

MATHEMATISCHES FORSCHUNGSINSTITUT OBERWOLFACH

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Mathematische Modelle in der Biologie

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The 1981 Oberwolfach Conference on Mathematical Biology organized by K.P.Hadeler (Tübingen) and W.Jäger (Heidelberg), continuing earlier meetings in 1975 and 1978 on this subject, brought together 41 mathematicians, biologists and physicists from nine countries. The topics covered a wide variety of biological fields, in which the application of mathematical methods appears to be adequate. In some areas of ecology or physiology the mathematical approach is successful, in others it is just in the initial stage, and much joint work has to be done. Lectures were given on population dynamics, genetics, epidemics, cell aggregation, immunology, the nervous system, membrane physiology and other topics. Reflecting this diversity of problems, the variety of mathematical subjects included ordinary and partial differential equations, difference and delay equations, stochastic processes and numerical methods. A considerable part of the time between and after the lectures was used for discussions in small groups of joint interest. For all these activities, the Oberwolfach Institute presented itself as an ideal place, and the participants are very grateful for the opportunity for interdisciplinary and international contacts and of passing a week of intense work in their field. Special thanks go to the staff of the house for excellent organization, accomodation and catering.

Vortragsauszüge

W. Alt:

Aggregation of leukocytes during inflammation: Analysis of a chemotaxis system

Infection of human tissue (say by bacteria) leads to the production of a diffusing chemical (chemoattractant) which triggers the chemotactic response of white blood cells (leukocytes) in the tissue and enhances their emigration out of the blood vessels. This situation is modelled by a strongly coupled parabolic system for the three concentrations (enlarged Keller-Segel-System). Assuming different time scales for the various events (chemotaxis, motility, reproduction and killing of bacteria etc.) as well as infections located at the outer boundary of the tissue, we [in joint work with D.A.Lauffenburger, Philadelphia] show that the chemotaxis system can approximately be described by a two-dimensional ordinary differential system, the approximation being valid for a certain large time interval. Infection-inflammation phase plane analysis exhibits various observed phenomena (as: transient aggregation of leukocytes, extinction of bacteria or tolerance of the infection) depending on the parameters (bacterial growth rate versus killing rate, chemotaxis coefficient and others). The introduction of a measure for the damage due to phagocytosis of bacteria explains the fact, that chemotactic aggregation has an overall positive effect on the defense response during inflammation.

St.N. Busenberg:

Epidemic models with spatial spread due to population migration

We consider a class of population models which involve diffusion terms that describe population migration. Here, the flux

of the subpopulation groups is assumed to be proportional to the gradient of a function of the total population. If p denotes the density of the total population, and p_i that of the i -th subpopulation, then we are led to consider non-linear diffusion terms of the form $\nabla \cdot (k \frac{p_i}{p} \nabla U(p))$, where U is a function of p only. In the special case of Fickian diffusion of the total population, U is the identity, $U(p) = p$. We give some general results concerning such migratory terms; and treat a particular $S \rightleftharpoons I \rightarrow R$ epidemic model with both migratory diffusion and with terms describing other modes of spatial spread of the infection. We derive threshold criteria, as well as stability results for the steady state solution. We also show that spatially nonhomogeneous, stable steady states are possible.

O. Diekmann:

Volterra integral equations and the dynamics of age-structured populations.

Models of population growth, which take into account that reproduction, mortality and/or interaction may depend on the age of the individuals, sometimes lead to a Volterra integral equation of convolution type. With such an equation one can associate a dynamical system acting on a space of forcing functions. This leads to standard proofs of, for instance, the Hopf bifurcation theorem. We discuss in some detail what these qualitative results can tell about

- 1) an epidemic model with temporary immunity
- 2) a model for the growth of a cannibalistic population.

An important part of the work consists of the analysis of a characteristic equation. The results are based on joint work with S.A. van Gils and R. Montijn.

W.Ebel:

A mathematical model for facilitated diffusion across membranes

A model for carrier facilitated diffusion is motivated and analysed. It is a system of three reaction diffusion equations with suitable boundary conditions.

