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MATHEMATISCHES FORSCHUNGSINSTITUT OBERWOLFACH

Tagungsbericht 50/1984

Mathematische Modelle in der Biologie

2.12. bis 8.12.1984

The 1984 Oberwolfach meeting on Mathematical Models in Biology, organized by K.P. Hadeler (Tübingen) and W. Jäger (Heidelberg) was the fourth meeting devoted to this topic in a series starting in 1975. 36 mathematicians, physicists, and biologists from ten countries came together.

The main topic of the conference was mathematical ecology: Dynamics of three interacting species, aggregating populations, oscillating population densities, age-structured populations, host-parasite interaction, zooplankton dynamics. Contributions from other biological areas were present, such as evolutionary processes, chemical reactions, models of cell aggregation, neural networks, in which similar mathematical tools can be used.

There were 29 lectures, and the official program was structured in such a way as to allow for very active discussions and a number of informal seminars with "volunteer" audiences. It appeared that scientific interaction was particularly active and personal relations, between visitors from so distant places, were cordial, non the least due to the Oberwolfach atmosphere including excellent organization, accomodation and catering for which special thanks go to staff and administration.



Vortragsauszüge

W. Alt:

Aggregation models with free boundary

Biological aggregation can be performed in different characteristic ways: Stationary aggregates (Slime molds), diffusive swarms (insects, slime bacteria) or more "ordered" swarms (birds, fishes). One-dimensional equations for the population density  $u = u(t,x)$  of the form

$$u_t = \{\mu u_x - uv\}_x$$

are analysed with different expressions for the random motility  $\mu = \mu(u)$  and the aggregative drift  $v(t,x)$  which, for fixed time  $t$ , satisfies an elliptic equation of the form

$$0 = \{n(u)v_x + g(u)\}_x - \phi v$$

Free boundaries appear in the parabolic case  $\mu \neq 0$ , where the motility  $\mu$  degenerates to zero, either at  $u = 0$  or at some maximal density  $u = u_{\max}$ . In the hyperbolic case  $\mu \equiv 0$  the two conditions at the free boundaries  $x = s_{\pm}(t)$  are  $\dot{s}_{\pm}(t) = v(t, s_{\pm}(t))$  and  $n(u)v_x + g(u) = K(u)$ , where  $K(u)$  models an additional outward pressure for individuals at the edge of a swarm.

Steady state and traveling pulses, as well as numerical simulations show that the models can reproduce some essential features of aggregate formation, swarm approximation and swarm separation.

E. Bohl:

A Remark on 3-dim. Models of the B.-Z.-Reaction

Three models of the B.Z.-Reaction have been studied. For them a method of finding appropriate parameters has been pointed out such that the resulting equations exhibit the dynamics to be modeled. On this basis a chaotic dynamic was explained as an affair of switching between two different limit cycles.

S. N. Busenberg:

Interaction of spatial diffusion and delays in models of genetic control by repression

A class of models based on the Jacob and Monod theory of genetic repression for control of biosynthetic pathways in cells is considered. Both spatial diffusion and time delays are taken into account. A method is developed for representing the effects of spatial diffusion as distributed delay terms. This method is applied to two specific models and the interaction between the diffusion and the delays is treated. The destabilizing of the steady-state and the bifurcation of oscillatory solutions are treated as functions of the delays and the diffusivities. The limits of very small and very large diffusivities are analyzed and comparisons with well-mixed compartment models are made.

V. Capasso:

A stochastic age-dependent epidemic model

A marked point process approach is presented here to model the evolution of an age-dependent epidemic system. Based on

the martingale properties of the associated counting processes estimators of the parameters of the system are generated following Aalen's methods. Asymptotic properties of the estimators are also desired.

K. L. Cooke:

A Multigroup Model for Diseases with Non-symptomatic Infectives

In some diseases, a large proportion of infected individuals are infectious to others, but may have no symptoms or only mild symptoms. Together with Dr. Jose M. Ferreira, we have formulated and analyzed a model for an endemic disease in a population with two groups, in each of which there are both symptomatic and non-symptomatic infectives. The basic reproductive rate,  $R$ , is expressed in terms of contact and recovery rates. It is proved that if  $R$  is greater than 1, there is a globally stable positive equilibrium state, but if  $R$  is less than 1, the only stable equilibrium state has zero infectives. The model is applied to a study of gonorrhoea incidence and comparisons are made with available data.

