1. Title of the project

The discreteness–continuity dichotomy in Individual-Based Population Dynamics using massively parrallel machines.

2. Applicants

Applicant	Affiliation	Discipline	NWO Foundation
Prof.dr.O.Diekmann	CWI/RUL	Mathematics, Theoretical Biology	SMC
Dr.B.W.Kooi	VUA	Mathematics, Computer Science	SLW
Prof.dr.S.A.L.M.Kooijman	VUA	Theoretical Biology	SLW
Prof.dr.J.A.J.Metz	RUL/CWI	Mathematics, Theoretical Biology	SLW
Dr.A.M.de Roos	UVA	Population Biology	SLW
Dr.B.Sommeijer	CWI	Numerical Analysis, Mathematics	SMC
Dr.P.Sloot	UVA	Computer science, Physics	FOM/SION
Dr.J.Kaandorp	UVA	Computer science, Physics	FOM/SION

3. Institute

Free University, Department of Theoretical Biology
de Boelelaan 1087, 1081 HV Amsterdam, e–mail: bas@bio.vu.nl

4. Abstract

Biological populations consist of discrete individuals with a unique physiological state, which interact among each other on a very local scale. In addition, random variation in, for example, individual growth occurs between fully indentical individuals. In models of population dynamics, this inherent discreteness and the consequent sources of stochasticity are often neglected, because the long–term behavior of populations are more suitably studied with continuous descriptions. A second school of research puts more emphasis on the influence of the inherent stochasticity and less on the full characterisation of the population dynamics as a function of parameters. We propose to study this *discreteness–continuity dichotomy* using massively parallel machines, since both approaches involve large–scale computation. To resolve the dichotomy comparisons are required between different approaches.

5. Duration of the project

4 year, starting in July 1995

6. Personnel

6.1 Senior-scientists

Group A: Free University, Theoretical Biology
- Prof.dr.S.A.L.M.Kooijman (modelling aspects of biological systems, VUA, 0.1 fte)

- Dr.B.W.Kooi (numerical analysis, computer science, VUA, 0.2 fte)

Group B: University of Amsterdam, Population Biology
- Dr.A.M.de Roos (structured population models, UVA, 0.2 fte)

Group C: CWI and University of Leiden
- Prof.dr.O.Diekmann (mathematics, CWI/RUL, 0.1 fte)
- Prof.dr.J.A.J.Metz (evolution theory, structured population models, CWI/RUL, 0.1 fte)
- Dr.B. Sommeijer (numerics, computer science, CWI, 0.1 fte)

Group D: University of Amsterdam, Mathematics and Computer Science
- Dr. P.M.A. Sloot (parallel computing, UvA, 0.1 fte)
- Dr. J.A. Kaandorp (parallel computing, FOM/MPR project "Portable parallel simulation of crystal nucleation and growth", 0.2 fte)

6.2 Junior-scientists and technicians

- Drs. J. van Wezel (System manager, VUA, 0.1 fte)
- Drs. A. Schoneveld (Complexity and parallelism of DCS, UvA, 0.2 fte)
- Drs. B. Overeinder (technical programmer, UvA, 0.5 fte)

7 Personel

7.1 Personel positions

Group A: 1 PhD–student (theoretical biology; 4 years) Group B: 1 Post–doc (theoretical biology; 2 years) Group C: 1 Post–doc (numerical analyst; 2 years) Group D: 1 Post–doc (computer science; 2 years)

7.2 Running budgets

To cover travelling costs for attending conferences and costs for acquisition, each group will need a running budget of 3kf on a yearly basis

7.3 Other costs

There are no other costs.

7.4 Other support

Group A: Free University, Theoretical Biology
- Prof.dr.S.A.L.M.Kooijman (VUA, 0.1 fte)
- Dr.B.W.Kooi (VUA, 0.2 fte)
- Drs. J. van Wezel (VUA, 0.1 fte)

Group B: University of Amsterdam, Population Biology
- Dr.A.M.de Roos (UVA, 0.2 fte)

Group C: CWI and University of Leiden
- Prof.dr.O.Diekmann (CWI, 0.1 fte)
- Prof.dr.J.A.J.Metz (RUL, 0.1 fte)

- Dr.B. Sommeijer (CWI, 0.1 fte)