Existence, uniqueness and boundedness of global solutions can be shown. There exist also stationary solutions, they are stable within a certain range of parameters.

W.J. Ewens:

Estimating genetic variation from restriction endonuclease data

The restriction endonuclease technique can be used, among other purposes, to estimate the degree of genetic variation in a population, a question of enduring interest to geneticists. The standard intuitive estimate of the extent of this variation is incorrect. In order to find a correct estimate, one must set up some model describing the genetic make-up and evolution of the population considered. It is not clear how detailed such a model must be in order to produce estimates, nor is it clear how detailed the model must be to produce variances of these estimates. Various possibilities are discussed and this leads to a general consideration of the modelling process in genetics.

E. Frehland:

Stochastic treatment of ionic movement through biological membranes within the concept of discrete transport systems

The discrete description of transport is adequate for systems with discontinuous structures and coupling between transport and other processes as e.g. chemical reactions. It has been successful for the description of complex ion transport

mechanisms through biological membranes, e.g. carrier mediated transport or hopping diffusion through narrow channels, which additionally may assume different conductivity states. The system is described by a discrete set of state variables. The time dependent probabilistic behaviour is given by a master equation for the probabilities of the different states. Transport observables as e.g. electric current are linearly coupled to the fluxes between different states. A general formula for the steady state transport fluctuations is derived. It is shown that as consequence of the vectorial character of transport observables at nonequilibrium the fluctuation dissipation theorem breaks down. Experimental applications and further consequences are discussed.

H.R. Gregorius and M. Ziehe:

The biological significance of discrete- and continuous-time models in the selection theory of population genetics

The majority of population genetic models proceeds from the assumption of either separated generations or continuously reproducing species. In order to be able to judge on possible evolutionary resemblances between these two models of reproduction one has to be as explicit as possible when specifying the biological meaning of the basic parameters used in the formulation of the two types of models. In particular, these parameters should be chosen in such a way that they can be applied to the discrete-time as well as to the continuous-time versions. This was demonstrated with the help of two examples. One referred to Fisher's continuous-time selection model based on gene frequencies, and the other considered a special model of genetic fecundity selection based on mating pairs. The latter example was formulated in the discrete- as well as in the continuous-time version.

For Fisher's model it was shown that under the assumption of Hardy-Weinberg proportions among zygotes and adults, and for frequency independent birth rates and mortalities, Fisher's

equation ($\dot{p}_i = p_i (m_i - \bar{m})$) defines a dynamical system on the state space of adult allelic frequencies if and only if fecundity selection does not take place and the genotypic mortalities are additive.

For the fecundity selection example it turned out that the continuous-time case produces a globally attractive equilibrium for all parameter values while for the separated generations case bifurcation occurs.

U. Großmann:

A mathematical model to simulate the combined exchange of oxygen and heat through the upper skin

A model of a microcirculatory unit has been developed to study oxygen exchange processes within the upper part of the skin. The model includes the loop-shaped capillary structure of the stratum papillare, the nonlinear binding of oxygen by hemoglobin and, in particular, the shift of the oxygen hemoglobin binding curve due to temperature variations. The corresponding nonlinear, elliptic boundary value problem is defined and the existence of at least one solution assured. After describing the numerical procedure to calculate an approximation to the solution, results of several calculations representing different supply situations are presented.

K.P.Hadeler:

Exclusion of periodic orbits in population genetic models

In the classical Fisher model of population genetics a Ljapunov function ensures the convergence to equilibrium. In other models such function is not known. In the case of two alleles, three genotypes, the space dimension is two, and the criteria of Dulac and Bendixson are of some help, at least in special cases, and after lengthy calculations. It is shown, that a suitable transformation leads to quasimonotone systems in the sense of Müller

and Kamke, and it is observed that for such systems the convergence problem is simple. This observation also greatly simplifies some proofs on ecological models.

