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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:

$$\dot{x}_i = \left( \sum_{p=1}^{n} k_{ip}x_p - \sum_{p, q} k_{pq}x_p x_q \right) x_i, \quad i = 1, \ldots, n.$$  

Besides the general case two simplifications are treated:

1. the nonhyperbolic case: $k_{ii} \equiv 0$ ($k_{ii} = 0$) and
2. cyclic symmetry: $k_{ii} = k_{i+1, i+1}$.

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

$$\dot{x}_i = x_i (x_{i-1} - \sum_{j=1}^{n} x_j x_{j-1}), \quad i = 1, \ldots, n$$  

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

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

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

$$\dot{x}_i = \Gamma_i(x) - \frac{x_i}{c} \phi(x), \quad i = 1, 2, \ldots, n$$  

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

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

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(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].

![Diagram of a flow reactor with energy rich and poor material inputs and outputs, self-replicative units, and dilution flux.](image)

**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 \( \phi \) 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 \( \phi \). Under "constant organization" \( \phi \) is adjusted to yield constant total concentration \( c \).

The self-replicative units may multiply either directly, then \( \Gamma_i \) is a linear function of \( x_i \), 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 \( \Gamma_i \). 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" \( \Gamma_i \), reflect the dynamical properties of the entities, self-productive biological macromolecules, primitive organisms etc., growing in the reactor. The constraint \( \phi \) corresponds to an isotropic dilution flux.

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

\[
\{ x = (x_1, \cdots, x_n) \in \mathbb{R}^n : x_i \geq 0, \sum_{i=1}^{n} x_i = c \}.
\]

Since \( S = c \) implies \( \dot{S} = 0 \), \( S_c^c \) 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 fulfill 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 $\Gamma_i$ 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:

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

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

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

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 $\Gamma_i(x)$. In the first case as in (1.2) the phase portrait $\mathcal{F}(n, \Gamma, c)$, 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 $\mathcal{F}$ 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,

$$k_{ij} = k_{i(j)} + d_{ij} \Rightarrow \phi = \sum_i k_{i(j)} x_i + \sum_{i,j} d_{ij} x_i x_j$$
and thus
\[ x_i' = x_i \left( \sum_p k_{ip} x_p - \sum_{p,q} k_{pq} x_p x_q \right) = x_i \left( \sum_p d_{ip} x_p - \sum_{p,q} d_{pq} x_p x_q \right). \]

\( k_{ii} \) does not enter the differential equations (1.2).

We remove this arbitrariness by putting
\[ k_{ii} = 0 \quad \forall i. \]  

(1.4)

In § 2 we present fixed point analysis of (1.2). A more detailed study of the phase portrait \( \mathcal{F}(n, f, 1) \) will be given under some supplementary assumptions. In § 3 we investigate the case \( k_{ii} \equiv 0 \)—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 \( \omega \)-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
\[
\begin{align*}
\dot{y}_1 &= y_1 (1 - y_1 - y_2), \\
\dot{y}_2 &= y_2 (1 - y_1 - y_2),
\end{align*}
\]

(1.5)

\((y_1 \geq 0, y_2 \geq 0)\), the phase portrait contains a line \( L \) of fixed points given by \( y_1 + y_2 = 1 \). The \( \omega \)-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).](image-url)
A possible way to take account of such small fluctuations is to replace the $\omega$-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 $\omega$-limit set of a point $x \in M$ is the set

$$\omega(x) = \{ y \in M : \exists n_0 \uparrow +\infty \text{ with } d(T_{n_0}(x), y) \to 0 \},$$

while the fluctuational limit set is

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

with

$$J(x, \epsilon, T) = \{ y \in M : \exists n_0 > T, \exists x_n \in M \text{ with } x_0 = x$$

and $d(T_{n_0}(x_n), x_{n+1}) < \epsilon$ such that $d(x_n, y) \to 0$ as $n \to \infty$.}

Roughly speaking, $J(x, \epsilon, T)$ is the set of points which may be approached asymptotically, starting from $x$, by superposition of the time evolution $T_t$ with some fluctuational "jumps" which are small and rare (if $\epsilon$ 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 $f - \omega(x)$ contains $\omega(x)$ but may be significantly larger.