Group D: University of Amsterdam, Mathematics and Computer Science
- Dr. P.M.A. Sloot (UvA, 0.1 fte)
- Dr. J.A. Kaandorp (FOM/MPR, 0.2 fte)
- Drs. A. Schoneveld (UvA, 0.2 fte)
- Drs. B. Overeinder (UvA, 0.5 fte)

All groups will bring in the local infrastructure. Group A, B and C will put forward a proposal to use the SP1 machine. If necessary we will forward a proposal to NCF to get access to the Cray 98 at SARA. The IC^3A systems can be used for developing the code without additional costs. The terms under which large scale production runs can be carried out on these systems will be negotiated with the director of the IC^3A.

7.5 Abstract

	1995	**1996**	**1997**	**1998**	**1999**	**Total**
Group A						
personel (positions)						
PhD-students	1/4	1	1	1	3/4	4
personel (costs in kf)	14	57	57	57	43	228
running budget (in kf)	3	3	3	3	12	
Group B						
personel (positions)						
post-docs			1/2	1	1/2	2
personel (costs in kf)			43.75	87.5	43.75	175
running budget (in kf)			3	3	3	9
Group C						
personel (positions)						
post-docs		1	1			2
personel (costs in kf)		87.5	87.5			175
running budget (in kf)		3	3			6
Group D						
personel (positions)						
post-docs	1/2	1	1/2			2
personel (costs in kf)	43.75	87.5	43.75			175
running budget (in kf)	3	3	3			9
total (in kf)	63.75	241	244	150.5	89.75	789

8. Publications

Metz, J.A.J. and Diekmann, O., editors. 1986. *The dynamics of physiologically structured populations*, Springer Lecture Notes in Biomathematics. Springer-Verlag.

Roos, A.M.de, 1988. Numerical methods for structured population models: The escalator boxcar train. Num.Meth.Part.Diff.Eq., 4:173–195.

Roos, A.M.de, McCauley, E. & Wilson, W.G. 1991. Mobility versus density–limited predator–prey dynamics on different spatial scales. Proc.R.Soc.Lond.B. 246:117–122.

Kooijman, S.A.L.M. 1993. Dynamic Energy Budgets in Biological Systems. Theory and applications in ecotoxicology. Cambridge University Press.

Sommeijer, B.P. 1993. Parallelism in the numerical integration of initial value problems, CWI Tract 99, CWI Amsterdam.

Kooi, B.W. & Kooijman, S.A.L.M. 1994. The transient behaviour of food chains in chemostats. J. Theor. Biol. 170:87–94.

Kaandorp, J.A. 1994. Fractal modelling: growth and form in biology. Springer-Verlag, Berlin, New York.

Sloot, P.M.A. 1994. Dynamical Complex Systems (DCS): A new approach to parallel computing in computational physics. Technical report FWI TR: CS 94 12, University of Amsterdam.

9. Research programme

Traditionally the dynamics of biological populations have been modelled using low–dimensional systems of ordinary differential equations (ODEs). These so–called "unstructured" formulations rest on the assumption that individuals are identical or can at least be represented by some "average" type, such that the total number of individuals making up a population suffices to characterise the state of the population. During the last decade it has become increasingly clear that realistic descriptions of the dynamic behaviour of populations should be based on the dynamic behaviour of individuals comprising it.

In the most realistic description the biological population should be viewed as a collection of discrete entities, *i.e.* the individuals, each characterized by a unique set of (physiological) traits. The population dynamical behavior (growth, development, reproduction, mortality) of all individuals taken together yield as a resultant the dynamics of the population as a whole. The individuals interact (locally or globally) with each other, as they, for example, compete for resources. In models of individual behavior these interactions are represented by feed–back loops via environmental variables, such as food density or total population size, which constitute the (often highly) non–linear parts of the population dynamic models.

The "unstructured" view of population dynamics and the "collection of individual entities" view are two extremes of a scale of complexity and realism. Various intermediate formulations do exist, specifying the population dynamics in terms of, for example, delay differential equations, partial differential equations and integral equations. These intermediate formulations are obtained on the basis of some set of simplifying assumptions, of which the "law–of–large–numbers" is invariably one. Assuming that the "law–of–large–numbers" holds, allows us to represent the finite number of discrete individuals by a density measure, such as a size–distribution of the individuals in the population over the plausible size range. The dynamics of the density measure are subsequently described by partial differential or integro–differential equations. Models that use a density measure to characterize the state of the population have become known under the heading of "physiologically structured population models" (Metz & Diekmann, 1986).