U. an der Heiden:

Neural Networks: Models and Dynamics

A mathematical description of the interaction in neuronal tissues among different classes of cell populations is given in the form of a system of integral equations: The populations are distributed in several areas R_1, R_2, \dots, R_n in the brain. The activity (locally averaged membrane potentials or impulse frequencies) $v(s_i, t)$ at location $s_i \in R_i$ at time t results from an integrated nonlinear transformation $U(s_i, s_j', t, t', v(s_j', t'))$ of activities at other locations $s_j' \in R_j, t' \leq t$, in addition to external influences $E(s_i, t)$:

$$v_i(s_i, t) = E(s_i, t) + \int_{-\infty}^t \sum_{j=1}^n \int_{R_j} U_{ij}(s_i, s_j', t, t', v(s_j', t')) ds_j' dt'.$$

It is shown that this general model comprises and gives coherent connection between most of the models for neural networks existing in the literature. The simplest conditions on U_{ij}, R_i , and E are derived for the existence of some basic types of behaviour such as multiple steady states, limit cycles, travelling waves etc.

Reference: U. an der Heiden, Analysis of Neural Networks, Lecture Notes in Biomathematics No.35, Springer-Verlag 1980

F.C. Hoppensteadt:

Some recent topics about biological clocks

Recent work on phase locking of biological clocks will be described. In particular, dynamic phase resetting experiments and rhythm splitting phenomena will be modeled and analyzed.

F. Jähnig:

Molecular Theory of Lipid Organization in Membranes

Lipid membranes can exist in an ordered state in which the long hydrocarbon chains are stretched, oriented parallel, and densely packed and in a disordered or fluid state. Between the two states a phase transition of first order occurs. These structural characteristics are described within a model of interacting flexible chains. One end of each chain is fixed in a common plane and the chains are otherwise free to organize themselves. The interactions include van der Waals interaction and steric hindrance, both treated in self-consistent field approximation. Flexibility is simulated by describing the chains as continuous lines with bend elasticity. The long-range order of the chains is calculated, and an analytic result is obtained for the phase transition temperature as a function of the molecular parameters elasticity constant and chain length. Demands upon the naturally occurring lipids for the adoption of the biologically necessary fluid state at physiological temperatures are derived.

K. Janáček:

A mathematical model of alkalization in an illuminated suspension of the alga Hydrodictyon reticulatum

Alkalization in an illuminated suspension of the alga Hydrodictyon reticulatum can be described by two empirical laws. The first of these follows from the purely exponential course of pH with time and may be formulated as follows: the rate of change of the chemical potential of protons is directly proportional to the difference between their final (steady-state) and actual chemical potentials. When, on the other hand, the final pH of the suspension is lowered by inflow of a strong acid in pH-stat equipment another law holds: the rate of

disappearance of free protons (or hydroxonium ions) from the medium is directly proportional to the above difference between their final and actual chemical potentials. Taking the two laws for granted, the alkalization is interpreted in terms of HCO_3^- , OH^- and CO_2 flows and HCO_3^- and CO_3^{2-} concentration changes.

G. Karigl:

A recursive approach to the theory of kinship and identity coefficients and some applications

A fundamental concept in the study of heredity in individual organisms and in the treatment of genetic relationships is that of gene-identity which was first introduced by C. W. Cotterman. Based on this notion several measures for the degree of relationship have been introduced such as the inbreeding coefficient, the coefficient of kinship and the identity coefficients. The investigation of these concepts yielded many useful applications especially in human genetics (G. Malecot, A. Jacquard and others).

All coefficients mentioned above - being essentially probabilities- fulfil certain recursive relations which permit calculations and give rise to generalizations to handle genetic relationships for any number of individuals. In order to emphasize the advantage of this approach the following two topics will be discussed:

1. A new recursive algorithm for the calculation of the kinship coefficient and of all nine condensed identity coefficients for any two individuals with given pedigree.
1. The problem of admissible regions in the simplex of identity coefficients of two non-inbred individuals.

