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Description:

In this project we combine expertise of the two participation groups in the study of the dynamics of populations as part of a food web community. The modelling is based on the Dynamics Energy Budget DEB theory as developed by Kooijman. This allows for a realistic modelling of mass and energy flow through ecosystems. The state of each population is described using two variables for the structural mass and energy reserves. Populations interact with each other but also with the abiotic environment, for instance, solar energy or chemical bounded energy is captured and used by the producers at the base of the ecosystem. The processes involved in the flow of mass and energy through the ecosystem leads to a mathematical formulation in terms of ordinary differential equations. In this project the emphasis is on two mathematical techniques which can be used to analyse the resulting governing equations.

In many cases the processes run at different time or space scales. Aggregation techniques (Auger and Poggiale) can be used to reduce the number of equations and consequently simplify the analysis of the model. This technique is applied to discrete time and continuous time systems.

In order to analyse the full as well as the reduced system, bifurcation analysis can be used to study the dependence of the long-term dynamics on parameter changes. Bifurcation points are values of parameters where this dynamic behaviour changes suddenly. Computer packages are available to calculate and continuate these bifurcation points. For this we use also the program written by M.P. Boer as part of the "NWO prioriteitenprogramma Niet Lineaire Systemen" NLS-project #61-254.

We conclude that the composition of the research team makes is possible to cover the whole spectrum from natural history knowledge, mathematical formulation of biotic systems in a biotic and abiotic environment, techniques to analyse the resulting mathematical model while the results can be interpreted in biological terms.

In order to support general theory development we worked on a number of case studies that should lead directly to publications. Here we give a short summary of the different subjects:

Quantitative steps in symbiogenesis and the evolution of homeostasis
The merging of two independent populations of heterotrophs and autotrophs into a single population of mixotrophs occurred frequently in evolutionary history. It is just one example of a wide class of related phenomena, known as symbiogenesis. The physiological basis is almost always (reciprocal) syntrophy, where each species uses the products of the other species. Symbiogenesis can repeat itself after specialization steps for assimilatory substrates. We discuss the quantitative aspects and delineate eight steps from two free-living interacting populations to a single fully integrated endosymbiontic one. The whole process of gradual interlocking of the two populations could be mimicked by incremental changes of particular parameter values. The role of products gradually degrade from an ecological to a physiological one. We found conditions where the free-living, epibiontic and endobiontic populations of symbionts can co-exist, as well as conditions where the endobiontic symbionts out-compete other symbionts. Our population dynamical analyses give new insights in the evolution of cellular homeostasis. We show how structural biomass with a constant chemical composition can evolve in a chemically varying environment if the parameters for the formation of products satisfy simple constraints. No additional regulation mechanisms are required for homeostasis within the context of the Dynamic Energy Budget (DEB) theory for the uptake and use of substrates by organisms. The DEB model appears to be closed under endosymbiosis. This means that when each free-living partner follows the DEB rules for substrate uptake and use, and they become engaged in an endosymbiontic relationship, a gradual transition to a single fully integrated system is possible that again follows the DEB rules for substrate uptake and use.

Aggregation methods in food chains with nutrient recycling
Food chain models under batch and chemostat conditions are studied where nutrient recycling is taken into account. The food chain is formed by a nutrient and two populations, prey and predator (producers and consumers). Species at both trophic levels digest their food source only partly. The unusable parts of the food not used for growth is ejected in the reactor as faeces together with metabolic products. The excreted material together with death material, detritus, is decomposed and this gives the recycling of the nutrient. In closed (batch-type environment) systems the elemental matter needed by producers must be provided through recycling where light energy from the environment supplies the necessary energy that fuels the life processes. In open (chemostat-type environment) systems this energy is added to the system via the chemical energy stored in the organic compounds in the inflow. An aggregation method is developed for situations in which each trophic level is characterized by differing time scales. This allows us the reduce the dimension of the model which gives good approximations after the fast transient. It is shown that in the chemostat case first-order approximations are needed in order to get the same qualitative long-term dynamics for both the full and the reduced model.

Bifurcation analysis of a predator-prey model with predators using hawk and dove tactics
Most classical prey-predator models do not take into account the behavioural structure of the population. Usually, the predator and the prey populations are assumed to be homogeneous, i.e. all individuals behave in the same way. In this work, we shall take into account different tactics that predators can use for exploiting a common resource, the prey population.