The theory of physiologically structured population models has been developed mainly by research groups in the Netherlands, in particular all members of the groups A, B and C have been involved. Group A (VUA) has developed and experimentally tested mathematical models of individual behavior based on energy budget considerations (Kooijman, 1993). The construction of population dynamical formulations from these individual level descriptions and the tools to analyse the models have been developed by the members of group B and C (CWI,RUL). These developments have been picked up by other groups, resulting in an alternative approach in which the "law–of–large–numbers" is not invoked and the population is represented as a collection of discrete individuals (Łomnicki, 1988; DeAngelis & Gross, 1992). The population dynamics is then studied by means of stochastic simulation of the behavior of all individuals. The latter approach of modelling population dynamics is usually referred to as "individual–based population models" in a general sense (Łomnicki, 1988; DeAngelis & Gross, 1992).

In accepting that the "law–of–large–numbers" holds, the inherent discreteness of the population dynamics is obviously neglected. The emphasis of researchers studying the more analytical physiologically structured population models is on the long–term dynamics of the population. That is, the attractors of the population model are of prime interest, as is their dependence on model parameters. Bifurcation analysis of the model equations is hence the central theme in studies of structured population models. Researchers studying individual–based simulation models of population dynamics put more emphasis on the inherent stochasticity of the process and in general do not explore in great detail the parameter dependence of the dynamics. The controversy arising between these two approaches centers around the *discreteness–continuity dichotomy* that is part of the "law–of–large–numbers". In the research program proposed here we plan to study the essence of the discreteness–continuitiy dichotomy to resolve part of the controversy. We have selected three important implications of the law–of–large–numbers for further investigation, which will be discussed below. The study of the implications of the law–of–large–numbers requires the expertise from different fields of science, ranging from theoretical biology, functional analysis, bifurcation analysis, numerical approximation techniques and parrallel computing, all of which are brought in by the different groups participating in this joint proposal.

Studies of the discreteness–continuity dichotomy require the comparison of the dynamics, as predicted by stochastic, individual–based simulation models and physiologically structured population models, specified in terms of integro–differential equations. Individual–based models will involve stochastic simulations of sometimes very large numbers of individuals (10^9), requiring enormous computational effort (TeraFlop applications). A very promising class of techniques can be identified by "natural solvers" (Sloot, 1994). These techniques have in common that they are inspired by processes from nature. An important examples of natural solvers is the Lattice Boltzmann method (a many particle system with a macroscopic behaviour that corresponds to the hydrodynamic equations; Succi et al., 1992). This class of solvers has become recently very important in parallel computing to model and simulate Dynamic Complex Systems (DCS). They have also been applied successfully in for example physics, chemistry, and economics. The problem of simulation and modelling of DCS, using these solvers, and the mapping of these solvers onto parallel platforms have been partly solved for relatively small problem sizes. A main challenge is to apply these parallel natural solvers in simulation models of biological systems, which are characteristically of considerably larger size. To this end extensions to the formalisms are needed, as well as methods to compute them.

To study the dynamics of physiologically structured population models, specific numerical methods have been developed for the resulting sets of equations (de Roos, 1988; de Roos, 1989; de Roos & Metz, 1991). Both approaches are very suitable for parallel computations, as individual organisms behave independently, apart from the (local) interactions via environmental feed–back loops. A first start to exploit parrallel computation techniques in the study of the dynamics and bifurcations in physiologically structured population models has been made in a current research program carried out at the CWI and funded as part of the NWO priority program on non–linear systems.

We propose to study three main issues involved in the discreteness–continuity dichotomy.

1. Inherent stochasticity
   Model formulations based on density measures neglect the inherent stochastic nature of the birth and death process of the biological organisms. It is clear that these models will deviate significantly from completely stochastic descriptions if the number of individuals in the popula-

tion is small. One of the first questions to resolve is to what level is the "law-of-large-numbers" safe to exploit?