J.P. Keener:

Genetic Effects on Epidemics

A model is presented for an epidemic in which individuals which contract a disease either recover with permanent immunity or die, and for which the response to infection is genetically related. It is assumed that there is a one locus, two allele genetic trait with genes A and a where A is dominant and the homozygote aa has a slight advantage with respect to recovery and death. The resulting system of nine nonlinear differential equations can be treated by singular perturbation techniques by supposing that genetic advantages are only slight. It is shown that Hardy-Weinberg proportions are rapidly attained and then, on a larger time scale the proportionality factor changes slowly. It is further shown that if there is a nonzero initial population of gene a, then the population of gene A approaches zero as time becomes infinite. This model is used to show that the use of myxomatosis to control rabbit populations is rendered less effective if there are present in the initial population a small number of mutants with resistance to myxomatosis.

P. Klein:

A Mathematical Model of the Development of Antibody-forming Cells

We have developed a mathematical model, based on experimental results, which focuses on the role antigen plays in controlling B lymphocyte differentiation. Immunocompetent cells (ICC) arising independently of antigen stimulation are activated by antigen to proliferate (immunologically activated cells-IAC). Another contact with antigen is needed for the terminal differentiation of IAC into short-lived antibody-forming cells (AFC). High doses of antigen can drive IAC into AFC thereby restricting

proliferation; exhaustion of antigen-reactive cells results in tolerance to the next antigen dose. Lower doses permit IAC to escape antigen and form long-lived memory cells (MC). Having higher avidity for antigen than ICC, MC can be either directly inactivated by low doses (low zone tolerance), or activated by medium doses to proliferate and differentiate into AFC, or exhausted by high doses through terminal differentiation. The model qualitatively agrees with experimental results and is used for suggesting experiments.

H.-A. Kolb:

Noise analysis of ion transport across membranes: Comparison of experimental data and theory

From the analysis of electrical noise generated by ion movement across biological and artificial membranes, information about the underlying molecular transport mechanisms may be obtained. In general two types of transport mechanisms are discussed, pore- and carrier-mediated ion transport. Using model systems it was found that the different types of transport mechanisms create different patterns of electrical noise which can be described theoretically by different approaches like the Nyquist-theorem, the Langevin-Ansatz, the master-equation etc. Furthermore, it will be shown that there is no one-to-one correspondence between experimental results and theoretical description.

D. Lauffenburger :

Consequences of Bacterial Motility and Chemotaxis for Population Growth and Competition

Most naturally occurring microbial ecological systems are not well-mixed or spatially uniform, so that the theories developed from well-mixed chemostat investigation may not be applicable. In particular, while the effects of growth

kinetic parameters on population growth and competition are well known, the effects of cell motility and chemotaxis are purely speculative.

We have developed simple mathematical models for growth and competition of bacterial populations in a finite domain, with the rate-limiting nutrient diffusing from a boundary source. Analyses of these models show that motility properties can have great influence on the outcome of single population growth on two-population competition. In particular, the results are no longer solely determined by growth kinetic properties. In fact, a population possessing inferior growth kinetic properties can outgrow a population with superior growth kinetic properties, if the motility properties of the first population are sufficiently superior in an easily determined way. Random motility turns out to be disadvantageous in this situation, and chemotaxis is helpful although not always enough to ensure population dominance.

A. Leung (with A. Lazer and D. Murio):

Monotone scheme for finite difference equations concerning steady-state prey-predator interactions

In this article a system of semilinear elliptic partial differential equations is studied. This system determines the equilibria of the Volterra-Lotka equations describing prey-predator interactions with diffusion, under Dirichlet boundary condition. To analyze the system, a new monotone scheme is presented. A rigorous foundation is given for numerical calculations by adapting a suitable finite difference method to the new monotone scheme. Many calculations of spatially dependent equilibria are made. Monotone sequences of functions are constructed which converge to upper and lower bounds for the solutions. In many examples, calculations indicate the the upper and lower bounds agree, suggesting uniqueness of positive coexistence states.

