SIAM J. APPL. MATH.
Vol. 38, No. 2, April 1980

0036-1399/80/3802-0009 $01.00/0

DYNAMICAL SYSTEMS UNDER CONSTANT ORGANIZATION II: HOMOGENEOUS GROWTH FUNCTIONS OF DEGREE $p=2$*

J. HOFBAUER,† P. SCHUSTER,‡ K. SIGMUND† AND R. WOLFF‡

Abstract. Qualitative analysis is presented for a system of differential equations, which play an important role in a theory of molecular self-organization:

$$\dot{x}_i=\left(\sum_{p=1}^{n} k_{ip}x_p-\sum_p\sum_q k_{pq}x_px_q\right)x_i, \qquad i=1,\cdots,n.$$

Besides the general case two simplifications are treated:
(1) the nonhyperbolic case: $k_{ij}\geqq 0$ ($k_{ii}=0$) and
(2) cyclic symmetry: $k_{ij}=k_{i+1,j+1}$.
Criteria for cooperation and exclusion are derived.

1. Introduction.

1.1. The origin of the problem. A recent kinetic approach towards a theory of molecular self-organization centers on the properties of a class of abstract dynamical systems called "hypercycles" and their physical realization (Eigen and Schuster [4]–[6]). Because of this basic importance the differential equations corresponding to hypercycles in their simplest form[1]

$$\dot{x}_i=x_i\left(x_{i-1}-\sum_{j=1}^{n} x_jx_{j-1}\right), \qquad i=1,\cdots,n \tag{1.1}$$

have been studied extensively by qualitative analysis [15].

Since hypercycles are just one class of a whole family of dynamical systems which are of certain importance in biophysical chemistry and theoretical ecology we made an attempt to analyze the corresponding generalized differential equations

$$\dot{x}_i=x_i\left(\sum_{p=1}^{n} k_{ip}x_p-\sum_{r=1}^{n}\sum_{s=1}^{n} k_{rs}x_rx_s\right). \tag{1.2}$$

This generalization does not only provide a better understanding of some interesting features of (1.1) like the appearance of a Hopf bifurcation observed for $n=5$ [15] but yields also important information on the origin of hypercycles and the probabilities of their formation.

Some of the questions to be discussed in this context are the following: where are the fixed points and, in particular, the stable equilibrium points? Are there periodic orbits, and in particular stable limit cycles? Are there bifurcations in the qualitative behavior of (1.2) when the parameters k_{ij} are allowed to vary? When is the system cooperative and when do we have exclusion?

1.2. The physical background, some basic definitions and properties. An equation of the form

$$\dot{x}_i=\Gamma_i(\mathbf{x})-\frac{x_i}{c}\phi(\mathbf{x}), \qquad i=1,2,\cdots,n \tag{1.3}$$

with $c>0$ and $\phi=\sum_{i=1}^{n}\Gamma_i$ has been called an equation under the constraint of "constant

* Received by the editors July 28, 1978, and in final revised form May 7, 1979.

† Institut für Mathematik der Universität Wien, Vienna, Austria.
‡ Institut für Theoretische Chemie und Strahlenchemie der Universität Wein, Vienna, Austria.

[1] Throughout this paper addition and subtraction of indices will always be understood modulo n.

(overall) organisation" by Eigen [3]. This constraint is closely related to but not identical with "constant forces" often applied in irreversible thermodynamics to simplify the analysis of complex systems. A situation simulated by (1.3) is, e.g. encountered in a flow reactor (Fig. 1). The use of a flow reactor to study evolution experiments has been discussed recently in great detail by Küppers [11].

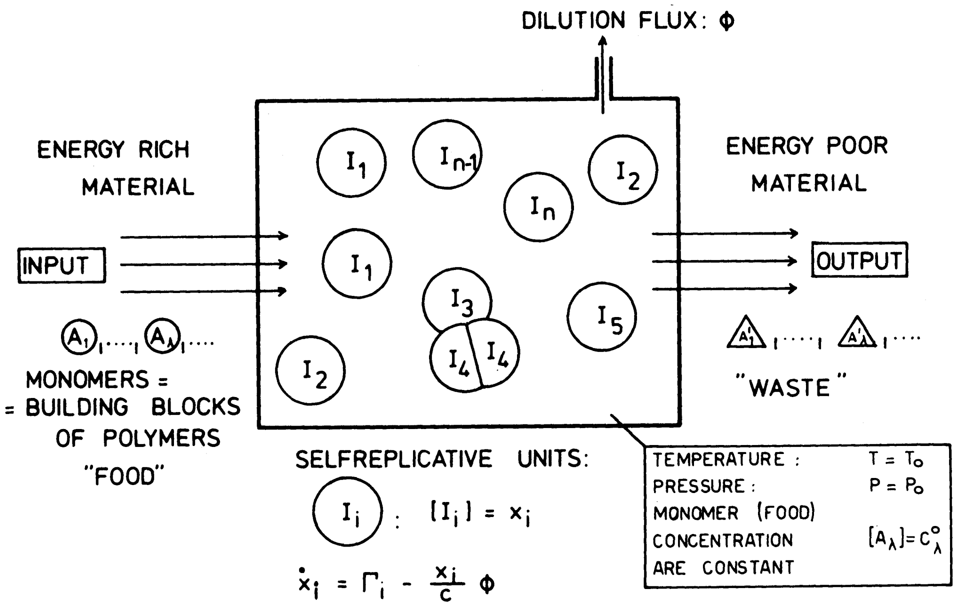

FIG. 1. *The evolution reactor. This kind of flow reactor consists of a reaction vessel which allows for temperature and pressure control. Its walls are impermeable to the self-replicative units (biological macromolecules like polynucleotides—e.g. phage RNA, bacteria or, in principle, also higher organisms). Energy rich material ("food") is poured from the environment into the reactor. The degradation products ("waste") are removed steadily. Material transport is adjusted in such a way that food concentration is constant in the reactor. A dilution flux ϕ is installed in order to remove the excess of self-replicative units produced by multiplication. Thus the sum of population numbers or concentrations,*

$$[I_1]+[I_2]+\cdots+[I_n]=\sum_{i=1}^{n} x_i = c,$$

may be controlled by the flux ϕ. Under "constant organization" ϕ is adjusted to yield constant total concentration c.

The self-replicative units may multiply either directly, then Γ_i is a linear function of x, or via catalytic help by another self-replicative entity. The former case has been treated extensively in previous papers [3], [4]. *Catalytic action leads to quadratic terms in the growth functions Γ_i. The dynamic behavior of purely catalytic systems is the subject of this paper.*

The experimental verification of evolution reactors has been discussed extensively by Küppers [11].

The "growth terms" Γ_i reflect the dynamical properties of the entities, selfreproductive biological macromolecules, primitive organisms etc., growing in the reactor. The constraint ϕ corresponds to an isotropic dilution flux.

With $S(\mathbf{x}) = x_1+\cdots+x_n$ one has $\dot{S} = \phi(1-(S/c))$. Let S_n^c denote the simplex

$$\left\{\mathbf{x}=(x_1,\cdots,x_n)\in\mathbb{R}^n : x_i \geqq 0, \qquad \sum_{i=1}^{n} x_i = c\right\}.$$

Since $S = c$ implies $\dot{S} = 0$, S_n^c is invariant. The constraint of constant organization thus leads to a stationary state with constant total concentration $S = \sum_i x_i = c$ (see also [5]).

The equations to be studied here (1.2) are a special case of (1.3) as they are obtained by putting

$$\Gamma_i = x_i \sum_{p=1}^{n} k_{ip} x_p.$$

We shall investigate their restriction to S_n^c (for S_n^1 we shall use simply S_n).

Additionally, the growth terms fulfil the relation $\Gamma_i = x_i G_i$ and hence (1.2) belongs to the class of ecological equations. Thus all species present in the system are assumed to be capable of self-induced replication. All constants in Γ_i refer to second order reaction rates, e.g. k_{ip} corresponds to catalytic help of species "p" with the replication of "i". In case the "species" are biological macromolecules, in particular polynucleotides, there are several kinetic mechanisms which provide physical explanation for the origin of the catalytic action [4], [5]. A second more formal consequence of the fact that (1.2) is an ecological equation may be deduced from the property:

$$x_i = 0 \to \dot{x}_i = 0.$$

Hence the boundary, $bd\, S_n$, consists of a hierarchically ordered set of m-subfaces $(m < n)$ which are globally invariant.

We have to thank the referee for pointing out that the restriction of (1.2) on S_n coincides there with a type of equation studied by Jenks in [8]–[10]. Indeed, using $\sum x_i = 1$, we may write (1.2) in the form

$$\dot{x}_i = \sum_{j,p,q} \delta_{ij}(k_{jp} - k_{pq}) x_p x_q x_j,$$

which is a special case of (1.1b) satisfying the condition (1.1c) from [8]. In that paper Theorem 2 gives a necessary and sufficient condition than S_n is positively invariant for Jenks equation: in our special case, this is trivially fulfilled. Theorems 3, 4 and 5 of [8] give conditions, in terms of the irreducibility of a certain tensor, for his system to have critical points in the interior of S_n. In our special case, the vertices of S_n are always critical points and the tensor is always reducible. Theorems 6–11 in [8] deal with critical points in the interior of S_n and give conditions for asymptotic stability, for instability and for the existence of strict Lyapunov functions in terms of a certain matrix $R(\xi)$. These results are of local character. In our more special systems, we study questions of exclusion and cooperation of a more global nature. In particular, we also take small fluctuations into account. Since for the equations of Jenks, $\sum x_i = c$ is invariant for all c, fluctuations may add up and significantly change the total concentration. In equations of the form (1.3), if $\phi > 0$, a fluctuation in total concentration will be subsequently canceled.

As deduced previously [5], there is a fundamental difference between dynamical systems with homogeneous and inhomogeneous growth functions $\Gamma_i(\mathbf{x})$. In the first case as in (1.2) the phase portrait $\mathscr{F}(n, \Gamma, c)$, does not depend on the total concentration c and hence we set $c = 1$ without losing generality. In the latter case which will be treated extensively, in a forthcoming paper, the dependence of $\mathscr{F}$ on c may be used to characterize the various dynamical systems with respect to their self-organizing properties.