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

DEFINITION. $x \in S_n$ is said to lead to exclusion for (1.2) if $f - \omega(x) \cap \text{bd } S_n \neq \emptyset$. Otherwise $x$ 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 $x \in \text{int } S_n$.

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 ($m \leq n$). Fixed points have to fulfil the conditions

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

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

$$\sum_{p=1}^{m} x_p = 1. \quad (2.1)$$

Elimination of $\phi$ yields $m - 1$ homogeneous linear equations

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

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 $\hat{x} = (\hat{x}_1, \ldots, \hat{x}_n)$. Since

$$\frac{\partial \phi}{\partial x_i} = \sum_{p=1}^{n} (k_{ip} + k_{ip}) x_p,$$
one obtains
\begin{equation}
    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
\end{equation}
(2.3)
\begin{equation}
    a_{ij} = \bar{x}_i (k_{ij} - \sum_{p=1}^{n} (k_{ip} + k_{pi}) \bar{x}_p) \quad \text{for } j \neq i.
\end{equation}

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 \(\omega_c\). 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 \(e_i = (\delta_{i1}, \ldots, \delta_{in})\) (\(\delta_{ij}\) is the Kronecker symbol) are fixed points \((l = 1, \ldots, n)\). The Jacobian has as the \(l\)th row \((-k_{1l}, -k_{2l}, \ldots, -k_{nl})\); for \(p \neq l\), the \(p\)th row consists of zeros except for the diagonal term \(k_{pl}\). As eigenvalues one obtains \(\omega_l = \omega_c = 0\) and \(\omega_p = k_{pl} (p = 1, \ldots, n, p \neq l)\).

2.4. Fixed points for \(S_2\). Apart from \(e_1\) (with eigenvalue \(k_{21}\)) and \(e_2\) (with eigenvalue \(k_{12}\)) we may have the fixed point
\begin{equation}
    \bar{x}_3 = \frac{1}{q} (k_{12}, k_{21})
\end{equation}
provided \(q = k_{12} + k_{21} \neq 0\). Its eigenvalue is
\begin{equation}
    \omega^{(3)} = -\frac{1}{q} k_{12} k_{21}.
\end{equation}
If \(k_{12} k_{21} > 0\), then \(\bar{x}_3 \in \text{int } S_2\). 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 \(k_{12} k_{21} \leq 0\), \(\bar{x}_3 \notin \text{int } S_2\) and we have exclusion: int \(S_2\) either consists of a single orbit or of fixed points.

2.5. Fixed points for \(S_3\). \(e_1\) has the eigenvalues \(k_{31}\) and \(k_{21}\); \(e_2\), the eigenvalues \(k_{12}\) and \(k_{32}\); and \(e_3\), the eigenvalues \(k_{23}\) and \(k_{13}\). Apart from linear degeneracies, there are four more possible fixed points:
\begin{equation}
    \bar{x}_4 = \frac{1}{q_4} (0, k_{23}, k_{32}) \quad \text{(where } q_4 = k_{23} + k_{32})
\end{equation}
has the eigenvalues
\begin{equation}
    \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},
\end{equation}
\(\bar{x}_5\) and \(\bar{x}_6\) are obtained by cyclic permutations. Finally
\begin{equation}
    \bar{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)})
\end{equation}
may lie in \(\text{int } S_3\). 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 \(k_{ij} \geq 0\) for \(1 \leq i, j \leq n\) (and \(k_{ij} = 0\) for all \(i\)).

With a nonhyperbolic equation of type (1.2) we associate a graph whose vertices are the species \(i\) \((i = 1, \ldots, n)\) and where there is a directed edge from \(i\) to \(j\) iff \(k_{ij} > 0\), 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 $\bar{x}$ in $\text{int} \, S_3$, then it is cooperative.