Continuous formulations approximate the stochastic birth and death processes by representing them with their expected values. Hence, birth and death are modelled using the average reproduction and mortality *rate* of individuals of a given type. The stochasticity neglected in this approximation can be seen as a source of internally generated noise. It is not *a priori* clear that this noise is negligible, as long as the number of individuals is large. The sometimes higly non–linear interactions between individual organisms could in principle amplify the small–amplitude noise and yield observable consequences at the level of the population.

2. Variation and selection

   Individual–based modelling of population dynamics makes it possible to take the, since Darwin well-known, variation between individuals and selection into account. Apart from the intrinsically stochastic reproduction and mortality events, individual organisms develop in a roughly deterministic way throughout their lifetime. This behaviour is partly fixed by values of parameters which can differ a little for different individuals making up the population. The consequences of this parameter variation among individuals is the second major theme in the discreteness–continuity dichotomy.

   Consistent models of the individual behaviour, as a function of their individual age and size and of the current food density they experience, have evolved and succesfully capture a large amount of biological detail at the individual level (see, for example, Kooijman, 1993). The particularly succesful theory of Dynamic Energy Budget models (Kooijman, 1993) to represent individual behavior implies that the stochastic variations in different parameters are not independent, but coupled by specific relations. These relations can hence be exploited to reduce the problem of parameter variation among individuals to stochastic variations in a single variable.

   By coupling parameter values of daughters to those of their mothers via an inheritance mechanism, it is possible to simulate evolution–processes for selection via competition already incorporated in the population dynamics. The environmental conditions to which individuals are adapted are not extrinsically determined constants. It contains not only the individuals of the species with which they interact, but also conspecifics. Furthermore, these conditions may fluctuate in various spatial and temporal scales. Especially a relative fast segregation of parameter values into two or more groups will be studied. This facilitates the investigation of the origin of species. Essential in this problem is that the properties of the individuals will change in time while evolution is based on mutation and selection. This means that the single individuals as part of a population interacting with other populations in ecosystems determine evolution. This shows the dichotomy between a description based on the discrete and continuum paradigm.

3. Local interactions

   As is already discussed, the interactions between individuals is always considered to act via feed–back loops that can be viewed as part of an individual's environment. Often this environment is assumed to be identical for all organisms, implying that individuals live in a homogeneous environmet. This assumption neglects the fact that interactions of an individual with its environment are necessarily localized, such that the homogeneity assumption is only valid if mixing is very rapid. Recent studies (de Roos et al., 1991) show that if interactions between individuals are local and mixing of individuals is restricted because individual mobility is limited, dynamics become strongly dependent on the spatial scale of observation. Local interactions immediately imply the generation of some form of spatial heterogeneity and only weak coupling of dynamics between regions of the spatial domain that are far apart. The extreme population oscillations that are observed in population models with homogeneous mixing remain localized under conditions of spatial subdivision and weak coupling (Jansen, 1994). On larger spatial scales this leads to a suppression of the oscillations. In well–mixed biological systems with a spatial homogeneous distribution of individuals over a uniform environment, oscillatory population behavior is indeed observed, as predicted by non–spatial models (Kooi & Kooijman, 1994). Many biological systems are, however, inherent spatially heterogeneous, which has severe consequences for the dynamics and also the evolution of populations (Boerlijst, 1994) because mutants experience changes in their neighbourhood caused by themselves.

A central goal of the study of local interactions is to understand the relation between the resulting spatial structure and the biological aspects of the life–histories of the individuals engaged in the interactions. Models with a spatial as well as with a realistic physiological structure have not been studied so far, by reason of the fact that they demand too much computing power. This links this subject with the previous one, for one approach is to follow individuals which move in a closed environment. The scientific focus will be on the generation of some fundamental understanding of the generation of spatial structure and its consequences for population dynamics, rather than on the study of specific biological case–studies. This requires a mixed approach, in which computational methods are constrasted with more analytical approximations.

Another type of spatial heterogeneity relevant for the interaction between populations is the often complex geometry of the physical environment in which interactions take place. For example, many sessile marine organisms live on a hard substrate with a complex geometry. The geometry has a strong influence on, for example, the availability of nutrients and/or light and hence on the population growth. Diffusion and transport processes through the environment play an overriding role. Lattice Boltzmann methods can be efficiently exploited to study models of such systems.