M. Levandowsky (joint work with B.S. White):

1. Diffusion Models of Sensory Responds by Microorganisms

Attention is drawn to differences in mathematical properties of Fick's diffusion equation and the Kolmogorov forward equation. The latter is shown to correspond to a plausible discrete model using the Itô stochastic calculus. The former, however, corresponds to an Itô equation which is physically unreasonable.

2. A birth-death model for the generation of Willis' "hollow curve" distribution of species per genus

The plant geographer Willis observed that, in groups of related plants or animals, the distribution of species per genus forms a "hollow curve", in which most genera have only one species, whereas some few have many species. Influenced by the recently developed "punctuated equilibrium" theory of speciation, we have developed a birth-death process in which new genera arise as speciation events representing particularly large "saltations" (on a geologic time scale). In contrast to Yule's model from 1925 in which all genera are equivalent from this viewpoint, in our process a new genus is much more likely to arise from a genus with many species than from a monospecific one.

This process leads asymptotically to a straight-line distribution in logarithmic coordinates with a slope -1 , which accords better than Yule's with modern taxonomic data. (e.g., Anderson 1974, Quarterly Review of Biology 49, 311).

P. Lory (joint work with A.Gilg and M.Horster):

Mathematical Modelling of Urine Formation in the Kidney

A mathematical model of the urine formation by the renal counterflow system is presented (passive mode). Special features incorporated in the model are:

(i) Pelvic urea reflux

(ii) Dichotomous merging of collecting ducts (CDs)

The mathematical treatment yields an extensive boundary value problem for 21 differential equations. It was solved by the multiple shooting method.

Conclusions: Exponential reduction of CD-tubes (ii) is decisive for maintaining high outer medullary CD urea concentration up to CD pelvic entry. Additional diffusion of urea from pelvis into inner medulla (i) enhances urea trapping in this zone. These properties are more effective in supplying urea to the inner medulla than CD urea diffusion alone.

D. Ludwig:

Harvesting Strategies for Fish Populations

It is difficult to regulate fisheries, because of lack of information about the dynamics of the stock. Sources of uncertainty are large fluctuations in recruitment due to environmental effects, and large errors in observations of catch and fishing effort. A statistical technique is proposed, to correct for the effects of observation error. Using this technique effective harvesting strategies can be formulated. They involve purposeful manipulation of the stock to both high and low levels, in order to obtain information about the dynamics of the stock.

M.C. Mackey:

The Dynamics of Recurrent Inhibition

Neurophysiologists have inferred the existence of recurrent inhibitory neuronal circuits in a number of situations. In this study it is argued that, in the face of constant activity in the input cell producing an excitatory potential E in the output cell soma, the dynamics of the output cell firing frequency $F(t)$ are approximated by

$$\frac{dI}{dt} = -\gamma I + \beta \tilde{F}(t-\tau) g(\tilde{F}(t-\tau)) \quad (1)$$

and

$$F(t) = \begin{cases} 0 & E - \theta < I(t) \\ E - I(t) - \theta & E - \theta \geq I(t) \end{cases} \quad (2)$$

where I is the inhibitory potential in the output cell, $g(.) \geq 0$ is a monotone decreasing function of the inhibitory interneuron firing frequency \tilde{F} , $\tilde{F} = \alpha F$, θ is the threshold for firing in the output cell, and $F_0, \alpha, \beta, \gamma$ and τ are constants.

The system (1)-(2) may exhibit a variety of dynamical behaviours including switching between multiple steady states and periodic and aperiodic oscillations about these steady states. These properties, in conjunction with estimates of neurophysiological parameters, are exploited to explain a variety of phenomena seen in the hippocampal mossy fibre - CA₃ pyramidal cell - basket cell inhibitory interneuron feedback network, in the Renshaw cell - α motoneuron circuit, and to explore the possible role of recurrent inhibition in controlling the dynamics in sympathetic preganglionic neurons.