O. Diekmann:

Nonlinear interaction during very short lifestages

A complicated prey-age dependent prey-predator model, incorporating a saturating functional response, is simplified by letting the age specific attack rate converge to a multiple of the delta "function" at prey age zero. In the simplified problem the prey recruitment rate is obtained from the prey birth rate by multiplication with an exponential reduction factor, where the argument of the exponential is implicitly defined by a consistency relation for the functional response.

For the case of egg eating predators and for the case of egg cannibalism, the stability boundary (for the unique nontrivial steady state) in a two dimensional (compound) parameter space is determined. Upon crossing of this boundary a Hopf bifurcation occurs.

J.-P. Gabriel:

Worm's sexuality from a mathematical point of view

The work presented here is a joint work with W. Hirsch and H. Hanisch. Its goal is the study of the possible relation between the sexual behavior of a parasitic worm and the statics and dynamics of its transmission. Very little is known today about the intimate life of parasitic worms and we think that a mathematical approach, based even on oversimplified models, can be helpful to shed some light on the underlying mechanisms of worms reproduction. It suggests, for example, that the usual dioecious organisms might be insufficient to describe their transmission.

M. R. Guevara:

Chaotic Cardiac Dynamics

Nonperiodic cardiac rhythms are often seen clinically on the electrocardiogram. Several different irregular rhythms can be induced in a population of spontaneously beating cardiac cells by stimulation with a periodic train of current pulses. Consideration of the phase-resetting response of the mutually entrained population to an isolated current-pulse stimulus leads to a formulation of the response to periodic stimulation in terms of a one-dimensional finite-difference equation. Analysis of this equation results in the identification of one particular experimentally observed nonperiodic rhythm as a mani-

manifestation of "chaotic" dynamics. This behaviour is found only at an intermediate level of the stimulus amplitude; it does not occur at higher or lower stimulus levels. The implications of this work for other forced biological oscillators will be discussed.

M. Gyllenberg:

A size structured model for the growth, budding and scar class distribution of populations of *Saccharomyces cerevisiae*

A size structured model for populations of *S. cerevisiae* is discussed. It is shown that under special conditions the system can be reduced to a scalar renewal equation. Using standard renewal theorems one can determine the asymptotic behaviour of the solutions: All solutions converge (in a damped oscillatory manner) towards a steady state. In the general case, when one cannot use renewal theory, the same result is obtained by spectral theory of  $C_0$ -semigroups.

K.P. Hadeler:

A birth and death process with killing and application to parasite infection

A birth and death process with killing and reestablishment of the population can be described by a degenerate first order system of partial differential equations, which can be reduced to a single renewal equation for one function (the probability of "no population"). The population can be interpreted as the parasite population within one host. With a transmission law, i. e. a nonlinear function coupling the immigration rate of parasites into hosts to the average parasite load, one arrives at a simplified version of an epidemic model introduced earlier by Hadeler and Dietz.

U. an der Heiden:

What and how does a frog see?

Seeing is not to be confused with "taking a photograph". Seeing always means evaluation and interpretation of an image. Frogs, like all other amphibians, have the problem to distinguish between prey, enemy, and other objects. In my lecture I discuss how neural networks in the retina and in the brain, in particular in the tectum opticum of amphibians participate in the analysis of the visual scene. The operations of these networks are described and modeled by systems of time- and space-dependent differential- and integral equations. These networks are able to separate moving from non-moving objects in the visual field, to discriminate various sizes and shapes of moving objects, and to give different responses to different orientations of the same object with respect to the direction of movement. The electrophysiological activity of a great number of different types of nerve cells observed experimentally in frogs, toads, and salamanders can be understood and predicted from the interactions of cells in the model network. Variation of a few of the network parameters is sufficient to generate many of the observed response types.