An easily verified but nevertheless important property of (1.2) is the fact that only the differences in rate constants determine the dynamics of the system. Indeed,

$$k_{ij} = k_{(j)} + d_{ij} \to \phi = \sum_j k_{(j)} x_j + \sum_{i,j} d_{ij} x_i x_j$$

and thus

$$\dot{x}_i = x_i\Big(\sum_p k_{ip}x_p - \sum_{p,q} k_{pq}x_px_q\Big) = x_i\Big(\sum_p d_{ip}x_p - \sum_{p,q} d_{pq}x_px_q\Big).$$

$k_{(j)}$ does not enter the differential equations (1.2).

We remove this arbitrariness by putting

$$k_{ii} = 0 \quad \forall i. \tag{1.4}$$

In § 2 we present fixed point analysis of (1.2). A more detailed study of the phase portrait $\mathcal{F}(n, \boldsymbol{\Gamma}, 1)$ will be given under some supplementary assumptions. In § 3 we investigate the case $k_{ij} \geqq 0$—called the "nonhyperbolic" case by Epstein [7]—and in § 4 we consider the case of cyclic symmetry where species "i" acts on "j" like "$i+1$" on "$j+1$". In both cases we give criteria for exclusion and cooperation of the corresponding dynamical systems.

1.3. Exclusion, cooperation and fluctuational limit sets. The term "exclusion" is frequently used in discussions of ecological differential equations, but its definition is subject to slight variations. It says roughly that at least one species vanishes, and hence could be translated as meaning that the ω-limit of the orbit describing the ecological system is not disjoint from the boundary of the concentration space. It may happen that the definition is too narrow, however.

For example, in the special case of the Volterra–Lotka equation

$$\begin{aligned} \dot{y}_1 &= y_1(1-y_1-y_2), \\ \dot{y}_2 &= y_2(1-y_1-y_2), \end{aligned} \tag{1.5}$$

($y_1 \geqq 0$, $y_2 \geqq 0$), the phase portrait contains a line L of fixed points given by $y_1 + y_2 = 1$. The ω-limit of every orbit starting from some point with coordinates $y_1 > 0$ and $y_2 > 0$ is a point on L and hence no species vanishes. Still, one usually speaks of exclusion (see for example McGehee and Armstrong [12]) since random fluctuations may move the system from one equilibrium point to another, eventually sending it to one of the axis $y_1 = 0$ or $y_2 = 0$ (see Fig. 2).

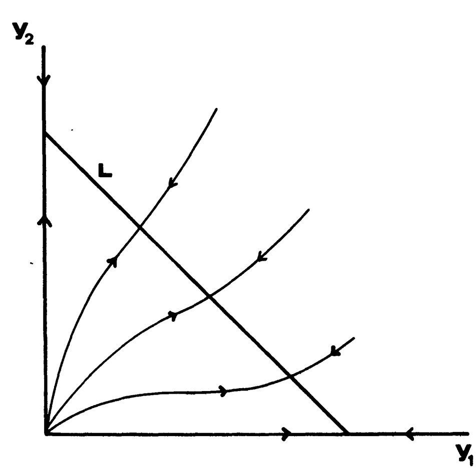

FIG. 2. *Phase portrait of the Lotka–Volterra equation* (1.5).

A possible way to take account of such small fluctuations is to replace the ω-limit set by the fluctuational limit set. If $T_t(t\in\mathbb{R})$ is a one-parameter group of homeomorphisms of a metric space (M, d), the ω-limit set of a point $\mathbf{x}\in M$ is the set

$$\omega(\mathbf{x})=\{\mathbf{y}\in M: \exists t_n\uparrow+\infty \text{ with } d(T_{t_n}(\mathbf{x}),\mathbf{y})\to 0\},$$

while the fluctuational limit set is

$$f-\omega(\mathbf{x})=\bigcap_{\varepsilon>0}\bigcap_{T>0} J(\mathbf{x},\varepsilon,T)$$

with

$$J(\mathbf{x},\varepsilon,T)=\{\mathbf{y}\in M: \exists t_n>T, \exists \mathbf{x}_n\in M \text{ with } \mathbf{x}_0=\mathbf{x}$$
$$\text{and } d(T_{t_n}(\mathbf{x}_n),\mathbf{x}_{n+1})<\varepsilon \text{ such that } d(\mathbf{x}_n,\mathbf{y})\to 0 \text{ as } n\to\infty\}.$$

Roughly speaking, $J(\mathbf{x},\varepsilon,T)$ is the set of points which may be approached asymptotically, starting from $\mathbf{x}$, by superposition of the time evolution T_t with some fluctuational "jumps" which are small and rare (if ε is small and T large). This notion is related to the "prolongational limit set" of Auslander and Seibert [1] and the "orbit-tracing" of Bowen [2]. Here we only note that $f-\omega(\mathbf{x})$ contains $\omega(\mathbf{x})$ but may be significantly larger.

If, for example, $\mathbf{x}$ is in the basin of attraction of a sink $\mathbf{y}$ of some ODE, then $f-\omega(\mathbf{x})=\omega(\mathbf{x})=\mathbf{y}$. On the other hand if we consider (1.5) for some $\mathbf{y}=(y_1,y_2)$ with $y_1>0$, $y_2>0$, then $\omega(\mathbf{y})$ is a point of the line L while $f-\omega(\mathbf{y})=L$. Thus $\omega(\mathbf{y})$ is disjoint from the boundary of the concentration space but not $f-\omega(\mathbf{y})$. This suggests the following definition.

DEFINITION. $\mathbf{x}\in S_n$ is said to lead to *exclusion* for (1.2) if $f-\omega(\mathbf{x})\cap bd\, S_n\neq\phi$. Otherwise $\mathbf{x}$ is said to be *cooperative*. Equation (1.2) is said to lead to exclusion (resp. to be cooperative) if the corresponding assertion is valid for all $\mathbf{x}\in \operatorname{int} S_n$.

2. Some preliminary results on fixed points.

2.1. Positions of the fixed points. The dynamical system (1.2) on S_n can be subdivided into a hierarchically ordered set of restrictions on m-subfaces ($m\leqq n$). Fixed points have to fulfil the conditions

$$\sum_{p=1}^{m} k_{ip}x_p-\phi=0, \qquad i=1,\cdots,m$$

with $x_i>0, \forall i=1,\cdots,m$ and $x_i=0, \forall i=m+1,\cdots,n$ (possibly after reordering of variables) as well as

$$\sum_{p=1}^{m} x_p=1. \tag{2.1}$$

Elimination of ϕ yields $m-1$ homogeneous linear equations

$$\sum_{p=1}^{m} (k_{1p}-k_{ip})x_p=0; \qquad i=2,\cdots,m. \tag{2.2}$$

Together with (2.1), these equations define linear subspaces of fixed points on the corresponding m-subface.

2.2. The Jacobian. Let $A=(a_{ij})$ be the Jacobian of (1.2) at a fixed point $\bar{\mathbf{x}}=(\bar{x}_1,\cdots,\bar{x}_n)$. Since

$$\frac{\partial\phi}{\partial x_j}=\sum_{p=1}^{n}(k_{jp}+k_{pj})x_p,$$

one obtains

$$\begin{aligned} a_{ii} &= \sum_{p=1}^{n} k_{ip}\bar{x}_p = \phi - \bar{x}_i \sum_{p=1}^{n} (k_{ip}+k_{pi})\bar{x}_p, \\ a_{ij} &= \bar{x}_i\Big(k_{ij} - \sum_{p=1}^{n} (k_{jp}+k_{pj})\bar{x}_p\Big) \quad \text{for } j \neq i. \end{aligned} \tag{2.3}$$

A has $n-1$ eigenvalues corresponding to eigenvectors in the plane parallel to the invariant simplex S_n, the remaining one will be denoted by ω_c. It tells us nothing about the behavior of (1.2) on S_n and we will often omit it.

2.3. The corners of S_n. The corners $\mathbf{e}_l \doteq (\delta_{1l}, \cdots, \delta_{nl})$ (δ_{ij} is the Kronecker symbol) are fixed points ($l = 1, \cdots, n$). The Jacobian has as the lth row $(-k_{1l}, -k_{2l}, \cdots, -k_{nl})$; for $p \neq l$, the pth row consists of zeros except for the diagonal term k_{pl}. As eigenvalues one obtains $\omega_l (=\omega_c) = 0$ and $\omega_p = k_{pl} (p = 1, \cdots, n, p \neq l)$.

2.4. Fixed points for S_2. Apart from $\mathbf{e}_1$ (with eigenvalue k_{21}) and $\mathbf{e}_2$ (with eigenvalue k_{12}) we may have the fixed point

$$\bar{\mathbf{x}}_3 = \frac{1}{q}(k_{12}, k_{21})$$

provided $q = k_{12} + k_{21} \neq 0$. Its eigenvalue is

$$\omega^{(3)} = -\frac{1}{q} k_{12} k_{21}.$$

If $k_{12}k_{21} > 0$, then $\bar{\mathbf{x}}_3 \in \operatorname{int} S_2$. For $k_{21} > 0$ it is a sink and the system is cooperative. For $k_{21} < 0$ it is a source and we have exclusion. If $k_{12}k_{21} \leqq 0$, $\bar{\mathbf{x}}_3 \notin \operatorname{int} S_2$ and we have exclusion: int S_2 either consists of a single orbit or of fixed points.