Predators fight together in order to keep or to have an access to captured prey individuals. Individual predators can use two behavioural tactics when they encounter to dispute a prey, the classical Hawk and Dove tactics. We assume two different time scales. The fast time scale corresponds to the intraspecific fighting between the predators and the interspecific handling and searching for the prey by the predators. The slow time scale corresponds to the (logistic) growth of the prey population and mortality of the predator. We take advantage of the two time scales to reduce the dimension of the model and to obtain an aggregated model that describes the dynamics of the total predator and prey densities at the slow time scale. We study two models, the first one with a Lotka-Volterra functional response (where the handling time is neglected) and the second one with a Holling type II functional response for the predator-prey interaction. We present the complete bifurcation analysis of the models and the effects of the different predator tactics on persistence and stability of the prey-predator community are discussed.

Key publications:

S.A.L.M. Kooijman. *Dynamic Energy and Mass Budgets in Biological Systems*, Cambridge University Press, 2000.

S.A.L.M. Kooijman. Quantitative aspects of metabolic organization; a discussion of concepts, *Phil. Trans. R. Soc. B*, 356:331–349, 2001.

Auger, P. and Bravo de la Parra, R. (2000). Methods of aggregation of variables in population dynamics, *Comptes rendus de l'Academie des science series III-Sciences de la vie-life*, 323:665–674.

Auger, P. and Pontier, D. (1998). Fast game theory coupled to slow population dynamics: the case of domestic cat populations, *Mathematical Biosciences*, 148:65–82.

Bernstein, C., Auger, P., and Poggiale, J.-C. (1999). Predator migration decisions, the ideal free distribution and predator-prey dynamics, *American Naturalist*, 153:267–281.

Kooi, B.W., Boer, M.P., and Kooijman, S.A.L.M. (1998). On the use of the logistic equation in food chains, *Bulletin of Mathematical Biology*, 60(2):231–246.

Kooi, B.W., Boer, M.P. and Kooijman, S.A.L.M. 1998. Consequences of population models on the dynamics of food chains, *Mathematical Biosciences*, 153:99–124.

Kooi B.W. and Kooijman S.A.L.M., 2000. Invading species can stabilize simple trophic systems, *Ecological Modelling*, 133(1-2):57-72.

Results of the van Gogh project:

Events:
April 03-07 2000: Visit Auger and Poggiale to Amsterdam
June 13–16 2000: Visit Kooi to Marseille
Febr. 18–22 2001: Visit Kooijman and Kooi to Lyon
June 14–16 2001: Visit Kooijman, Kooi, Auger and Poggiale to Paris
Febr. 24–28 2002: Visit Kooijman and Kooi to Lyon

We had one meeting in Amsterdam and two meetings in Lyon and all participated in the annual meeting of the French Society for Theoretical Biology in Paris, June 2001, where Kooijman was invited speaker.

Forthcoming events:
June 24-28, 2002: Auger, Poggiale and Kooi participate in the conference on Mathematical Modelling of population dynamics Bodlewo, Poland. `http://www.math.us.edu.pl/cmmpd/` Auger is invited speaker and Poggiale and Kooi give oral presentations.
July 2-6 2002: Auger, Poggiale and Kooi participate in the 5th ESMTB Conference, Milano, Italy. `http://ecmtb.mat.unimi.it/` Auger and Kooi give oral presentations.
July 13-16 2002 Annual Meeting of the Society for Mathematical Biology and International Conference on Mathematics and Biology Interdisciplinary Connections in Living Systems University of Tennessee, Knoxville, USA. `http://www.tiem.utk.edu/smb02/` Kooijman is invited speaker.

Publications:
Kooi, B.W., Poggiale, J.C. and Auger, P. 1998. Aggregation methods in food chains. *Mathematical and Computer Modelling*, 27(4):109-120.

Submitted papers:
B.W. Kooi, J.C. Poggiale, P. Auger and S.A.L.M. Kooijman. Aggregation methods in food chains with nutrient recycling, *Ecological Modelling.* submitted 2001/07/02.

Papers in preparation:
S.A.L.M. Kooijman, P. Auger, J.C. Poggiale and B.W. Kooi, Quantitative steps in symbiogenesis and the evolution of homeostasis, *Biological Reviews.*
P. Auger, B.W. Kooi, R. Bravo de la Parra and J.C. Poggiale. Bifurcation analysis of a predator-prey model with predators using hawk dove tactics, *Theor. Pop. Biol.*
J.C. Poggiale, B.W. Kooi, P. Auger and S.A.L.M. Kooijman. Aggregation methods in food chains with different time scales, *SIAM.*

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