# Application for project grant Faculty of Biology, Vrije Universiteit[1]

# 1    Applicant

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# 2    Title of proposal

The role of food web structures in the dynamics of ecosystems; Project codename: DEBsys.

# 3    Responsible group leader

Prof. Dr. S.A.L.M. Kooijman; Institute Ecological Sciences; ACES; SENSE

# 4    Abstract of proposal

After maturation of the Dynamic Energy Budget (DEB) theory for the uptake and use of resources by individuals, the analysis of the dynamics of populations consisting of individuals that follow the rules specified by the DEB theory, and the analysis of food chains of such populations in chemostats environments, we recently entered the next phase: the analysis of canonical communities. These three-species communities consist of producers, consumers and decomposers that live in a spatially homogeneous environment that is fully closed for mass, and fully open for energy. We follow all chemical transformations and dissipating heat fluxes in this idealized ecosystem, and analyse its dynamical properties, including its longterm behaviour (both locally and globally). The present proposal aims to replace the population of consumers by food webs of increasing complexity, and to study how this affects the dynamic properties of the system. The hope is to develop a modular setup for the analysis of the dynamics of ecosystems as a way to avoid models of extreme complexity. Moreover we aim to quantify the activities of the system in a small number of summerizing statistics that make sense in the context of the DEB theory, and can be measured in real world ecosystems.

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[1]Kooijman, 27 april 1999

# 5    Composition of the research group

| name | discipline | paid by | hrs/ week |
|------|-----------|---------|-----------|
| Dr. B.W. Kooi | mathematics | VUA | 2 |
| Dr. C. Zonneveld | biology | VUA | 2 |
| Prof. Dr. S.A.L.M. Kooijman | biology | VUA | 1 |
| vacant | biomathematics | VUA | 36 |
| Dr. M. Berg | ecology | VUA | 1 |
| Prof. Dr. N.M. van Straalen | ecology | VUA | 0.5 |

# 6    Description of the project

## 6.1    Motivation and historical background

Around 1979, Diekmann, Metz and Kooijman felt the need to develop a theoretical framework for structured populations, to evaluate the consequences of effects of toxicants on individuals on population dynamics. Little was available in the ecological literature at that time to relate population dynamics to properties of individuals, and we thought this to be essential from a fundamental point of view. A NWO-grant was obtained for de Roos, and in retrospection we can state that this initiative triggered a huge effort, world wide, on developing theory for individual based population dynamics. This can be illustrated by pointing to the session on this topic in the coming symposium on Theory and Mathematics in Biology and Medicine in Amsterdam (June 1999) of the European Society for Theoretical and Mathematical Biology; the session turned to be the most popular among 9 others, and even had to be splitted into parts.

The development of the Dynamic Energy Budget (DEB) theory (Kooijman, 1993) for the uptake and use of resources by organisms played an important role in our understanding of the dynamics of realistic physiologically structured population dynamics, because it is simple enough to be applicable in this context. In fact, it was initially developed for this purpose, although it is now also used as a framework to model sub-organismal organization, even down to the molecular level (Kooijman, 1998; Kooijman, 1999; Nisbet et al., 1999). Studies of the behaviour of food chains revealed complex dynamics as soon as the chains have more than 2 trophic levels (Kooi and Kooijman, 1994b; Kooi and Kooijman, 1995; Kooi et al., 1997a; Boer et al., 1998; Kooi et al., 1998b; Kooi et al., 1999a; Boer et al., 1999b; Boer et al., 1999a; Hanegraaf et al., 1999). Multiple attractors appear, some of them of the chaotic type. Methods have been developed to analyse bifurcation patterns systematically (Boer et al., 1999a) and to reduce the complexity (Kooi et al., 1998a), but we still have to invest a considerable effort along this line. Realistic models for food chain dynamics are found to be inconsistent with some popular formulations in the literature, which turn out to violate the conservation law for mass (Kooi et al., 1997b), and frequently leads to new insights. I mention the result that an increase in complexity of the food web, or in biodiversity if you wish, can increase stability (Kooi and Kooijman, 1999a), while the reverse is generally stated by mathematical biologists, on the basis of the work of May in the early 70's, who used linear functional responses to describe trophic relationships among (unstructured) populations. A more subtle treatment of variations in the nutritional values

of prey for predators turned out to have a substantial stabilizing impact on food chain dynamics (Hanegraaf et al., 1999). The study of reactions of food webs to perturbations has only be initiated (Berg, 1998e).