2.5. Fixed points for S_3. $\mathbf{e}_1$ has the eigenvalues k_{31} and k_{21}; $\mathbf{e}_2$, the eigenvalues k_{12} and k_{32}; and $\mathbf{e}_3$, the eigenvalues k_{23} and k_{13}. Apart from linear degeneracies, there are four more possible fixed points:

$$\bar{\mathbf{x}}_4 = \frac{1}{q_4}(0, k_{23}, k_{32}) \quad (\text{where } q_4 = k_{23} + k_{32})$$

has the eigenvalues

$$\omega_1^{(4)} = \frac{1}{q_4}(k_{23}(k_{12} - k_{32}) + k_{32}k_{13}) \quad \text{and} \quad \omega_2^{(4)} = -\frac{1}{q_4} k_{23}k_{32},$$

$\bar{\mathbf{x}}_5$ and $\bar{\mathbf{x}}_6$ are obtained by cyclic permutations. Finally

$$\bar{\mathbf{x}}_7 = \frac{1}{q_7}(\omega_1^{(4)}, \omega_1^{(5)}, \omega_1^{(6)}) \quad (\text{where } q_7 = \omega_1^{(4)} + \omega_1^{(5)} + \omega_1^{(6)})$$

may lie in int S_3. The explicit formula for the eigenvalues is rather complicated. In general, it is not a rational function of the k_{ij}'s.

3. The nonhyperbolic case. In this paragraph we consider the so-called nonhyperbolic case, where we assume that $k_{ij} \geqq 0$ for $1 \leqq i, j \leqq n$ (and $k_{ii} = 0$ for all i).

With a nonhyperbolic equation of type (1.2) we associate a graph whose vertices are the species i ($i = 1, \cdots, n$) and where there is a directed edge from i to j iff $k_{ji} > 0$, i.e., iff i catalyzes j. The graph is said to be irreducible if each i can be reached from each

j through a directed arc. It is said to be Hamiltonian if it contains a directed circuit (an arc that returns to its starting point) which covers all vertices of the graph without self-intersection.

In [16] it is shown that if the graph of a nonhyperbolic system (1.2) is a circuit, then the system is cooperative. It would be interesting to know whether some converse of this is true or more precisely whether the graph of every cooperative hyperbolic system (1.2) has to be Hamiltonian. Numerical evidence supports this, but we can only prove it for $n=3$ (for $n=2$ it is trivial). For $n=4$ we can only show that a cooperative system has to be irreducible.

3.1. The case $n=3$. Up to permutations of the indices, there are 16 different graphs shown in Fig. 3. We prove first

THEOREM 1. *If the nonhyperbolic system* (1.2) *has a unique fixed point* $\bar{\mathbf{x}}$ *in* int S_3, *then it is cooperative.*

Proof. Equation (1.2) is now

$$\begin{aligned} \dot{x}_1 &= x_1(k_{12}x_2+k_{13}x_3-\phi),\\ \dot{x}_2 &= x_2(k_{21}x_1+k_{23}x_3-\phi),\\ \dot{x}_3 &= x_3(k_{31}x_1+k_{32}x_2-\phi) \end{aligned} \tag{3.1}$$

and the fixed point $\bar{\mathbf{x}}$ in int S_3 satisfies

$$k_{12}\bar{x}_2+k_{13}\bar{x}_3=k_{21}\bar{x}_1+k_{23}\bar{x}_3=k_{31}\bar{x}_1+k_{32}\bar{x}_2 \tag{3.2}$$

as well as $\bar{x}_1>0$, $\bar{x}_2>0$, $\bar{x}_3>0$. We have in int S_3

$$\frac{d}{dt}\left(\frac{x_1}{x_2}\right)=\left(\frac{x_1}{x_2}\right)^{\cdot}=\left(\frac{x_1}{x_2}\right)(k_{12}x_2+k_{13}x_3-k_{21}x_1-k_{23}x_3). \tag{3.3}$$

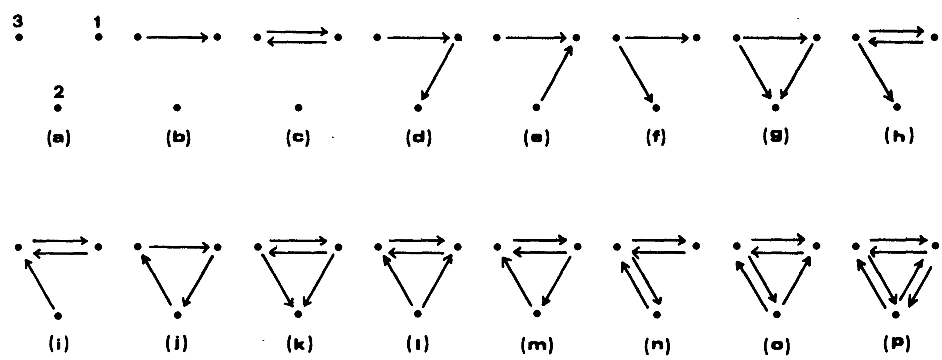

FIG. 3. *Possible graphs of the nonhyperbolic equation* (1.2) *with* $n=3$.

Let L_3 be the line where $(x_1/x_2)^{\cdot}=0$. This line passes through $\bar{\mathbf{x}}$ and intersects the edge $x_3=0$ somewhere between $\mathbf{e}_1$ and $\mathbf{e}_2$ (the coordinates x_1 and x_2 of the point of intersection satisfy $k_{21}x_1=k_{12}x_2$ by (3.2), and hence $0\leqq x_1\leqq 1$).

Let l_1, l_2, resp. l_3 be the lines through $\bar{\mathbf{x}}$ and $\mathbf{e}_1$, $\mathbf{e}_2$ resp. $\mathbf{e}_3$. Let P_1 be an arbitrary point on l_1 between $\mathbf{e}_1$ and $\bar{\mathbf{x}}$; let Q_2 (resp. Q_3) be the intersection of $P_1\mathbf{e}_3$ (resp. $P_1\mathbf{e}_2$) with l_2 (resp. l_3). Let P_2 (resp. P_3) be the intersection of $Q_3\mathbf{e}_1$ (resp. $Q_2\mathbf{e}_1$) with l_2 (resp. l_3). Then the intersection of $P_2\mathbf{e}_3$ and $P_3\mathbf{e}_2$ is a point Q_1 on l_1 (see Fig. 4: a proof of the last statement is in [16]).

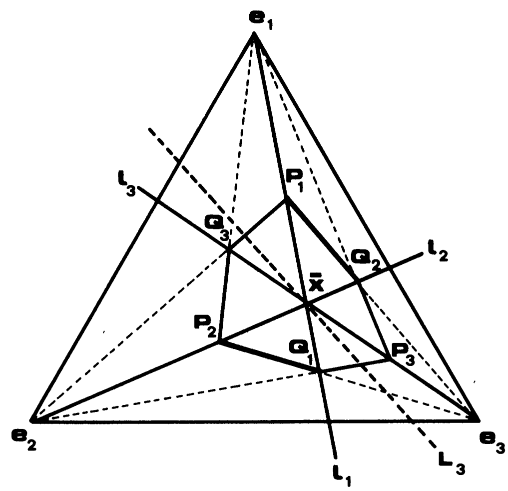

FIG. 4. *Geometric construction for the proof of Theorem* 1.

Consider now the two opposite edges P_1Q_2 and P_2Q_1 of the hexagon $P_1Q_2P_3Q_1P_2Q_3$. Since they are both colinear with $\mathbf{e}_3$, the ratio (x_1/x_2) is constant on each of them. On the other hand, the two edges are separated by L_3, and it follows that on P_1Q_2, we have $(x_1/x_2)^{\cdot}<0$, while on P_2Q_1 we have $(x_1/x_2)^{\cdot}>0$. Thus all orbits through P_1Q_2 and P_2Q_1 point into the hexagon. The same is true for the other edges of the hexagon. Since P_1 was arbitrary, it follows that $\bar{\mathbf{x}}$ is the ω-limit (and the fluctuational ω-limit) of every orbit in int S_3. Thus the system is cooperative.

THEOREM 2. *If the graph of the nonhyperbolic system* (1.2) *with* $n=3$ *is not Hamiltonian, the system leads to exclusion.*

Proof. Apart from the case considered in the previous theorem, we may have the following two situations:

(a) There is no fixed point in the interior of S_3. In this case, the theorem of Poincaré–Bendixson implies exclusion.

(b) There is a straight line of fixed points through int S_3 (see § 2.1). Since this line intersects *bd* S_3, we have exclusion again. Hence the theorem is proved.

As an illustration let us consider an equation whose graph is given by (**n**) in Fig. 3. This means that we have (3.1) with $k_{12}=k_{21}=0$. Equation (3.3) becomes

$$\left(\frac{x_1}{x_2}\right)^{\cdot}=\left(\frac{x_1}{x_2}\right)x_3(k_{13}-k_{23}). \tag{3.4}$$

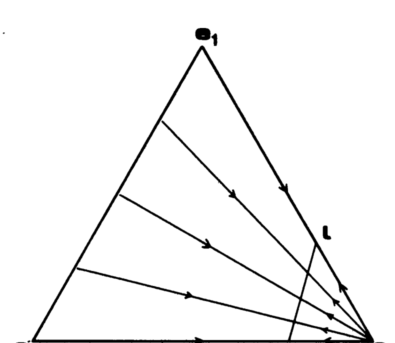

FIG. 5. *Phase portrait of a dynamical system corresponding to graph* (*n*) *in Fig.* 3.

If $k_{13}-k_{23}\neq 0$, one of the species 1 or 2 must vanish, we have a situation as in part (a) of the last proof. If $k_{13}=k_{23}$, the ratio (x_1/x_2) is constant. Let l be the line of fixed points of (3.1) given by $k_{13}x_3=k_{31}x_1+k_{32}x_2$. We then have a situation as in part (b) of the last proof. The phase portrait is sketched in Fig. 5. The fluctuational limit set of every point in int S_3 consists of $l\cap S_3$, which is not disjoint from the boundary. The situation is similar to that in § 1.3, Fig. 2, and hence we have exclusion.

Note that all graphs in Fig. 3 except (**j**), (**m**), (**o**) and (**p**) lead to exclusion.

3.2. The case $n=4$.

THEOREM 3. *If the graph of the nonhyperbolic equation* (1.2) *with* $n=4$ *is not irreducible, then the system leads to exclusion.*

Proof. There exists a proper subset D of $\{1, 2, 3, 4\}$ which is closed, i.e., such that no directed edge leads from a vertex in D to a vertex in the complement D' of D.

(1) If D' consists of one point, say $\{1\}$, then no species catalyzes species 1 and hence $\dot{x}_1\leqq 0$. This implies exclusion.