M. Mimura:

Nonlinear degenerate diffusion equations occurring in population dynamics

We consider a spatially aggregation population model which provides the homogenizing process due to density-dependent diffusion and the dehomogenizing one due to a certain long-range transport. The result asserts that, by a balance between two processes, an initial distribution of populations forms itself into a traveling solitary wave pattern for large time, which exhibits phenomenologically a kind of aggregation of a species.

P. de Mottoni:

Bifurcation of Stable Stationary Solutions Exhibiting Space Segregation for a Competition System with Migration

(Report based on a joint work with A.Schiaffino and A.Tesei)

We are mainly interested in investigating how the qualitative properties of elementary models of population dynamics are affected if more complex features are accounted for. A typical situation is encountered in competition systems, where it can be shown that the standard tenet of competitive exclusion, valid in the constant coefficient case, is violated if the coefficients are periodic. In the present contribution, we focus on existence and stability properties of stationary solutions of a system describing competition between two species in a bounded space region, only one of which is able to migrate, and find a lethal environment at the boundary. We get a complete characterization of the stable, stationary solutions, which turn out to exhibit a marked space dependence.

Assume that in the absence of any migration, only one species can survive. Slow migration of this species allows the other species to survive near the boundary, where the first species is kept at a low level. If the rate of migration is high enough the migrating species is doomed to extinction, while the competing species attains a space-homogeneous distribution.

F. Rothe:

A nonhomogeneous predator-prey system with patchiness

Predator-prey systems with one diffusion and one sedentary species as for example

$$u_t - \Delta u = u(\bar{+} 1 \pm a(x)v)$$

$$v_t = v(\pm 1 - \varepsilon v \mp b(x)u) \equiv pv$$

(upper signs correspond to diffusing predator, lower signs to diffusing prey, $\varepsilon, a(x), b(x) > 0$) admit a whole continuum

of equilibria (\bar{u}, \bar{v}) such that $\bar{u} > 0$, $\bar{v} \geq 0$ exhibiting different "patches" $\Omega_p = \{x \in \Omega | \bar{v}(x) = 0\}$. For initial data $u_0 > 0$, $v_0 \geq 0$ we have convergence in the limit $t \rightarrow \infty$ to the equilibrium (\bar{u}, \bar{v}) determined by the compatibility condition $\{\bar{v} = 0, \bar{p} > 0\} \subset \{v_0 = 0\} \subset \{\bar{v} = 0\}$.

This can be shown using a Ljapunov functional. Using upper and lower solutions one can show existence of an equilibrium (\bar{u}, \bar{v}) satisfying the compatibility condition for given initial data.

K. Schumacher:

Global oscillations in time-discrete host-parasite models

Fairly different models simulating the bud moth-forest interaction have been presented by A. Fischlin, W. Baltensweiler, D. Ludwig, D.D. Jones, C.S. Holling and H. Thieme. In all these models computer studies show global oscillations in the abundance of the parasites and the host for certain ranges of the parameters. In this talk an analytic result for time-discrete two component host-parasite models is presented which guarantees the existence of a compact globally attracting invariant set \mathcal{L} in the phase plane, if the stationary point (\bar{x}, \bar{y}) is ejective. It is shown that \mathcal{L} is bounded away from (\bar{x}, \bar{y}) and that every sequence which starts in \mathcal{L} oscillates in a certain sense around (\bar{x}, \bar{y}) .

H. Thieme:

Linear and Nonlinear Renewal Theorems in Population Dynamics and Epidemics

I. We consider a linear model for the development of a population which includes spatial diffusion, age structure and seasonal variations. The rates of diffusion, mortality and birth are age and time dependent. The dependence on time is periodic with period 1. If $I(t, a, x)$ denotes the number of individuals at location x with age a at time t , it turns

out that $I(t, a, x) \sim \alpha e^{\lambda t} \tilde{I}(t, a) v(x)$ for $t \rightarrow \infty$, with $\alpha > 0$, $\lambda \in \mathbb{R}$, \tilde{I} periodic in t with period 1.