With the extension of the DEB theory to include mass fluxes, it became evident that predator-prey relationships comprise only one aspect of interactions among populations. For a proper understanding of the dynamics of ecosystems it is essential to consider all types of mass exchange between populations, including the release of nutrients, the growth of producers on these nutrients and the indirect effects on consumers (Kooijman and Nisbet, 1999). The environment in which the system is living and the nutrient exchange across its borders has a mayor impact on the long term behaviour of the system, with intriguing implications for evolutionary theory. Most of the food chain analyses have been done in chemostat environments, where the dynamics of the chain breaks down at throughput zero, because these analyses did not include recycling of nutrients. With an extended DEB theory that covers both heterotrophic and autotrophic systems, we now feel ready to include these trophic interactions via nutrients in simple ecosystems. A start has been made with the formulation of a Canonical Community, which has three basic components, producers, consumers and decomposers, and is fully closed in terms of mass, and fully open in terms of energy. A preliminary study of its dynamical properties indicates that an attempt to include simple food webs is feasible and instructive.

## 6.2    Aims and methodology

A sequence of spatially homogeneous ecosystems of increasing complexity will be studied that are fully closed for mass and fully open for energy; the temperature is taken to be constant. Light, total nitrogen and total carbon are tunable (i.e. under experimental control). This setup has peculiar implications for the potential dynamic behaviour of the system, because particular information from the initial conditions, namely total nitrogen and carbon, never gets lost. All mass transformations and energy fluxes in the system will be followed in the context of the DEB theory.

Four minerals are followed (ammonium, carbon dioxide, oxygen, water), but oxygen and water are assumed to be available *at libitum*. Up to to three types of detritus are followed (dead reserves, dead structure, feaces; the latter only present in more than 2 species communities). The digestion of reserve-detritus is complete, so reserve-detritus is transformed into reserves of the consumer (or predator) and minerals; this means that feaces is derived from structure-detritus only, and all types of feaces have the same elemental composition. Decomposers mineralize detritus completely, but reserve-detritus are easier to decompose than structure-detritus, and structure-detritus is easier to decompose than feaces. The decomposition of reserve-detritus releases ammonia, that of structure-detritus is neutral in ammonia release or requirement, while the decomposition of feaces requires ammonia. All structural masses will have the same elemental composition; this also holds for the reserves.

We start with the assumption that the individuals of all species follow the rules as specified by the DEB theory for 1D-isomorphs, and the masses of all individuals can be added (which partly removes the individual-structure of population dynamics). The energy parameters of all consumers (and predators) will be chosen identical, at first; then we reduce turnover rates for increasing trophic position. For 3 and 4 species ecosystems we will also evaluate the behaviour 3D-isomorphic consumers (and predators). This analysis

is substantially more difficult, and requires a.o. a full specification of size preferences in the predation process; maximum body size is a function of the trophic position of the species. Body size scaling relationships of parameter values, as implied by the DEB theory, then become important. We will study several scenarios.

The following sequence of systems will be studied, where the configuration is indicated with $P$ for producer, $D$ for decomposer, $C$ for consumer, with an index for the trophic level. Level 0 only feeds on producers and decomposers; consumers of level $i$ only feeds on level $i-1$; $jC_i$ means $j$ species of consumers of trophic level $i$. The listed configurations are a subset of all possible configurations.

- 1 species (mixothrophs); Two types of detritus: dead reserves and structure that result from aging.

- 2 species (producers, decomposers): $\{P, D\}$. Two types of detritus: dead reserves and structure of both producers and decomposers that result from aging of both species.

- 3 species (producers, decomposers, consumers): $\{P, D, C_0\}$. Three types of detritus: dead reserves and structure that result from aging of the consumers; feaces derived from producers and decomposers that result from grazing by consumers; Aging of producers and decomposers in negligibly is slow relative to grazing. The configuration is called the Canonical Community.

- 4 species by adding a competing consumer, or a predator: $\{D, P, C_0, C_1\}$; $\{D, P, 2C_0\}$. The competing consumers can differ in their preferences for decomposers relative to producers.

- 5 species by adding a consumer, this is done in 5 different ways: $\{D, P, C_0, C_1, C_2\}$; $\{D, P, C_0, 2C_1\}$; $\{D, P, 2C_0, C_1\}$; $\{D, P, 3C_0\}$.

- 6 species by adding a consumer, this is done in 8 different ways: $\{D, P, C_0, C_1, C_2, C_3\}$; $\{D, P, C_0, C_1, 2C_2\}$; $\{D, P, C_0, 2C_1, C_2\}$; $\{D, P, C_0, 3C_1\}$; $\{D, P, 2C_0, C_1, C_2\}$; $\{D, P, 2C_0, 2C_1\}$; $\{D, P, 3C_0, C_1\}$; $\{D, P, 4C_0\}$.