(2) Suppose that D' consists of 3 points, say $\{1, 2, 3\}$. By assumption, species 4 catalyzes no other species, i.e., $k_{i4}=0$ for $i=1, 2, 3$. Therefore the first three equations of (1.2), i.e., the equations for $\dot{x}_1$, $\dot{x}_2$ and $\dot{x}_3$, look like (3.1), the only difference being that ϕ is now of another form. This difference plays no role in the following considerations. The expression for $(x_1/x_2)^{\cdot}$ is given by (3.3) again; $(x_2/x_3)^{\cdot}$ and $(x_3/x_1)^{\cdot}$ are similar. It may be that one of these expressions is always of the same sign. The corresponding quotient (x_i/x_j) then converges either to 0 or to $+\infty$, or it remains constant. In each of these cases one has exclusion.

The remaining alternative is that there exists a solution $(\bar{x}_1, \bar{x}_2, \bar{x}_3)$ of (3.2) with $\bar{x}_1>0$, $\bar{x}_2>0$, $\bar{x}_3>0$. We want to show that in this case one has "internal equilibration," i.e., that $(x_i/x_j)\to(\bar{x}_i/\bar{x}_j)$ for $1\leqq i, j\leqq 3$. But this can be shown just as in the proof of Theorem 1, the only difference being that we have $x_1+x_2+x_3\leqq 1$ instead of $x_1+x_2+x_3=1$. Nothing changes except that instead of hexagons in S_3, we get pyramids with corresponding hexagonal bases. (A similar case is treated in [16]).

Now let S^* be the subset of S_4 satisfying (3.2). This is an invariant 2-simplex. As coordinates in S^*, we may use x_4 and $y=x_1(1+x_2(\bar{x}_1/\bar{x}_2)+x_3(\bar{x}_1/\bar{x}_3))(=x_1+x_2+x_3$ on $S^*)$. It is easy to see that on S^*, (1.2) becomes

$$\dot{y}=y(qy-\phi),\qquad \dot{x}_4=x_4(ky-\phi) \tag{3.5}$$

with

$$x_4+y=1,\qquad \phi=y(qy+kx_4),$$

$$k=\left(1+x_2\frac{\bar{x}_1}{\bar{x}_2}+x_3\frac{\bar{x}_1}{\bar{x}_3}\right)^{-1}\left(k_{41}+k_{42}\frac{\bar{x}_2}{\bar{x}_1}+k_{43}\frac{\bar{x}_3}{\bar{x}_1}\right)$$

and

$$q=\left(1+x_2\frac{\bar{x}_1}{\bar{x}_2}+x_3\frac{\bar{x}_1}{\bar{x}_3}\right)^{-1}\left(k_{12}\frac{\bar{x}_2}{\bar{x}_1}+k_{13}\frac{\bar{x}_3}{\bar{x}_1}\right).$$

Equations (3.5) always lead to exclusion (if $q=k$ all points are fixed points; otherwise either $y\to 0$ or $y\to 1$). Since all orbits of (1.2) in int S_4 converge to S^*, it follows that (1.2) leads to exclusion.

(3) Consider finally the case where D' consists of 2 points, say $\{1, 2\}$. If one of these species is not end-point of an oriented edge, then this species has to vanish and we have exclusion. The remaining alternative is that $k_{12}>0$ and $k_{21}>0$. It is shown in [16] that in such a situation one has internal equilibrium in the sense that

$$\frac{x_1}{x_2}\to\frac{k_{12}}{k_{21}}.$$

Let S^* now denote the subset of S_4 where $k_{21}x_1=k_{12}x_2$. S^* is an invariant 3-simplex. As coordinates on S^*, we may use x_3, x_4 and $y=x_1(1+(k_{21}/k_{12}))(=x_1+x_2$ on $S^*)$. On S^*, (1.2) becomes

$$\begin{aligned}
&\dot{y}=y(qy-\phi),\\
(3.6)\qquad &\dot{x}_3=x_3(k_3y+k_{34}x_4-\phi),\\
&\dot{x}_4=x_4(k_4y+k_{43}x_3-\phi),
\end{aligned}$$

where $y+x_3+x_4=1$, $\phi=y(qy+k_3x_3+k_4x_4)+x_3x_4(k_{34}+k_{43})$,

$$\begin{aligned}
q&=\left(1+\frac{k_{21}}{k_{12}}\right)^{-1}k_{21},\\
k_3&=\left(1+\frac{k_{21}}{k_{12}}\right)^{-1}\left(k_{31}+k_{32}\frac{k_{21}}{k_{q2}}\right),\\
k_4&=\left(1+\frac{k_{21}}{k_{12}}\right)^{-1}\left(k_{41}+k_{42}\frac{k_{21}}{k_{12}}\right).
\end{aligned}$$

Reestablishing condition $k_{ii}=0$ so as to get (3.6) with $q=0$ one obtains a system of the form (3.7) which is studied in § 3.3. We show there that we have exclusion. Since every orbit of the nonhyperbolic (1.2) in int S_4 converges to S^*, exclusion holds again and the proof is completed.

Up to permutation of the indices, there are 8 irreducible graphs without Hamiltonian arc. They are shown in Fig. 6. Numerical solutions indicate that we always have exclusion and lend some weight to the conjecture that in order to be cooperative, the nonhyperbolic system must have a Hamiltonian graph and thus must be at least as complex as a hypercycle.

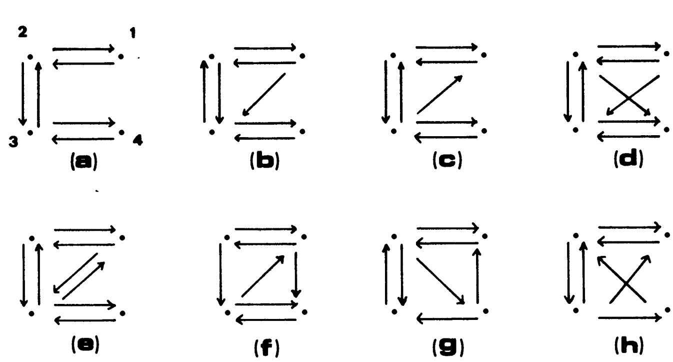

FIG 6. *Possible irreducible graphs without Hamiltonian arcs for the nonhyperbolic equation* (1.2) *with* $n=4$.

3.3. A system with exclusion. In order to complete the proof of Theorem 3, we have to show that the (not necessarily nonhyperbolic) system

$$\begin{aligned} \dot{x}_1 &= x_1(-\phi), \\ \dot{x}_2 &= x_2(-q_2x_1+h_2x_3-\phi), \\ \dot{x}_3 &= x_3(-q_3x_1+h_3x_2-\phi) \end{aligned} \tag{3.7}$$

(where $h_2, h_3>0$ and $q_2, q_3 \in R$) leads to exclusion. We shall only consider the case where $q_3>0$ and $q_2>0$, the other cases being trivial. There is then a unique fixed point C in int S_3. We shall see that C is a saddle point—this is enough to guarantee exclusion. With $A=h_2h_3+h_3q_2+h_2q_3$, the coordinates of C are $x_1=A^{-1}h_2h_3$, $x_2=A^{-1}h_2q_3$, $x_3=A^{-1}q_2h_3$. Let us make a change of variables, putting $x_2=x$, $x_3=y$ and obtaining $x_1=1-x-y$. Interchanging x and y means just permuting the indices 2 and 3. We obtain

$$\phi=-q_2x-q_3y+xy(h_2+h_3+q_2+q_3)$$

and

$$\frac{\partial\phi}{\partial x}=-q_2+(h_2+h_3+q_2+q_3)y+2q_2x.$$

Equation (3.7) becomes

$$\begin{aligned} \dot{x} &= x(-q_2(1-x-y)+h_2y-\phi)=F_1(x, y), \\ \dot{y} &= y(-q_3(1-x-y)+h_3x-\phi)=F_2(x, y). \end{aligned} \tag{3.8}$$

At the point C one gets

$$\frac{\partial\phi}{\partial x}=A^{-1}q_2(h_3^2+h_3q_3+q_3h_2),$$

$$\frac{\partial F_1}{\partial x}=A^{-2}h_2h_3q_2q_3(k_2+q_2-h_3-q_3),$$

$$\frac{\partial F_1}{\partial y}=A^{-2}h_2h_3q_3[(q_2+h_2)^2-q_2q_3]$$

and for the determinant of the Jacobian at C:

$$-A^{-2}(h_2h_3)^2q_2q_3[(h_2+q_2)(h_3+q_3)-q_2q_3]^2<0,$$

which implies that C is a saddle. The phase portrait is sketched in Fig. 7.

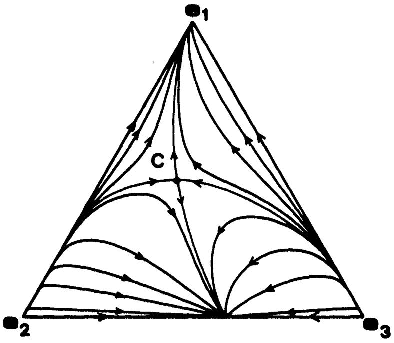

FIG. 7. *Phase portrait of equation* (3.7).

4. Cyclic symmetry. The study of (1.2) is greatly simplified in the case of cyclic symmetry, i.e., under the assumption that $k_{i,j}=k_{i+1,j+1}$ for all i, j. We still assume (without restriction of generality) that $k_{ii}=0$, but drop the condition $k_{ij}\geqq 0$. Denoting $k_{i,i+j}$ by $k_j (j=0, 1, \cdots, n-1)$ one obtains the equation

$$\dot{x}_i = x_i(G_i - \phi) \tag{4.1}$$

with

$$G_i = \sum_{j=1}^{n-1} k_j x_{i+j}$$

and

$$\phi = \sum_{j=1}^{n-1} k_j\left(\sum_{i=1}^{n} x_i x_{i+j}\right).$$

Note that the point $C=(1/n, \cdots, 1/n)$ is always an equilibrium point of (4.1). We shall see that in most cases it is the only fixed point in int S_n.