H.W. Hethcote:

Optimal ages of vaccination for measles

The great diversity throughout the world in the recommended ages of vaccination for measles indicates that there is no general agreement on the best vaccination strategies. This paper shows how a modeling approach can be used to determine ages of vaccination which minimize the lifetime expected risk due to measles in a population. Although no two-dose strategy is theoretically optimal, there can be practical

reasons for using two doses in some countries. However, in developing countries where there are limited resources for measles vaccination, the calculations show that vaccination of a large fraction at one optimal age is much better than vaccination of half as many children at two ages. Optimal ages of vaccination are calculated from approximate measles seroconversion rate curves and estimated parameter values for Kenya, parts of South America, and the USA. Thus, current data and a model are used to obtain general and specific suggestions regarding vaccination strategies for measles.

J. Hofbauer:

#### The selection mutation equation

Fisher's Fundamental Theorem of Natural Selection is generalized to the selection mutation model with special mutation rates  $\epsilon_{ij}$  depending only on the target gene ( $\epsilon_{ij} = \epsilon_i$ ), by taking 
$$V(x) = \frac{1}{w} \sum_{i=1}^n x_i^{2\epsilon_i} \quad (\epsilon = \sum \epsilon_i)$$
 as generalized mean fitness

function. The selection mutation equation is then the gradient of  $V$  if the probability simplex is equipped with Shahshahani's metric. For other mutation rates this is not true, and a theorem of Akin implies the existence of periodic orbits for a suitable chosen selection field. In a particular 3-allelic example with cycling symmetric mutation rates stable limit cycles are found.

F.C. Hoppensteadt:

#### Networks of neuron analog circuits

A new circuit analog of a nerve cell was described. This is based on modulation of a voltage controlled oscillator by signals entering through a circuit analog of a chemical

synapse. Phase-locking of frequency encoded information is described for the von Euler mechanism of respiration control. This demonstrates synchronization of breathing with stride by runners.

S. Levin:

### Coevolution

A review is given of the modelling of evolutionary problems involving interacting populations. These range from the "gene - for - gene" systems of cereal plants and their fungal parasites, in which the genetic basis of resistance and virulence is well understood and encoded at reciprocal loci in parasite and host, to diffuse coevolution in which many species interact. A detailed discussion is given of the evolution of reduced levels of virulence in the myxoma virus introduced to control European rabbits in Australia. Analytic results are given for simplified models of the S-I-R type, and more detailed discussions are given for computer simulations of the spatio temporal dynamics.

M. C. Mackey:

### Globally Asymptotic Properties of Proliferating Cell Populations

This paper presents a general model for the cell division cycle in a population of cells. Three hypotheses are used: (1) There is a substance (mitogen) produced by cells which is necessary for mitosis; (2) The probability of mitosis is a function of mitogen levels; and (3) At mitosis each daughter cell receives exactly one-half of the mitogen present in the mother cell. With these hypotheses we derive expressions for the  $\alpha$  and  $\beta$  curves, the distributions of mitogen and cell

cycle times, and the correlation coefficients between mother-daughter ( $\rho_{md}$ ) and sister-sister ( $\rho_{ss}$ ) cell cycle times.

The distribution of mitogen levels is shown to be given by the solution to an integral equation, and under very mild assumptions we prove that this distribution is globally asymptotically stable. We further show that the limiting logarithmic slopes of  $\alpha(t)$  and  $\beta(t)$  are equal and constant, and that  $\rho_{md} \leq 0$  while  $\rho_{ss} \geq 0$ . These results are in accord with the experimental results in many different cell lines. Further, the transition probability model of the cell cycle is shown to be a simple special case of the model presented here. The most novel aspect of this model is the demonstration that the probabilistic behaviour noted in populations of cells may arise from a totally deterministic mitotic division mechanism operating in a region dominated by "chaotic" dynamics.

M. Markus:

#### Time Patterns in Glycolysis: Model and Experiments

A model of sugar metabolism (glycolysis) is analyzed using enzymic rate laws that have been obtained in great detail from kinetic measurements. A large variety of periodic, quasi-periodic and chaotic solutions are obtained for periodic substrate input flux. At sinusoidal input flux, conditions exist at which oscillations having a period in the range of minutes are modulated with a period in the range of hours. The degree of randomness of the chaotic oscillations, as indicated by the Liapunov dimension, can be considerably higher under amplitude or frequency modulated input than under sinusoidal input. Furthermore, it is shown that up to four attractors can coexist in phase space under the same set of bifurcation parameters, and that the dynamics of the system follows complex hysteresis loops.