**Proof.** Equation (1.2) is now

\begin{align*}
\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{align*}

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

\begin{equation}
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
\end{equation}

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

\begin{equation}
\frac{d}{dt} \left( \frac{x_1}{x_2} \right) = \left( \frac{x_1}{x_2} \right) (k_{12}x_2 + k_{13}x_3 - k_{21}x_1 - k_{23}x_3).
\end{equation}

![Fig. 3. Possible graphs of the nonhyperbolic equation (1.2) with $n = 3$.](image)

Let $L_3$ be the line where $(x_1/x_2)^2 = 0$. This line passes through $\bar{x}$ and intersects the edge $x_3 = 0$ somewhere between $e_1$ and $e_2$ (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 $0 \leq x_1 \leq 1$).

Let $l_1, l_2, \text{resp.} \, l_3$ be the lines through $\bar{x}$ and $e_1, e_2 \text{ resp.} \, e_3$. Let $P_1$ be an arbitrary point on $l_1$ between $e_1$ and $\bar{x}$; let $Q_2$ (resp. $Q_3$) be the intersection of $P_1e_3$ (resp. $P_1e_2$) with $l_2$ (resp. $l_3$). Let $P_2$ (resp. $P_3$) be the intersection of $Q_3e_1$ (resp. $Q_2e_1$) with $l_2$ (resp. $l_3$). Then the intersection of $P_2e_3$ and $P_3e_2$ is a point $Q_1$ on $l_1$ (see Fig. 4: a proof of the last statement is in [16]).
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 collinear with \( e_3 \), 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 \( x_1/x_2 < 0 \), while on \( P_2Q_1 \) we have \( x_1/x_2 > 0 \). 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 \( \mathcal{F} \) is the \( \omega \)-limit (and the fluctuational \( \omega \)-limit) of every orbit in \( \text{int } S_3 \). 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 \( \text{int } S_3 \) (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

\[
\frac{x_1}{x_2} = \frac{x_1}{x_2} x_3(k_{13} - k_{23}).
\]

**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 \( \text{int} S_3 \) 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 \( \dot{x}_1 \leq 0 \). 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., \( k_{4i} = 0 \) 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 \( \phi \) is now of another form. This difference plays no role in the following considerations. The expression for \( x_1 / x_3 \) is given by (3.3) again; \( x_2 / x_3 \) and \( x_3 / x_1 \) are similar. It may be that one of these expressions is always of the same sign. The corresponding quotient \( x_1 / x_3 \) 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 \( (\bar{x}_i / \bar{x}_j) \to (\bar{x}_i / \bar{x}_j) \) for \( 1 \leq i, j \leq 3 \). But this can be shown just as in the proof of Theorem 1, the only difference being that we have \( x_1 + x_2 + x_3 \leq 1 \) 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 \( y = x_1 (1 + x_2 (\bar{x}_1 / \bar{x}_2)) + x_3 (\bar{x}_1 / \bar{x}_3) \) (or \( x_1 + x_2 + x_3 \) on \( S^* \)). It is easy to see that on \( S^* \), (1.2) becomes

\[
\begin{align*}
\dot{y} &= y(qy - \phi), \\
\dot{x}_4 &= x_4(ky - \phi)
\end{align*}
\]

with

\[
x_4 + y = 1, \quad \phi = y(qy + kx_4),
\]

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

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 \( \text{int} S_4 \) 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

\[
\dot{y} = y(qy - \phi),
\]

\[
\dot{x}_3 = x_3(k_3y + k_{34}x_4 - \phi), \quad \dot{x}_4 = x_4(k_4y + k_{43}x_3 - \phi),
\]

where $y + x_3 + x_4 = 1$, $\phi = y(qy + k_3x_3 + k_{44}x_4) + x_3x_4(k_{34} + k_{45})$, \[q = (1 + \frac{k_{21}}{k_{12}})^{-1} \frac{k_{21}}{k_{21}}, \]

\[k_3 = (1 + \frac{k_{21}}{k_{12}})^{-1} \left( k_{31} + k_{32} \frac{k_{21}}{k_{42}} \right), \]

\[k_4 = (1 + \frac{k_{21}}{k_{12}})^{-1} \left( k_{41} + k_{42} \frac{k_{21}}{k_{12}} \right). \]