4.1. Some general results.

4.1.1. The eigenvalue at the point *C*. A simple computation starting from (2.3) shows that the Jacobian of (4.1) at C is of the form

$$A = \begin{bmatrix} c_0 & c_1 & c_2 & \cdots & c_{n-1} \\ c_{n-1} & c_0 & c_1 & \cdots & c_{n-2} \\ \vdots & \vdots & & & \vdots \end{bmatrix}$$

with $c_i = (1/n)(k_i - 2\bar{k})$ and $\bar{k} = (1/n)\sum_{j=1}^{n-1} k_j$.

The matrix A is circulant; hence its eigenvalues can be easily computed by using the formula in [14, p. 198], for example. One obtains

$$\omega_j = \sum_{l=0}^{n-1} c_l \lambda^{jl} = \frac{1}{n}\sum_{l=0}^{n-1} k_l \lambda^{jl}, \qquad j=1, \cdots, n-1, \quad \lambda = \exp\left(\frac{2\pi i}{n}\right). \tag{4.2}$$

Furthermore the nth eigenvalue corresponding to ω_c is equal to $-\bar{k}$. For convenience we will denote it by $-\omega_0(\omega_0=\bar{k})$.

4.1.2. A change of variables. We shall use the following change of variables, which can be viewed as Fourier transformation on the space $\mathbb{Z}_n$ of indices modulo n,

$$y_p = \sum_{i=1}^{n} \lambda^{ip} x_i \qquad (p=0, \cdots, n-1).$$

One then has

$$x_i = \frac{1}{n}\sum_{p=0}^{n-1} \lambda^{-ip} y_p \qquad (i=1, \cdots, n).$$

The new variables y_p obviously represent the eigenvectors which correspond to the eigenvalues ω_p defined by (4.2), see also [15].

The y_p are complex numbers. Since the x_i are real and $\sum_{i=1}^n x_i = 1$, we have the relations

$$
\begin{aligned}
\bar{y}_p &= y_{n-p} \qquad (p = 1, \cdots, n-1), \\
y_0 &= 1.
\end{aligned}
\tag{4.3}
$$

Equation (4.1) then becomes

$$
\begin{aligned}
\dot{y}_p &= \sum_{i=1}^{n} \lambda^{ip} \dot{x}_i = \sum_{i=1}^{n} \lambda^{ip} x_i \left(\sum_{j=1}^{n-1} k_j x_{i+j} - \phi \right) \\
&= \sum_{j=1}^{n-1} k_j \left(\sum_{i=1}^{n} \lambda^{ip} x_i x_{i+j} \right) - \left(\sum_{i=1}^{n} \lambda^{ip} x_i \right) \phi \\
&= \sum_{j=1}^{n-1} k_j \frac{1}{n^2} \sum_{i=1}^{n} \lambda^{ip} \left(\sum_{l=0}^{n-1} \lambda^{-il} y_l \right) \left(\sum_{m=0}^{n-1} \lambda^{-(i+j)m} y_m \right) - \phi y_p \\
&= \sum_{j=1}^{n-1} k_j \frac{1}{n^2} \sum_{l,m=0}^{n-1} \left(\sum_{i=1}^{n} \lambda^{i(p-l-m)} \right) \lambda^{-jm} y_l y_m - \phi y_p.
\end{aligned}
$$

Since

$$
\sum_{i=1}^{n} \lambda^{i(p-l-m)} = n \delta_{p,l+m},
$$

we obtain

$$
\begin{aligned}
\dot{y}_p &= \sum_{j=1}^{n-1} k_j \frac{1}{n} \sum_{m=0}^{n-1} \lambda^{-jm} y_{p-m} y_m - \phi y_p \\
&= \sum_{m=0}^{n-1} \left(\frac{1}{n} \sum_{j=1}^{n-1} k_j \lambda^{-jm} \right) y_{p-m} y_m - \phi y_p \\
&= \sum_{m=0}^{n-1} \omega_{-m} y_m y_{p-m} - \phi y_p
\end{aligned}
$$

or

$$
\dot{y}_p = \sum_{m=0}^{n-1} \omega_m \bar{y}_m y_{p+m} - \phi y_p. \tag{4.4}
$$

For $p = 0$, using $y_0 = 1$, one obtains

$$
\phi = \sum_{m=0}^{n-1} \omega_m |y_m|^2 = \sum_{m=0}^{n-1} \operatorname{Re} \omega_m |y_m|^2 \tag{4.5}
$$

and therefore (4.1) is transformed into

$$
\dot{y}_p = \sum_{m=1}^{n-1} \omega_m \bar{y}_m (y_{p+m} - y_p y_m) \qquad (p = 1, \cdots, n-1). \tag{4.6}
$$

From this follows, incidentally, that for even n, the system (4.1) contains an invariant $n/2$-dimensional subsystem of the same type. More precisely, the set $S_n \cap \{y_1 = y_3 = \cdots y_{n-1} = 0\}$ is easily seen to be invariant, and we can check that the restriction to this set is of the form (4.1), with $k_i + k_{(n/2)+i} (i = 1, \cdots, n/2)$ instead of k_i.

4.1.3. The function *P*. For the study of (4.1) the function

$$P(\mathbf{x}) = x_1 x_2 \cdots x_n \tag{4.7}$$

is very convenient. On S_n, its maximum is attained in C, its minimum 0 is attained on bdS_n.

One obtains

$$\begin{aligned} \dot{P} &= P \sum_{i=1}^{n} (G_i - \phi) \\ &= P[(k_1 + \cdots + k_{n-1}) - n\phi] \\ &= nP(\omega_0 - \phi) \\ &= -nP \sum_{m=1}^{n-1} \operatorname{Re} \omega_m |y_m|^2. \end{aligned} \tag{4.8}$$

In terms of the x_i's, a short computation shows that

$$\dot{P} = nP \sum_{j=1}^{n-1} (k_j - \bar{k}) \Big(\sum_{i=1}^{n} (x_i - x_{i+j})^2 \Big). \tag{4.9}$$

An immediate consequence of (4.8) is

THEOREM 4. (1) *If C is a sink, it is the ω-limit of every orbit in* int S_n *and the system is cooperative.*

(2) *If C is a source, the ω-limit of every orbit in* int S_n *(with the exception of C) lies on bdS_n, and the system leads to exclusion.*

Hence, in these two cases the qualitative analysis reduces to an investigation of the central fixed point.

4.1.4. The occurrence of Hopf bifurcations. Let us consider the case where $n \geqq 5$ and where exactly one pair of conjugate eigenvalues of C are on the imginary axis, while all other eigenvalues are in the left half-plane. We may thus assume $\operatorname{Re} \omega_1 = 0$ $(\omega_1 \neq 0)$ and $\operatorname{Re} \omega_i < 0$ for $i \neq 1, n-1$. Then (4.8) reduces to

$$\dot{P} = -nP \sum_{m=2}^{n-2} \operatorname{Re} \omega_m |y_m|^2 \geqq 0.$$

We want to show that C is asymptotically stable, with int S_n as basin of attraction. For this it is enough to show that the set $\{\dot{P} = 0\} = \{y_m = 0, m = 2, \cdots, n-2\}$ contains no invariant set with the exception of C (which is the point $(1, 0, \cdots, 0)$ in y-space). Since on this set

$$\dot{y}_i = \sum_{m=0}^{n-1} \omega_m \bar{y}_m y_{i+m} \qquad (i = 2, \cdots, n-2),$$

the assumption that $\dot{y}_i = 0$ for $i = 2, \cdots, n-2$ leads to

$$0 = \dot{y}_2 = \sum_{m=0}^{n-1} \omega_m \bar{y}_m y_{m+2} = \omega_{n-1} y_1^2$$

and hence $y_i = 0$ for $i = 1, \cdots, n-1$. Therefore C is the only invariant set.

Suppose now that $\mu \mapsto \underset{\sim}{k}(\mu) = (k(\mu), \cdots, k_n(\mu))$ is a path in the parameter space, where μ varies in an interval with 0 as an inner point. Let us assume that

(i) for $\mu < 0$ one has $\operatorname{Re} \omega_i < 0$ $(i = 1, \cdots, n-1)$;

(ii) for $\mu = 0$ $\operatorname{Re} \omega_1 = 0$ $(\omega_1 \neq 0)$ and $\operatorname{Re} \omega_i < 0$ $(i = 2, \cdots, n-2)$;

(iii) for $\mu > 0$ Re $\omega_1 > 0$ and Re $\omega_i < 0$ $(i = 2, \cdots, n-2)$;
and furthermore that $(\mathrm{Re}\, \omega_1(\mu))'_{\mu=0} > 0$.

Since for the case (ii) C is asymptotically stable, the Hopf bifurcation theorem applies (see [13]). This means that if $\mu > 0$ is sufficiently small, there exists a stable limit cycle. Note that for $n = 5$ and $k_1 > 0$, $k_2 = k_3 = k_4 = 0$ we have the case of the symmetric hypercycle treated in [15], where we offered numerical evidence for the existence of the stable limit cycle. The situation for $n = 3$ and $n = 4$ will be treated in the next section.

4.2. Qualitative discussions for low dimensions. The case $n = 2$ is trivial: We have exclusion iff $k_1 \leqq 0$, and cooperation otherwise.