Fluorescence measurements in yeast extracts under periodic glucose input show responses with periods 1,2,3,4,5,7 and 9 times the input period, quasiperiodic oscillations and chaos in the predicted range of control parameters.

In whole yeast cells, synchronization of oscillating glycolysis and oscillating membrane potential is observed.

J. A. J. Metz:

A model for size and age dependent population processes in Daphnia magna and other simple ectotherms

Starting from simple energetic considerations on the individual level a model is built for the dynamics of populations of simple ectotherms. Individual growth is modelled by a von Bertalanffy growth equation coupled to a Holling (or Monod) functional response. Birth rate is modelled by assuming that a fixed fraction of the ingested energy is channeled to reproduction as soon as the length exceeds a fixed value. All these assumptions are born out by experiments on individual Daphnia magna. When food becomes scarce maintenance is assumed to take priority. When total intake cannot keep pace with maintenance the animal dies. Apart from this extreme case death is dependent only on age. The population state is given by the age distribution together with the instantaneous age length relation. The development of the population process is generated by a set of coupled first order partial differential equations together with a boundary condition representing births.

If feeding conditions are constant the age length relation soon stabilizes and a linear age dependent process remains, the dominant eigenvalues of which can be studied in terms of the biological parameters of the process. Using this dominant eigenvalue as the measure of population growth we studied the dependence of the conclusions from routine toxicity tests on the feeding regime.

If food availability is coupled dynamically to population size we get a model for population regulation. If the boundary equilibrium is unstable there is a unique interior equilibrium, the characteristic equation of which equals that of a delay differential equation. This we shall study in the near future. Numerical work suggests the occurrence of a Hopf bifurcation (in accordance with experimentally observed oscillations) and subsequent periodic doubling. The lecture ends with a discussion of some of the methodological problems inherent to the modelling process.

Masayasu Mimura:

Pulse-like patterns of spatially aggregating population models

A model of non-local reaction-diffusion equations related to spatial aggregation of biological individuals

$$\begin{aligned} u_t &= [d u_x - \chi s_x \cdot u]_x + f(u) \\ (*) \quad s_t &= k \cdot u - s \end{aligned} \quad t > 0, x \in \mathbb{R}$$

is discussed where  $d, \chi > 0$  const.,  $f(u)$  is a cubic-like function with  $f(0) = f(1) = 0$ ,  $f'(0) < 0$ ,  $f'(1) < 0$ ,  $k(x)$  is a kernel specified by  $k(x) = \frac{1}{2} (1 + \beta |x|) e^{-\beta |x|}$  with const.  $\beta > 0$ . When  $d, \chi$  are sufficiently small, it is shown that there is a set  $\Omega \subset \mathbb{R}_+^2$  such that (\*) has two different types of pulse-like stationary solutions for any  $(\beta, a) \in \Omega$ . Also it is numerically investigated that one (large pulse) is stable and the other (small pulse) is unstable.

R.M. Nisbet:

Stage-structure models: Theory and application to zooplankton dynamics

Gurney, Blyte and I have recently studied the systematic formulation of "stage-structure" models in which complex life histories are modelled in ways that yield the population dynamics in terms of solution of delay-differential equations. I shall briefly review the "tool-kit" of available techniques and illustrate their use in models of both marine and fresh-water zooplankton.

Yasumasa Nishiura:

Stability of layer type solutions of Reaction-Diffusion system and their orbital connection

In the process of pattern formation, "front" plays an important role. A new stable pattern is frequently created by the movement of "fronts".

In other words, this is a transition from an unstable layer solution to a stable one.

Using a typical reaction-diffusion system with zero flux boundary conditions and sigmoidal nonlinearity, we will show the stability (instability) of interior (boundary) layer solution, respectively, and consider the orbital connection problem in infinite dimensional space between them.

Leny Nusse:

Persistent regularity in the chaotic dynamical behaviour in some discrete biological models

We consider a general discrete growth model for one single species population with nonoverlapping generations. We write  $N_t$  for the number of individuals per unit area in generation  $t$ .

Consider the model  $N_{t+1} = F(N_t)$  where  $F$  is some nonlinear differentiable function from the set of nonnegative real numbers into itself such that  $F$  has one or more critical points (that are points at which the derivative vanishes), and  $F$  vanishes at zero. We assume that  $F$  is a chaotic Axiom A map.