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{equation}
\begin{align*}
\dot{x}_1 &= x_1(-\phi), \\
\dot{x}_2 &= x_2(-q_2 x_1 + h_2 x_3 - \phi), \\
\dot{x}_3 &= x_3(-q_3 x_1 + h_3 x_2 - \phi)
\end{align*}
\end{equation}

(where $h_2, h_3 > 0$ and $q_2, q_3 \in \mathbb{R}$) 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 $A = h_2 h_3 + h_3 q_2 + h_2 q_3$, the coordinates of $C$ are $x_1 = A^{-1} h_2 h_3, x_2 = A^{-1} h_2 q_3, x_3 = A^{-1} q_2 h_3$. 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

$$
\phi = -q_2 x - q_3 y + xy(h_2 + h_3 + q_2 + q_3)
$$

and

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

Equation (3.7) becomes

\begin{equation}
\begin{align*}
\dot{x} &= x(-q_2(1 - x - y) + h_2 y - \phi) = F_1(x, y), \\
\dot{y} &= y(-q_3(1 - x - y) + h_3 x - \phi) = F_2(x, y).
\end{align*}
\end{equation}

At the point $C$ one gets

$$
\frac{\partial \phi}{\partial x} = A^{-1} q_2 (h_2^2 + h_3 q_3 + q_3 h_2),
$$

$$
\frac{\partial F_1}{\partial x} = A^{-2} h_2 h_3 q_2 q_3 (k_2 + q_2 - h_3 - q_3),
$$

$$
\frac{\partial F_1}{\partial y} = A^{-2} h_2 h_3 q_3 [(q_2 + h_2)^2 - q_2 q_3]
$$

and for the determinant of the Jacobian at $C$:

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

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

\begin{figure}[h]
\centering
\includegraphics[width=0.5\textwidth]{phase_portrait.png}
\caption{Phase portrait of equation (3.7).}
\end{figure}
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 \( k_{i,j} = 0 \), but drop the condition \( k_{i,j} \geq 0 \). Denoting \( k_{i,i+j} \) by \( k_j (j = 0, 1, \cdots, n-1) \) one obtains the equation

\[
(4.1) \quad \dot{x}_i = x_i (G_i - \phi)
\]

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 \( \text{int} \ S_n \).

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

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

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

\[
\omega_j = \sum_{l=0}^{n-1} c_l \lambda^{l j} = \frac{1}{n} \sum_{l=0}^{n-1} k_l \lambda^{l j},
\]

(4.2)

\[ j = 1, \cdots, n-1, \quad \lambda = \exp \left( \frac{2 \pi i}{n} \right). \]

Furthermore the \( n \)th eigenvalue corresponding to \( \omega_n \) 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 \( n \),

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

One then has

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

The new variables \( y_p \) obviously represent the eigenvectors which correspond to the eigenvalues \( \omega_p \) 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

$$\bar{y}_p = y_{n-p} \quad (p = 1, \cdots, n-1),$$

$$y_0 = 1.$$  \hspace{1cm} (4.3)

Equation (4.1) then becomes

$$\dot{y}_p = \sum_{i=1}^{n} \lambda^{ip} x_i = \sum_{i=1}^{n} \lambda^{ip} x_i \left( \sum_{j=1}^{n-1} k_j x_{i+j} - \phi \right)$$

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

$$= \sum_{i=1}^{n-1} k_i \frac{1}{n} \sum_{i=1}^{n} \lambda^{ip} \left( \sum_{i=0}^{n-1} \lambda^{-iy} \right) \left( \sum_{m=0}^{n-1} \lambda^{-(i+j)m} y_m \right) - \phi y_p$$

$$= \sum_{i=1}^{n-1} k_i \frac{1}{n} \sum_{l,m=0}^{n-1} \left( \sum_{i=1}^{n} \lambda^{i(p-l-m)} \right) \lambda^{-lm} y_ly_m - \phi y_p.$$  \hspace{1cm} (4.4)