4.2.1. The case $n = 3$. By (4.2) the eigenvalues of (4.1) at C are

$$\omega_{1,2} = -k_1 - k_2 \pm i\sqrt{3}(k_2 - k_1).$$

By (4.9)

$$\begin{aligned}\dot{P} &= \frac{P}{2}(k_1 + k_2)[(x_1 - x_2)^2 + (x_2 - x_3)^2 + (x_3 - x_1)^2] \\ &= \frac{3P}{2}(k_1 + k_2) \sum_{i=1}^{3} \left(x_i - \frac{1}{3}\right)^2.\end{aligned}$$

4.2.1.1. If $0 < k_1 + k_2$, then C is a sink and the system is cooperative according to Theorem 4.

4.2.1.2. If $k_1 + k_2 = 0$, then $\dot{P} = 0$. If, in this case, $k_1 = k_2 (=0)$, then every point in S_3 is a fixed point. If $k_1 \neq k_2$, then C is an equilibrium point of center type, and the only fixed point in the interior of S_3. (Indeed, one sees easily that $\dot{x}_1 = 0$ implies $x_2 = x_3$, and

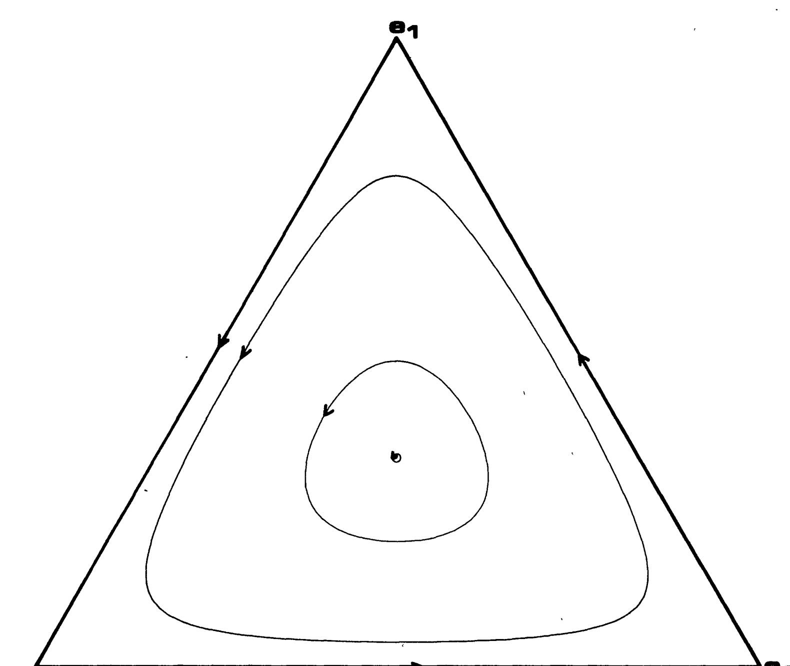

FIG. 8. *Phase portrait of the dynamical system according to equation* (4.1) *with* $n = 3$ $(k_1 = -0.5; k_2 = 0.5)$.

$\dot{x}_2 = 0$ implies $x_3 = x_1$.) Thus in this case every point in the interior of S_3 is on a periodic orbit given by $P = \text{const.}$ around the center C, which is therefore stable, but not asymptotically stable (see Fig. 8). In both cases we have exclusion.

4.2.1.3. If, finally, $k_1 + k_2 < 0$, the point C is unstable, and every other orbit in the interior of S_3 converges to its boundary. In case k_1 and k_2 have different sign, the points $\mathbf{e}_1$, $\mathbf{e}_2$ and $\mathbf{e}_3$ (whose eigenvalues are k_1 and k_2) are of saddle type and are the only fixed points on bdS_3. In this case, every point in the interior of S_3 (apart from C) has the set bdS_3 as ω-limit (see Fig. 9). If k_1 and k_2 are negative the points $\mathbf{e}_1$, $\mathbf{e}_2$ and $\mathbf{e}_3$ are sinks and

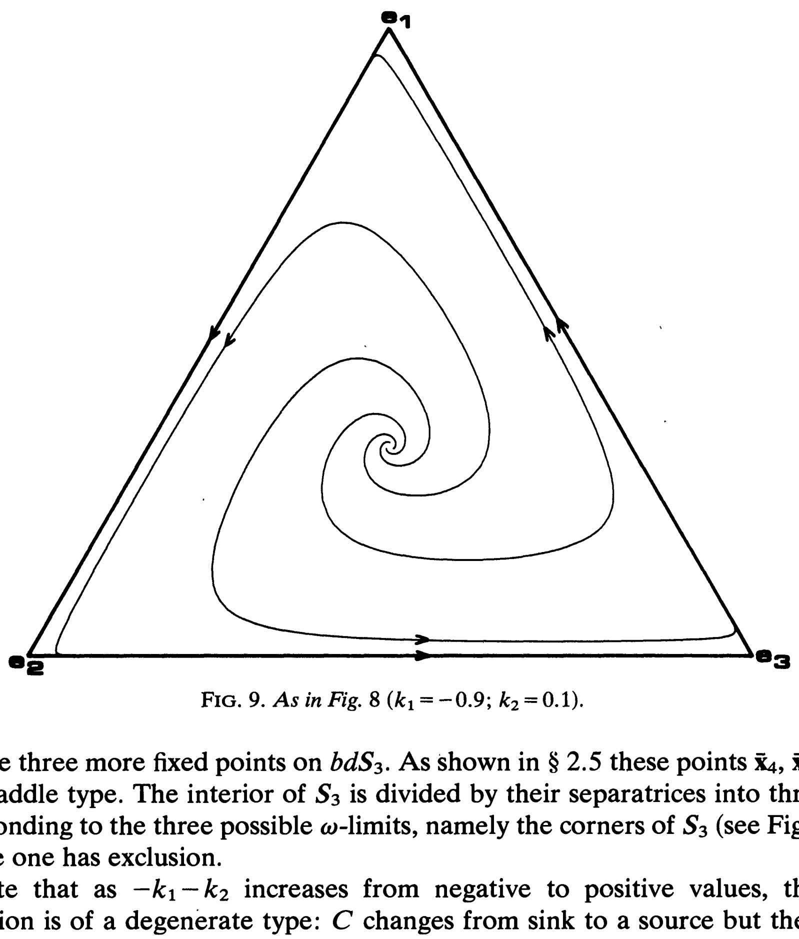

FIG. 9. *As in Fig.* 8 ($k_1 = -0.9$; $k_2 = 0.1$).

there are three more fixed points on bdS_3. As shown in § 2.5 these points $\bar{\mathbf{x}}_4$, $\bar{\mathbf{x}}_5$ and $\bar{\mathbf{x}}_6$ are of saddle type. The interior of S_3 is divided by their separatrices into three parts corresponding to the three possible ω-limits, namely the corners of S_3 (see Fig. 10). In any case one has exclusion.

Note that as $-k_1 - k_2$ increases from negative to positive values, the Hopf bifurcation is of a degenerate type: C changes from sink to a source but there is no stable periodic orbit emerging around C. This is due to the fact that for the critical value $k_1 + k_2 = 0$, the point C is not asymptotically stable. In the formulation of the Hopf bifurcation theorem as found in [13, p. 87], the condition H5 is not valid. This is in contrast to the corresponding situation for $n = 4$.

4.2.2. The case $n = 4$. By (4.2) the eigenvalues of (4.1) at C are

$$\omega_2 = \tfrac{1}{4}(k_2 - k_1 - k_3),$$
$$\omega_{1,3} = \tfrac{1}{4}(-k_2 \pm i(k_1 - k_3)).$$

It is easy to see that the eigenspace corresponding to ω_2 is the line where $x_1 = x_3$ and $x_2 = x_4$, the one corresponding to $\omega_{1,3}$ is the plane $x_1 + x_3 = \tfrac{1}{2}$.

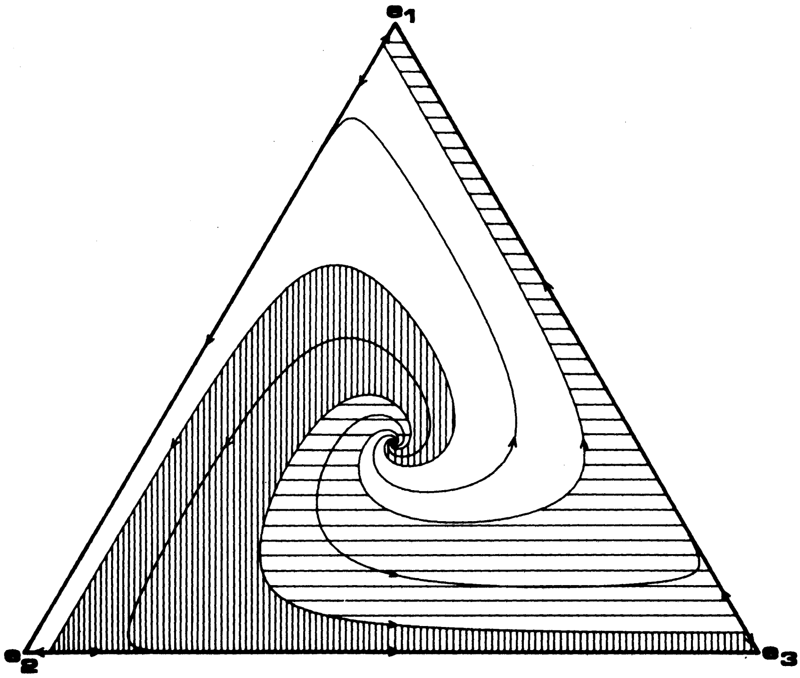

FIG. 10. *As in Fig.* 8 ($k_1=-0.1$; $k_2=-2.9$). *Basins of the sinks in e_1, e_2 and e_3 are hatched.*

Using (4.9) one obtains

$$\begin{aligned}\dot P &= P\{4(k_1+k_3-k_2)(x_1+x_3-\tfrac12)^2+k_2[(x_1+x_2-\tfrac12)^2+(x_1+x_4-\tfrac12)^2]\}\\ &= P\{4(k_1+k_3-k_2)(x_1+x_3-\tfrac12)^2+\tfrac12k_2[(x_1-x_3)^2+(x_2-x_4)^2]\}.\end{aligned}$$

4.2.2.1. If $k_1+k_3>k_2>0$, then C is a sink and an attractor whose basin is the interior of the simplex S_4. The system is therefore cooperative.

4.2.2.2. If $k_1+k_3<k_2<0$, then C is a source and the ω-limit of every point in the interior of S_4, except C, lies on the boundary. We have exclusion.