The following results have been obtained:

1. There is no chaos; in other words, any arbitrarily chosen initial value that will lead to aperiodic (chaotic) behaviour, has probability zero.
2. The periodic points for  $F$  with period  $n$  can be computed for each positive integer  $n$ .
3. One can associate a nonnegative real number with the model measuring the complexity of the dynamical behaviour.
4.  $F$  is  $C^1$ -omega stable, i.e. the structure of the nonwandering set of  $F$  doesn't change under small smooth  $C^1$  perturbation.
5.  $F$  is  $C^2$ -structurally stable, provided that  $F$  satisfies some reasonable conditions.

Remark 1: Assume that  $f \in C^3(X, X)$  has the following properties: (i)  $f$  has a negative Schwarzian derivative, (ii) the set of critical points of  $f$  are contained in the domains of attraction. (iii)  $f$  is contracting on the set of asymptotically stable periodic points. Then  $f$  is an Axiom A map.

Remark 2: The standard examples  $N_{t+1} = N_t \{ 1 + n(1 - \frac{N_t}{K}) \}$  and  $N_{t+1} = N_t \exp [n(1 - \frac{N_t}{K})]$  will be discussed.

Otto E. Rössler:

### Chaos in simple autonomous $C^1$ systems

Two simple O.D.E.s will be considered:

- (1)  $\dot{x} = -x - f(z)$ ,  $\dot{y} = x - y$ ,  $\dot{z} = y - z$ ; with  $f(z) =$  slanted letter V.
- (2)  $\dot{x} = -y - z$ ,  $\dot{y} = x$ ,  $\dot{z} = a(1 - |y|) - bz$ .

The first is a variant to the well-known Danziger-Elmergreen model of hormonal regulation. The second is the simplest "two-level oscillator" (the averaged amplitude of the  $x, y$

oscillator,  $|y|$ , forming a second oscillator with  $z$ ). Both reproduce chaos (for  $f(z) = 84.2|z| + 75.8z$ , or  $a = 0.65$ ,  $b = 0.2$ , respectively), the second in addition K.A.M. tori if  $b = 0$  (and  $a = 0.2$ , e.g.). Both can be investigated analytically with the method of Poincaré half maps which reveals a rich (both folded and cut) structure even for one of the two linear half systems already. A complete catalogue of 3-variable single-threshold piecewise linear systems (as prototypic models of more realistic systems including boundary value problems for biological P.D.E.s) is in preparation. Four-variable analogs to Eqs. (1) and (2) produce hyper chaos and K.A.M. hyper tori, respectively.

Coauthors: Claus Kahlert and Bernhard Uehleke.

Franz Rothe:

#### Periods and thermodynamics in the Volterra-Lotka model

The classical predator-prey system of Volterra and Lotka can be converted to a Hamiltonian system. The canonical partition function is explicitly  $z(\beta, \lambda, \mu) = z(\beta\lambda)z(\beta\mu)$  with  $z(\gamma) = e^{\gamma(1 - \log \gamma)} \Gamma(\gamma)$ . Because this is the Laplace transform of the energy-period function, one gets asymptotic expansions for the periods of small and large orbits. On the other hand, the period is a convolution integral, which is shown to satisfy a convexity in appropriate logarithmic scales. This implies monotonicity of the periods and allows to compare periods for different parameter values.

Michelle Schatzman:

#### Cooperation and competition models in neurophysiology

A number of models describing phenomena in neurophysiology of development of visual cortex can be mathematically expressed

with an integrodifferential equation involving a convolution term (convolution in space) and a nonlinearity. Depending on the kind of nonlinearity different asymptotic behaviours are obtained. Those asymptotic behaviours describe the final state of a system in evolution, and give hints on how definite structures arise from arbitrary initial data.

D. Schenzle:

An age-structured model for recurrent epidemics

The problem of recurrent epidemics of infections like measles is reconsidered, using a model with age-dependent contact rates and taking into account the grade-wise mode of operation of schools. The main idea is, that with the beginning of each new school year a whole cohort of children becomes exposed to a high intra-school infection rate. This creates an annually recurring "shove" on infection transmission, giving rise to coexisting periodic incidence patterns with periods of one, two or several years. Model simulation results conform to differing observations from countries where new school years start in fall or spring, i.e. after or before summer vacation. The model especially describes to some detail the pre- and post-vaccination measles data from England.