Since

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

we obtain

$$\dot{y}_p = \sum_{i=1}^{n} k_i \frac{1}{n} \sum_{m=0}^{n-1} \lambda^{-lm} y_{p-m} y_m - \phi y_p$$

$$= \sum_{m=0}^{n-1} \left( \frac{1}{n} \sum_{i=1}^{n} k_i \lambda^{-lm} \right) y_{p-m} y_m - \phi y_p$$

or

$$\dot{y}_p = \sum_{m=0}^{n-1} \omega_m \bar{y}_m y_{p+m} - \phi y_p.$$  \hspace{1cm} (4.5)

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

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

and therefore (4.1) is transformed into

$$\dot{y}_p = \sum_{m=0}^{n-1} \omega_m \bar{y}_m (y_{p+m} - y_p y_m) \quad (p = 1, \cdots, n-1).$$  \hspace{1cm} (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

$$P(x) = x_1 x_2 \cdots x_n$$

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

One obtains

$$\dot{P} = P \sum_{i=1}^{n} (G_i - \phi)$$

$$= P[(k_1 + \cdots + k_{n-1}) - n\phi]$$

$$= nP(\omega_0 - \phi)$$

$$= -nP \sum_{m=1}^{n-1} \text{Re} \omega_m |y_m|^2.$$  \(4.8\)

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

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

An immediate consequence of (4.8) is

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

(2) If $C$ is a source, the $\omega$-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 $n \geq 5$ and where exactly one pair of conjugate eigenvalues of $C$ are on the imaginary axis, while all other eigenvalues are in the left half-plane. We may thus assume $\text{Re} \omega_1 = 0$ ($\omega_1 \neq 0$) and $\text{Re} \omega_i < 0$ for $i \neq 1$, $n - 1$. Then (4.8) reduces to

$$\dot{P} = -nP \sum_{m=2}^{n-2} \text{Re} \omega_m |y_m|^2 \geq 0.$$  \(4.8\)

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 \{$P = 0$\} = \{$y_m = 0, m = 2, \cdots, n - 2$\} contains no invariant set with the exception of $C$ (which is the point $(1, 0, \cdots, 0)$ in $y$-space). Since on this set

$$y_i = \sum_{m=0}^{n-1} \omega_m y_{m+i} (i = 2, \cdots, n - 2),$$

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

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

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

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

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

(ii) for $\mu = 0$ $\text{Re} \omega_1 = 0$ ($\omega_1 \neq 0$) and $\text{Re} \omega_i < 0$ ($i = 2, \cdots, n - 2$);
(iii) for $\mu > 0$ Re $\omega_1 > 0$ and Re $\omega_i < 0$ ($i = 2, \ldots, n-2$; and furthermore that (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 $k_1 \equiv 0$, 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)

$$\dot{p} = \frac{P}{2}(k_1 + k_2)[(x_1 - x_2)^2 + (x_2 - x_3)^2 + (x_3 - x_1)^2]$$

$$= \frac{3P}{2}(k_1 + k_2) \sum_{i=1}^{3} \left(x_i - \frac{1}{3}\right)^2.$$

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 $x_1 = 0$ implies $x_2 = x_3$, and

![Fig. 8. Phase portrait of the dynamical system according to equation (4.1) with $n = 3$ ($k_1 = -0.5; k_2 = 0.5$).](image_url)
\( \dot{x}_2 = 0 \) 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 \( e_1, e_2 \) and \( e_3 \) (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 \( \omega \)-limit (see Fig. 9). If \( k_1 \) and \( k_2 \) are negative the points \( e_1, e_2 \) and \( e_3 \) are sinks and there are three more fixed points on \( bdS_3 \). As shown in § 2.5 these points \( \bar{s}_4, \bar{s}_5 \) and \( \bar{s}_6 \) are of saddle type. The interior of \( S_3 \) is divided by their separatrices into three parts corresponding to the three possible \( \omega \)-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

\[
\omega_2 = \frac{1}{4}(k_2 - k_1 - k_3), \\
\omega_{1,3} = \frac{1}{4}(-k_2 \pm i(k_1 - k_3)).
\]