This gives 17 configurations to be studied as functions of parameter values. Bifurcation analysis will be used to analyse the long term properties of the system using advanced software (AUTO, CONTENT, LOCBIF, BASE, CONTIN); and computer simulations will be used to analyse transient behaviour. The general idea is to produce a systematic catalogue of potential behaviour. We will try to reduce the more than 3 species communities to a Canonical Community, and we will compare their behaviour with 2 and 1 species communities. This comparison concerns both the structure (relative amounts of masses of the various components) and the function of the ecosystem (turnover rates of the various components).

We will try to find answers for the following specific questions

- What is the long term behaviour of the system for an increasing complexity of the food web?

- How can we quantify the global stability of the system, and how does this change as a function of the complexity of the food web?

- How does the system reacted to penetrating invading predators or competitors?

- How do we quantify the metabolic activity of the system?

- Is it possible to replace the food web by a single population of generalized consumers with some appropriate input-output behaviour, such that the dynamics of the system is hardly affected?

Our hypothesis is that systems such as $D, P, 3C_0$ can exist at steady state, even in the situation of a point attractor for the system, because of the chemical heterogeneity of the prey (structure and reserves) in combination with difference in the ability to digest these compounds among competing species. If true, the competitive exclusion principle requires reformulation. The system $D, P, C_0, 3C_1$, for example, can probably only exist for oscillatory attractors of the system. This is of major significance, because it is extremely difficult to preserve asymptotic diversity in accepted food web models, as predicted by the competitive exclusion principle. This serious handicap is rarely felt by frequently used empirical models, because those models are only 'run' during a restrictive period and avoid the exposure of this unrealistic property, or treat the structure as given (which introduces inconsistencies). These and many other questions about the long term behaviour of the system are part of the systematic investigation of the asymptotic behaviour of the system. It is likely that the analyses of these physiologically more realistic systems will lead to conclusions that differ from accepted insights about potential ecosystem behaviour. I only mention that particular forms of size selectivity by predators (selection of embryos versus adults) can turn out to represent another route for escaping the competitive exclusion principle and preserving diversity.

We know, of course, that real world ecosystems are not closed and are not homogeneous. We even believe that it is essential to open the system to stabilize its behaviour and to incorporate long term trends in its behaviour. We will partially explore the effects of inputs and leaks of nutrients and organic matter. The study of spatially heterogenous systems, however, is beyond the scope of the present proposal. We do believe that spatially heterogenous systems can only be understood, after homogenous systems are known better.

The focus of the study is on ecosystem consequences of food webs, and the extend to which foodwebs can be approximated by a single generalized consumer population for ecosystem studies that are more realistic in other respects. This simplification is essential for a deeper understanding of ecosystem dynamics, because complex models with many variables and parameters hardly assist such an understanding.

## 6.3 Context

This study can be seen as essential preliminary research that is required for a myriad of sensible future developments that can be envisioned, e.g. inclusion of competing producers, with preferential grazing activity of the various species of consumers; more types of nutrients; the relationship between diversity in biomass composition and diversity of species in communities; the occurrence of epidemics and other internal processes that affect stability of the system; genetic variability in relation to the process of sympatric speciation; and last but not least spatial heterogeneity.

This list is not meant to be exhaustive; it illustrates that research of these more realistic aspects of ecosystem behaviour can only be productive if it is set up in a systematic way

that is fully consistent with physical chemical principles, and that basic aspects have to be studied first.

One of the direct applications of the results of the present study is in the functioning of the organic carbon pump, that removes carbon from the upper layers of the ocean to deeper layers, via sinking of feacal pellets, and enhances carbon dioxide absorption from the atmosphere. One of the important questions about the mechanism of the organic carbon pump, and the rate at which it operates, is in the role of nutrients such as nitrogen, phosphorus and iron.

In collaboration with Henk Dijkstra (Inst. Marine & Atmospheric Research, Utrecht), we presently study a single species community of mixotrophs. This system is simple enough to incorporate in global circulation models to study effects of life on the global carbon cycle. Spatial heterogeneity is provided by the global circulation model; the ocean cells differ in temperature and light, and this model environment provides rules for mass exchange, which also apply to biota. We think that this project is sufficiently innovative to receive financial support in the near future. Our hope is that the present project will allow us to increase realism without increasing the complexity of the model too much.

Parallel to this study, the research program "Manipulation of above- and belowground biodiversity as tool in the restoration of ecosystem functioning" will be running within the Research School Sense (Berendse, LUW, coordinates). This experimentally oriented project is focused on plants and soil invertebrates. Although the DEB theory is recently extended to include plants, we feel that more research has to be invested in testing this extension to experimental data at the level of the individual. The study of dynamical aspects of plant populations on the basis of the DEB theory is not yet feasible, let alone ecosystem dynamics in which vascular plant play a key role. The relevance of the proposed project to the biodiversity research program is in addressing fundamental questions about the relationship between diversity and ecosystem functioning and stability. This includes the effects of nutrient (nitrogen) enrichment on biodiversity; we expect that this proposal will lead to fundamental insight into the paradox of enrichment, for instance. Another potential link is the quantitative understanding of mass transfer in symbiontic relationships (cf mycorrhiza). We expect that this project will contribute to other research projects in the department of Theoretical Biology, that focus on the range of predator-prey to (endo)symbiontic relationships in an evolutionary context.