II. We consider an epidemic model of S-I-S type with spatial spread. It turns out that, for small inputs of initial infectives, the epidemic develops in a very typical manner. In particular the development does not depend on the spatial distribution of the initial infectives.

M.A. Viergever:

Solution methods for cochlea models

Solution methods for mathematical models of the mechanics of the cochlea are discussed on the basis of a two-dimensional model. A one-dimensional description is not accurate enough. Besides, the techniques by which it can be solved are not representative for multi-dimensional models. Three-dimensional models, on the other hand, have thus far only allowed asymptotic solutions.

The two-dimensional model is described by a boundary value problem consisting of Laplace's equation on a rectangle, Neumann conditions on three of the four boundaries, and a Robin (Cauchy) condition on the fourth boundary. This problem can be solved by means of various numerical techniques. The solution techniques must be computationally fast, however, to enable evaluation of the model upon experimental data. This is why many asymptotic approximations have been tried. The talk covers the most important numerically exact and asymptotic methods, including a discussion of the possibilities to extend them to three-dimensional problems.

H.O. Walther (joint work with U. an der Heiden):

Chaos in differential delay equations related to physiological control systems

Consider the equation

$$(*) \quad \dot{x}(t) = f(x(t-1)) - \alpha x(t),$$

where α is a positive parameter, and f a hump function. Such equations were proposed as simple models for e.g. growth of the population of red blood cells, or for self-inhibition in the nervous system.

Numerical experiments indicated that -depending on α and the shape of the hump f - the equilibrium $t \mapsto x_0$ can be stable, or unstable with an attracting closed orbit "around" it - or that solutions oscillate in a very irregular fashion with no nice attractor appearing. Of course, the latter suggested one or another type of chaotic motion.

We prove existence of Li-Yorke-Chaos for a restricted class of hump functions f in equation (*). This chaos is seen in the spacing of the intersection points of solutions with a certain level $x = a$. The structure behind is an unstable closed orbit (periodic solution) in the state space $C = C([-1,0], \mathbb{R})$ together with a special homoclinic solution which merges into the closed orbit in finite time.

P. Waltman:

Competition in the Chemostat

A brief review of the mathematical and experimental results of competition in the chemostat was given. The constant input nutrient was changed to a logistic term, reflecting a renewable resource, giving a system of three nonlinear ordinary differential equations. This system was analysed and regions in parameter space determined where competitive exclusion occurs. Outside this region, bifurcation can occur. In particular, a stable limit cycle in one (planar) face of the positive octant can bifurcate into a limite cycle in the open positive octant, yielding coexistence of the competing predators.

L. Demetrius:

Macroscopic Parameters in Complex Systems: The Role of Ergodic Theory in Population Dynamics

Several deterministic models in population biology and related sciences are characterized by systems consisting of a large number of interacting elements or systems with chaotic dynamics. This high dimensionality and the chaotic dynamics render predictions of the behavior of these systems difficult. This paper considers statistical representations of these models and outlines a class of algorithms to derive macroscopic variables from the deterministic laws describing the individual elements. We emphasize the thermodynamic analogues of these variables and discuss their significance in understanding the global behavior of these models.

W. Jäger:

A diffusion reaction system modelling growing surfaces

Pattern formation has been studied mainly in the situation where the underlying manifold is not growing. J. Murray treated the case of diffusing substances on growing surfaces where the growth is externally given. The system of equations studied in this lecture has been suggested by Murray and Jäger in 1980. An activator substance (combined with an inhibitor) is diffusing on a surface, activating the growth of the surface. This is modelled by diffusion-reaction equations containing diffusion coefficients depending on the growth (change of the metric on the manifold) and an additional dispersive term caused by growth. The growth is modelled by an ordinary differential equation for the metric. It may lead to instabilities causing (transient) patterns in the activator and inhibitor distribution. The growing manifold takes up the pattern if diffusion, reaction and growth parameters are in a proper range. A series of computer simulations by Jäger and Pöppe shows that the equations produce these phenomena. For the analytic treatment a quasi-steady state approach is suggested.

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