It is easy to see that the eigenspace corresponding to \( \omega_2 \) is the line where \( x_1 = x_3 \) and \( x_2 = x_4 \), the one corresponding to \( \omega_{1,3} \) is the plane \( x_1 + x_3 = \frac{1}{2} \).
Using (4.9) one obtains
\[ \dot{P} = P\{4(k_1 + k_3 - k_2)(x_1 + x_3 - \frac{1}{2})^2 + k_2[(x_1 + x_2 - \frac{1}{2})^2 + (x_1 + x_4 - \frac{1}{2})^2]\}\]
\[ = P\{4(k_1 + k_3 - k_2)(x_1 + x_3 - \frac{1}{2})^2 + \frac{1}{2}k_2[(x_1 - x_3)^2 + (x_2 - x_4)^2]\}\]

**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 \( \omega \)-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
\[ \dot{P} = 4P(k_1 + k_3)(x_1 + x_3 - \frac{1}{2})^2 \]

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 \( P = \text{const.} \) and \( \phi = 0 \). Also,
\[ \dot{x}_1 = x_1(k_1x_2 + k_3x_4) \]
\[ = x_1k_1(x_2 - x_4). \]

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 \((x_1, x_3) = 0\) and similarly \((x_2, x_4) = 0\). 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.

\[ \begin{align*}
\phi &= \frac{1}{4}(k_1 + k_3), \\
\dot{x}_1 &= x_1(k_1x_2 + k_3x_4 - \phi), \\
\dot{x}_3 &= x_3(k_3x_2 + k_1x_4 - \phi)
\end{align*} \]

and

\[ \dot{x}_1 + \dot{x}_3 = (k_1 - k_3)(x_1x_2 + x_3x_4 - \frac{1}{8}). \]

In the case $k_1 = k_3$, the plane $x_1 + x_3 = \frac{1}{2}$ is invariant (it consists of fixed points). The $\omega$-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 $P = 0$ only for a discrete set of times. If $k_1 + k_3 > 0$, this implies that every orbit in the interior has $C$ as $\omega$-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.
4.2.2.4. The case \( k_2 = k_1 + k_3 \). In this case
\[ \dot{P} = 2k_2P[(x_1 - x_3)^2 + (x_2 - x_4)^2]. \]
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 \( \omega \)-limit is, the fluctuational \( \omega \)-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 \( \text{Re} \omega_{1,3} = k_2 = 0 \), ((ii) from § 4.1.4)) the point \( C \) is asymptotically stable by § 4.2.2.3.2. Hence the hypotheses of the Hopf bifurcation 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 \( m \)-surfaces and facilitates a combinatorial analysis for the low dimensional cases \((m \leq 3)\).

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:

$$
\begin{align*}
\dot{x}_i &= (k, x_j - \phi)x_i, \\
\dot{x}_j &= (k, x_i - \phi)x_j.
\end{align*}
$$

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

![Diagram of a simplex mapped onto a polygon](image)

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

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

($\beta$) $n$ 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, $\tilde{x}_k$: $(\tilde{x}_i = \tilde{x}_j = \frac{1}{2}, \tilde{x}_k = 0, \forall k \neq i, j, k = 1, \ldots, n)$.

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 $k \leq l \leq m$. A given triangle does occur in $bdS_n$ iff the indices fulfill the following conditions:

$$m = \min (k + l, n - k - l),$$

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

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:

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

($\beta$) 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 $N(k, k, m) = n$;

$l = m$: $(k, l, l), 2l + k = n, N(k, l, l) = n$.

($\gamma$) 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 $S_n(n \leq 9)$ to 3-subsaces*

<table>
<thead>
<tr>
<th>$n$</th>
<th>Class of triangles $(k, l, m)$</th>
<th>Number of triangles $N(k, l, m)$</th>
</tr>
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</tr>
<tr>
<td>4</td>
<td>(112)</td>
<td>4</td>
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<tr>
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<td>(112)</td>
<td>5</td>
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<tr>
<td></td>
<td>(122)</td>
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</tr>
<tr>
<td>6</td>
<td>(112)</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>(123)</td>
<td>12</td>
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<tr>
<td></td>
<td>(222)</td>
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<td>7</td>
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<td>7</td>
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<td></td>
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<tr>
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<td>3</td>
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