4.2.2.3. The case $k_2=0$. One has

$$\dot P = 4P(k_1+k_3)(x_1+x_3-\tfrac12)^2$$

and

$$\phi=(k_1+k_3)(x_1+x_3)(x_2+x_4).$$

4.2.2.3.1. The case $k_1+k_3=0$. Then $P=$ const. and $\phi=0$. Also,

$$\begin{aligned}\dot x_1 &= x_1(k_1x_2+k_3x_4)\\ &= x_1k_1(x_2-x_4).\end{aligned}$$

If $k_1=0$, the system consists only of fixed points. If $k_1\neq 0$, then one also has

$$\dot x_3 = x_3k_1(x_4-x_2).$$

Thus one obtains $(x_1x_3)^{\cdot}=0$ and similarly $(x_2x_4)^{\cdot}=0$. The points on the line where $x_1=x_3$ and $x_2=x_4$ are fixed points. All other points in the interior of S_4 are periodic points, i.e. each orbit is on the intersection of two sets $x_1x_3 = \text{const.}$ and $x_2x_4 = \text{const.}$ (see Fig. 11). In any case one has exclusion.

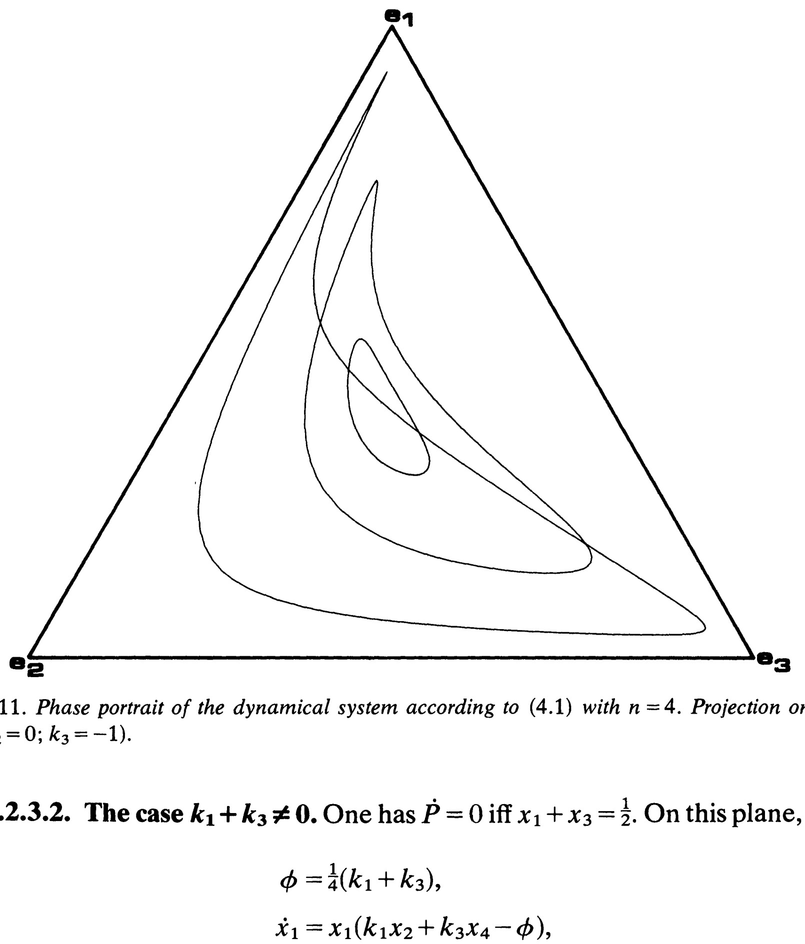

FIG. 11. *Phase portrait of the dynamical system according to* (4.1) *with* $n = 4$. *Projection onto a face* ($k_1 = 1$; $k_2 = 0$; $k_3 = -1$).

4.2.2.3.2. The case $k_1 + k_3 \neq 0$. One has $\dot{P} = 0$ iff $x_1 + x_3 = \frac{1}{2}$. On this plane, one has

$$\phi = \tfrac{1}{4}(k_1 + k_3),$$
$$\dot{x}_1 = x_1(k_1x_2 + k_3x_4 - \phi),$$
$$\dot{x}_3 = x_3(k_3x_2 + k_1x_4 - \phi)$$

and

$$\dot{x}_1 + \dot{x}_3 = (k_1 - k_3)(x_1x_2 + x_3x_4 - \tfrac{1}{8}).$$

In the case $k_1 = k_3$, the plane $x_1 + x_3 = \frac{1}{2}$ is invariant (it consists of fixed points). The ω-limit of orbits in int S_4 depends on the sign of k_1, but one has always exclusion.

In the case $k_1 \neq k_3$, the situation is slightly more complicated. On the plane $x_1 + x_3 = \frac{1}{2}$, one has $\dot{x}_1 + \dot{x}_3 = 0$ iff $x_1x_2 + x_3x_4 = \frac{1}{8}$ or, since $x_2 + x_4 = \frac{1}{2}$, iff

$$4x_1(4x_2 - 1) = 4x_2 - 1.$$

This is the case iff $x_1 = \frac{1}{4}$ or $x_2 = \frac{1}{4}$. If $x_1 = \frac{1}{4}$ but $x_2 \neq \frac{1}{4}$ then $\dot{x}_1 \neq 0$, and vice versa; in any case, apart from the fixed point C, there is no invariant set on the plane $x_1 + x_3 = \frac{1}{2}$. Thus $\dot{P} = 0$ only for a discrete set of times. If $k_1 + k_3 > 0$, this implies that every orbit in the interior has C as ω-limit (hence C is asymptotically stable, see Fig. 12) and the system is cooperative. If $k_1 + k_3 < 0$, then $P \to 0$ and one has exclusion.

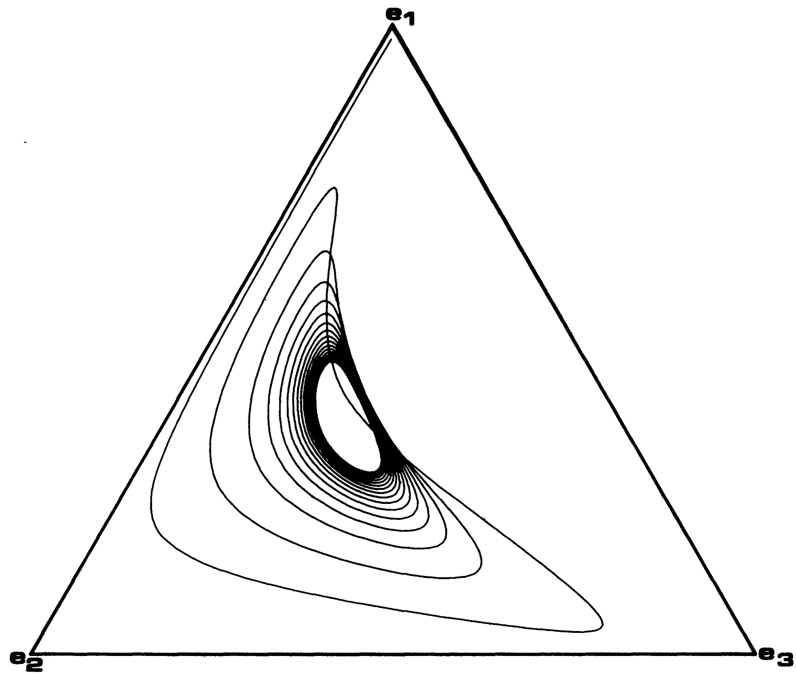

FIG. 12. *As in Fig.* 11 ($k_1 = k_2 = 0$; $k_3 = 1$).

4.2.2.4. The case $k_2 = k_1 + k_3$. In this case

$$\dot{P} = 2k_2 P[(x_1 - x_3)^2 + (x_2 - x_4)^2].$$

If $k_2 = 0$, we obtain the situation discussed in § 4.2.2.3.1. If $k_2 \neq 0$, then $\dot{P} = 0$ only for the points on the line where $x_1 = x_3$ and $x_2 = x_4$. On this line, every point is a fixed point. No matter what the ω-limit is, the fluctuational ω-limit has points in common with bdS_4 and the system leads to exclusion.

4.2.2.5. The case where $k_2 > 0$ and $k_1 + k_3 < k_2$. This case seems to be the most difficult to analyze. Note that (4.1) always has two fixed points, $(\frac{1}{2}, 0, \frac{1}{2}, 0)$ and $(0, \frac{1}{2}, 0, \frac{1}{2})$, on the boundary and that their eigenvalues are $-\frac{1}{2}k_2$ and $\frac{1}{2}(k_1 + k_3 - k_2)$. In the case considered here, these two points are sinks, while the four corners are unstable. Numerical computations indicate that we have exclusion (Fig. 13).

4.2.2.6. The case where $k_2 < 0$ and $k_1 + k_3 > k_2$. This case is obtained from the "stable" case in § 4.2.2.1 by letting the real part of the conjugate pair of eigenvalues $\omega_{1,3}$ cross the imaginary axis. In the critical case where Re $\omega_{1,3} = k_2 = 0$, ((ii) from § 4.1.4)) the point C is asymptotically stable by § 4.2.2.3.2. Hence the hypotheses of the Hopf birfurcation theorem are satisfied and we have a stable periodic orbit in the interior of S_4 (see Fig. 14).

4.3. Hierarchy of restrictions. Cyclic symmetry reduces the number of different restrictions to m-subfaces and facilitates a combinatorial analysis for the low dimensional cases ($m \leqq 3$).

4.3.1. $m = 1$: All corners of S_n are equivalent, the eigenvalues being $\omega_l = k_l$ ($l = 1, \cdots, n = 1$).