We do feel that a parallel development of experimental and theoretical research programs on ecosystem dynamics is an essential preliminary phase to formulate a feasible future research programme where both approaches are integrated more intensively. At present the theoretical problems connected with spatially heterogeneous systems are too complex to be feasible to address.

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# 7 Working programme

## 7.1 Time schedule

Oct 1999 start of project

March 2000 completion of literature about ecosystem models (first round)

Oct 2000 completion of setup of a software environment for computer simulations studies

March 2001 completion of first round of simulation studies with a 3 trophic food chain

Oct 2001 completion of bifurcation analysis of with a 3 trophic food chain, and comparisons with1 and 2 species communities

March 2002 completion of simulation studies with a 4 trophic food chain, and 4 trophic a food web

Oct 2002 completion of bifurcation analysis with a 4 trophic food chain and web

March 2003  completion of a reduction of the food web of consumers by a single generalized population of consumers

Oct 2003  completion of the comparison of the behaviours of systems with increasing complexity

## 7.2  Publication outline

Provisional titles and completions dates

March 2001  The transient behaviour of communities with a 3 trophic food chain; comparison with Canonical Community dynamics

Oct 2002  The longterm beviour of communities with 4 trophic food webs

March 2003  The transient beviour of communities with 4 trophic food webs; the relationship between stability and biodiversity

Oct 2003  The modular reduction of food web dynamics in a simple ecosystem

Oct 2003  literature review on the dynamics of ecosystems

Oct 2003  PhD- thesis

## 7.3  Progress monitoring

The research progress will be monitored by a scientific committee for this project, chaired and composed by van Straalen. The committee will meet twice a year.

The project will also be brought into the informal ALW working group on Theoretical Biology, which monitors progress in two-days yearly meetings at NIOZ (Texel).

The project will also be subjected to the review system of SENSE.

# 8  Positioning within international research programmes

The project fits well into the NWO-priority program on Nonlinear Systems (Kooijman is national coordinator on the sub-program on population dynamics), the NWO-priority programme on Massively Parallel computational methods (Kooi is coordinator), and in the NOP2 programme on global change. We aim at a EU project on the role of plankton in the global carbon cycle in the period of the project; which will have tight links with this proposal. The project will be included into DEBweb, an international group collaborating on DEB modelling (Hallam, Knoxville; Nisbet, Santa Barbara; Lika, Crete) which meets regularly.

# 9  Required qualifications of researcher to be appointed

Mathematical biology; a training in dynamical system theory and ecology.

# 10 Laboratory animals

No animals are used

# 11 Recombinant DNA

No recombinant DNA is used

# 12 Special fields of research

The topic of research has relevance for non-linear systems and biodiversity

# 13 Applied research

This project is of applied relevance to conservation biology

# 14 Renewed application

This is the first time we propose this research

# 15 Financial assistance of research group from other sources

The project would benefit considerably from a number of projects currently running at the department for Theoretical Biology, and some projects that have been completed recently. I mention

- Modelling the ecosystem of the North Sea; Funded by RIKZ, this project aims to evaluate current models for the ecosystem of the North Sea, and to setup a modular modelling framework that helps to understand the dynamics of the system and its reactions on perturbations for various nature.

- Analysis of routine biodegradation tests; Funded by STW-NWO, this project aims to develop realistic models for biodegradation of organic compounds.

- Individual-based population dynamics; Funded by NWO (priority program Massive Parallel Computational methods), this project aims to evaluate the discrete nature of individuals in population dynamics.

- Impact of *Emiliania* on the global carbon flux; Funded by NOP2, this project aims to evaluate to role of *Emiliania* in the global carbon cycle.

- Sulphur and carbon fluxes in microbial mats; Funded by NWO (priority program Perturbation of Earth Systems), this project aimed to model the ecophysiology of microbial coastal ecosystems, in relation the DMS production.

- Structured population dynamics: Funded by NWO (priority program Non-linear Systems), this project aimed to analize the dynamics of food chains in structured populations.

More details about these projects (and other projects) can be found at `http://www.bio.vu.nl/thb/`

# 16   Funds requested

Apart from the standard exploitation costs, a travel fund of 10 kf is requested.

# 17   Motivation of requested funds

The travel fund is needed to participate in the rather intense international collaborative exchange within DEBweb.

# 18   Approval by the research institute

This proposal has been written on invitation by the institute.

# 19   Signature