Konrad Schumacher:

A mathematical model for the larch - larch bud moth hypothesis

The larch - larch bud moth hypothesis states that the observed oscillations of the abundance of the larch bud moth originate from a physiological change of the larch needles as a reaction of the larch to the defoliation by larval feeding. We analyse a discrete  $2 \times 2$  recursion where one variable is the size of the bud moth population in the egg-stage and the other measures the physiological state of the larch. The model differs from

previous models by Van den Bos and Rabbinge (1976), Fischlin and Baltensweiler (1979), and Fischlin (1982) in the functional relationships between the physiological state of the larch, the defoliation, the food consumption, and the starvation mortality. It can be shown that the appearance of undamped oscillations follows from biologically reasonable assumptions on these functions. Numerical simulations exhibit a good agreement of the modelled oscillations with the observed oscillations in the upper Engadine valley.

Horst Thieme:

Existence and uniqueness of solutions to the "Dutch" Daphnia model

Proving existence and uniqueness of solutions to the Daphnia model presented by J.A.J. Metz in his talk is not straightforward due to a discontinuity of the birth rate excluding an easy application of Banach's fixed point theorem. This difficulty can be overcome by establishing the relation  $n(t,a) < \text{const.} \cdot \partial_a l(t,a)$  between the age distribution  $n(t, \cdot)$  of the Daphnia population and the age distribution  $l(t, \cdot)$  of the length of individual daphniae at time  $t$ . This requires an assumption involving an actual biological restriction, namely the relation  $K l_y \geq l_b$  between the lengths  $l_b, l_y$  of individuals at birth and at the beginning of reproduction respectively and the fraction  $K$  of assimilated food put into metabolic maintenance and growth.

Paul Waltman:

Persistence in model ecosystems

A system of ordinary differential equations of the form  $x' = F(x)$ ,  $x(0) = x_0$ ,  $x \in \mathbb{R}^n$ ,  $x_0 \in \mathbb{R}_n^+$  is said to be persistent if

$\liminf_{t \rightarrow \infty} x_i(t) > 0$  for each component,  $x_i(t)$  and uniformly persistent if  $\liminf_{t \rightarrow \infty} x_i(t) \geq \alpha > 0$ . Conditions are provided whereby solutions of the population equations

$$u' = f(u,v,w)$$

$$v' = g(u,v,w)$$

$$w' = h(u,v,w)$$

are persistent. The conditions are all on the boundary  $\partial R_3^+$  where the dynamics are assumed to be well understood, since the flow there is at most two dimensional. The methods are those of dynamical systems.

Comments at the closing of the Fourth Oberwolfach Conference  
on Mathematical Biology, December, 1984.

This concludes the Fourth Oberwolfach Conference on Mathematical Biology. Since the first conference in 1975, we have seen significant biological problems come into all of the presentations. This is a significant change in the style of these meetings, and it is an excellent sign that participants are going outside mathematics to find problems from the life sciences that have significant mathematical content.

Mathematical Biology is a body of mathematical topics that are applicable to diverse life science problems. Most of the participants in this conference could understand most of the presentations even though the biological problems were widely varied. Mathematics made this possible. For example, we have seen that mathematical methods from population biology apply to ensembles of chemical reactions and to networks of neurons as well as to ecological problems.

Whole areas of the life sciences lie waiting to be resolved, and mathematical methods will play decisive roles in many of them. These include DNA sequence and structure, and perhaps

more important: How does a brain work? New and interesting mathematics and rediscoveries of old problems and techniques in exciting new settings can be expected from studies of these problems, much like function iteration problems from ecology stimulated breathtaking reinterpretations and extensions of classic work over the past decade. In particular, the problems of brain dynamics are even more challenging, and they offer even richer mathematical structure and relevance to life.

Professor Hadeler and Jäger, the conference organizers, have played major roles in nurturing Mathematical Biology over the past decade, both in Germany and internationally. We owe them our gratitude, and we hope that they will continue to provide us the opportunity to get together through future Oberwolfach meetings. As we return to our home countries at a time when Applied Mathematics groups are dwindling internationally, it is highly important that we work hard to create and nurture programs in Mathematical Biology.

Thank you.

F. C. Hoppensteadt

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