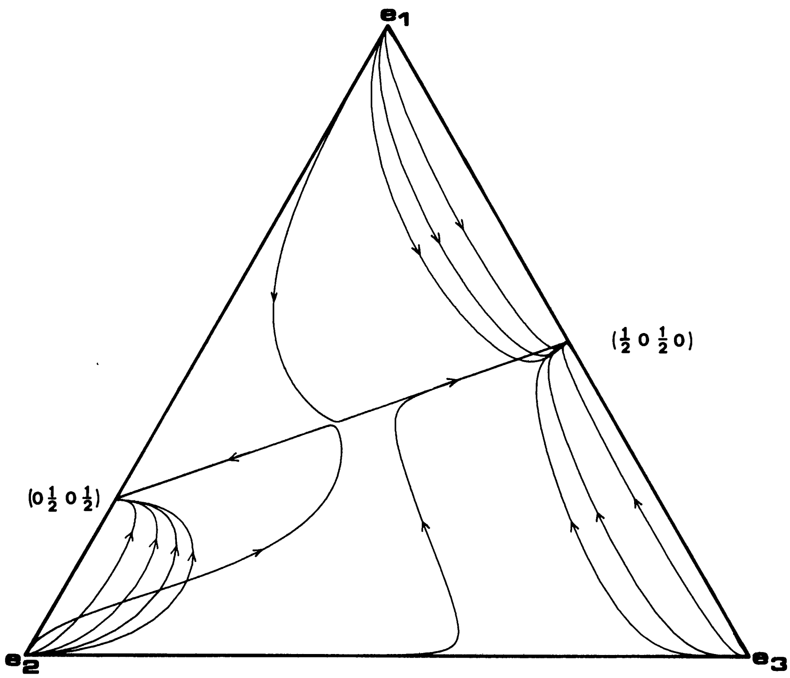

FIG. 13. *As in Fig.* 11 ($k_1=1$; $k_2=4$; $k_3=2$).

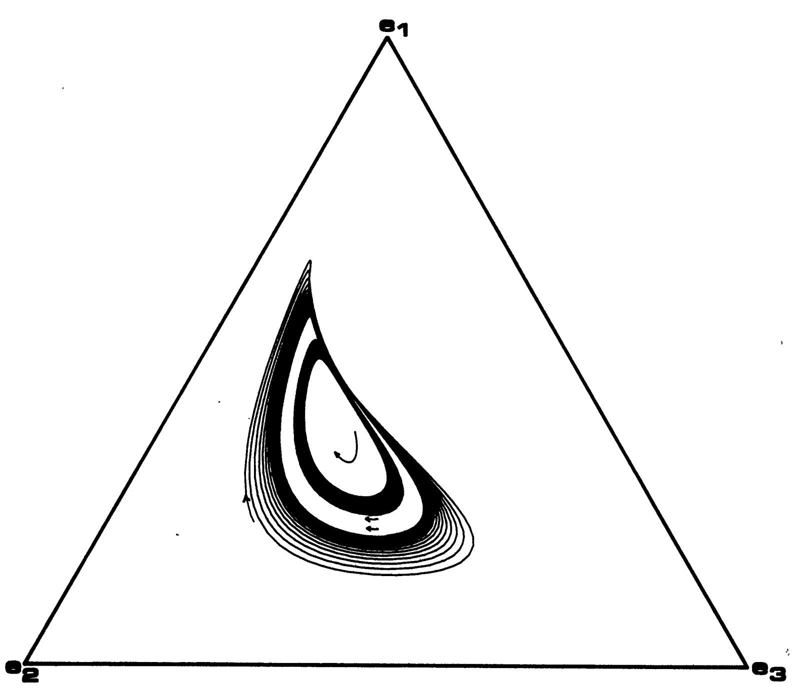

FIG. 14. *As in Fig.* 11 ($k_1=1.98$; $k_2=-.02$; $k_3=-1.02$). *The stable limit cycle is approached very slowly by the two spirals.*

4.3.2. $m=2$: We assign an order $r=\min\{|j-i|, n-|j-i|\}$ to the edge $\overline{ij}$. Due to cyclic symmetry the order r is sufficient to determine the dynamical system of the corresponding restriction:

$$\text{edge } \overline{ij}, \text{ order } r \begin{cases} \dot{x}_i=(k_r x_j-\phi)x_i, \\ \dot{x}_j=(k_{n-r}x_i-\phi)x_j. \end{cases}$$

For schematic illustration we map the simplex S_n onto a polygon P_n (see Fig. 15).

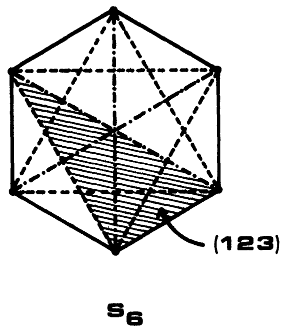

FIG. 15. *The simplex S_6 is mapped onto a regular polygon. A face of type* (123) *is hatched for illustrations.*

(α) n is odd: There are edges up to the order $r=(n-1)/2$, n of each class.

(β) n is even: There are n edges of each class up to the order $r=(n-2)/2$ and $n/2$ edges of the order $r=n/2$. The latter edges are symmetric since $k_r=k_{n-r}$.

In case there is a single fixed point ($k_{n/2}\neq 0$) it is placed in the middle of the edge, $\bar{\mathbf{x}}_{ij}$: ($\bar{x}_i=\bar{x}_j=\frac{1}{2}$, $\bar{x}_k=0$, $\forall k\neq i, j$, $k=1,\cdots,n$).

4.3.3. $m=3$: We can classify the various 3-faces on S_n by triples of indices (k, l, m) which represent the orders of the three edges of this face. Again the dynamical system is determined by the three indices. Without losing generality we assume $k\leqq l\leqq m$. A given triangle does occur in bdS_n iff the indices fulfill the following conditions:

$$m=\min(k+l, n-k-l),$$
$$k+l+m=n-i(1-\delta_{lm}), \qquad i=0, 1, \cdots.$$

The numbers of triangles of a given class is given by

$$N(k, l, m)=n\frac{1+(1-\delta_{kl})(1-\delta_{lm})}{1+2\delta_{kl}\delta_{lm}}.$$

Several results can be deduced easily from these conditions. Examples are:

(α) Triangles with three equivalent edges ($k=l=m$) do occur iff n is an integer multiple of 3. Then $k=n/3$ and $N(k, k, k)=n/3$.

(β) There are two classes of triangles with two equivalent edges
$k=l$: (k, k, m), $m=\min(2k, n-2k)$, $k<[(n-1)/3]$ and $N(k, k, m)=n$;
$l=m$: (k, l, l), $2l+k=n$, $N(k, l, l)=n$.

(γ) For $n=4$ there is only one type of restriction to a 3-subface, namely (1, 1, 2).

For illustration see the restrictions up to S_9 in Table 1. The hypercycle with cyclic symmetry ($k_2=\cdots=k_{n-1}=0$) has been treated for arbitrary n and m in [15].

TABLE 1
Restrictions of $S_n (n \leqq 9)$ to 3-subfaces

n	Class of triangles (k, l, m)	Number of triangles $N(k, l, m)$
3	(111)	1
4	(112)	4
5	(112)	5
	(122)	5
6	(112)	6
	(123)	12
	(222)	2
7	(112)	7
	(123)	14
	(133)	7
	(223)	7
8	(112)	8
	(123)	16
	(134)	16
	(224)	8
	(233)	8
9	(112)	9
	(123)	18
	(134)	18
	(144)	9
	(224)	9
	(234)	18
	(333)	3

Acknowledgments. The authors thank Prof. Dr. Manfred Eigen for many stimulating discussions. Generous supply with computer time by the "Interuniversitäres Rechenzentrum, Wien" and financial support by the Austrian "Fonds zur Förderung der Wissenschaftlichen Forschung," (Project Nrs. 2261 and 3502) as well as the "Bundesministerium für Wissenschaft und Forschung" is gratefully acknowledged.

Note added in proof. Recently, Taylor and Jonker, *Evolutionary stable strategies and game dynamics*, Math. Biosci. 40 (1978), pp. 145–156 and Zeeman in *Population dynamics from game theory* (to be published) have found that equation (1.2) plays a fundamental role in a theory of social behaviour of animals. We refer also to Hofbauer, Schuster and Sigmund, *A note on evolutionary stable strategies and game dynamics*, to appear in J. Theoret. Biol.

REFERENCES

[1] J. AUSLANDER AND P. SEIBERT, *Prolongations and stability in dynamical systems*, Ann. Inst. Fourier, 14 (1964), pp. 237–268.

[2] R. BOWEN, *ω-limit sets for Axiom A diffeomorphisms*, J. Differential Equations, 18 (1975), pp. 333–339.

[3] M. EIGEN, *Selforganization of matter and the evolution of biological macromolecules*, Die Naturwissenschaften, 58 (1971), pp. 465–526.

[4] M. EIGEN AND P. SCHUSTER, *The hypercycle, a principle of natural selforganization. Part A: Emergence of the hypercycle*, Die Naturwissenschaften, 64 (1977), pp. 541–565.

[5] ———, *The hypercycle, a principle of natural selforganization. Part B: The abstract hypercycle*, Ibid., 65 (1978), pp. 7–41.

[6] ———, *The hypercycle, a principle of natural selforganization. Part C: The realistic hypercycle*, Ibid., 65 (1978), pp. 341–369.

[7] I. EPSTEIN, *Coexistence, competition and hypercyclic interaction in some systems of biological interest*, to be published.

[8] R. D. JENKS, *Homogeneous multidimensional differential systems for mathematical models*, J. Differential Equations, 4 (1968), pp. 549–565.

[9] ———, *Irreducible tensors and associated homogeneous nonnegative transformations*, Ibid., 4 (1968), pp. 566–572.

[10] ———, *Quadratic differential systems for interactive population models*, Ibid., 5 (1969), pp. 497–514.

[11] B. O. KÜPPERS, *Towards an experimental analysis of molecular selforganization and precellar Darwinian evolution*, Naturwissenschaften, 66 (1979), to appear.

[12] R. MCGEHEE AND R. ARMSTRONG, *Some mathematical problems concerning the ecological principle of competitive exclusion*, J. Differential Equations, 23 (1977), pp. 30–52.

[13] J. MARSDEN AND M. MCCRACKEN, *The Hopf bifurcation and its applications*, Applied Mathematical Sciences, Vol. 19, Springer, New York, 1976.

[14] R. M. MAY, *Stability and Complexity in Model Ecosystems*, Princeton University Press, Princeton, NJ, 1973.

[15] P. SCHUSTER, K. SIGMUND AND R. WOLFF, *Dynamical systems under constant organization I: Topological analysis of a family of non-linear differential equations—a model for catalytic hypercycles*, Bull. Math. Biophysics, 40 (1978), pp. 743–769.

[16] ———, *Dynamical system under constant organization III: Cooperative and competitive behavior of hypercycles*, J. Differential Equations, 32 (1979), pp. 357–368.