Superficially the setting sketched above suggests that biological populations are comparable with other "many–particle" systems. As such, the proposed research belongs to the class of projects that wil use parrallel computers as a research tool for applications. The behavior of individuals is, however, a mixture of continuous changes, like growth in size, and stochastic processes, like giving birth and dying. The individual properties that change continuously over time have a strong influence on the probability to give birth or to die. Moreover, the aspect of not completely faithful reproduction of individuals (discrete entities) and the ensuing evolution of traits is unique for biological problems. Taken together, these aspects imply that the research will also involve studies of implementation techniques that may be of importance to a larger field of science.

In addition to studies of population consisting of discrete entities, the discreteness–continuity dichotomy can only be resolved by comparison. The requested support for the entire research project is therefore necessarily spread out over the different groups participating. The proposed PhD–candidate is supposed to focus on the aspects of inherent stochasticity (point 1 above) and variation and selection among individuals (point 2) in homogeneously mixed environments. One of the proposed Post–doc candidates will focus on the influence of local interactions and spatial heterogeneity (point 3) and its consequences for dynamics and evolution (point 2 above). Both aspects can not do without comparison with more analytical approaches, such as the recently started project on the numerical analysis of phsyiologically structured population models (NWO priority program on non–linear systems), in which the expertise of the Applied Mathematics and the Numerical Mathematics group of the CWI are essential. A second Post–doc will therefore have to supply the analytical approaches to the problems as contrast. The stochastic simulation studies with individuals as discrete entities will exploit parallel implementation techniques such as the Lattice Boltzmann method. The third Post–doc requested will primarily focus on the extension and development of these methods for application to biological problems, which require new techniques because of their characteristically large size.

Algorithms

A very suitable method for modelling spatially distributed systems taking into account explicit individual movement through the domain is the lattice Boltzmann method. In addition, the lattice Boltzmann solver allows for domain decomposition and can be mapped onto a parallel platform.

Physiologically structured population continuum models are formulated in terms of non–linear hyperbolic partial differential equations, coupled to a set of ordinary differential describing the dynamics of the relevant environment variables. The coupling terms in these sets of equations contain measures of the population distribution. De Roos has developed an efficient numerical method for dealing with general nonspatial physiologically structured populations models, based on an interesting combination of biological and mathematical insight (de Roos, 1989). At CWI numerical integrators for similar initial value problems were already studied intensively Sommeijer (1993). Navier-Stokes problems in computational fluid dynamics have a number of aspects in common with this kind of problems. There is, however, a important difference, namely the fact that at each time the total integral of the density has to be calculated. Individuals interact via the environment and indirect via the density distribution of individuals because the influence of the population on the environment is connected to this quantity. As mentioned before, recently a start has been made to exploit parrallel computation techniques in the numerical method developed by de Roos (1989) to numerically analyse the dynamics of physiologically structured population models. This concerns a joint project between the Applied Mathematics and the Numerical Mathematics group of the CWI and the Population Biology group of the University of Amsterdam.

Programming languages

A central decision regarding the development of distributed software is the method exploited for parallelization (H. Ball 1990). Distributed applications can be built directly on top of the hardware, on top of an operating system, or in a special language for distributed programming. To develop a framework that will also be accessible for a larger community of biological researches we intend to use as much as possible an existing sequential laguage, like C^{++} or Fortran, plus standard package (PVM) for developing parallel program executable on networked Unix computers and multi–processor system.

PVM (Geist et al. 1994) is a public domain software package which allows a heterogeneous collection of workstations and supercomputers to function as a single high-performance parallel machine. PVM is portable and runs on a wide variety of modern platforms. It has been well accepted by the global computing community and used successfully for solving large-scale problems in science, industry, and business. PVM is designed to link computing resources and provide users with a parallel platform for running their computer applications, irrespective of the number of different computers they use and where the computers are located. PVM can also be used on highly parallel systems such as Cray T3D, and Thinking Machines CM-5.

The package PVM seems to be a promissing environment to implement the programs because it is operating system and the hardware independent to a high extent. Performance issues, dealing primarily with communication overheads, will be analyzed. The choice of programming language, operating system and machine hardware will be reconsidered as soon as more promissing developments are reported. The primary aim will be the implementation of parallelized numerical methods for solving population dynamics on parallel machines.

Computer systems to be used

At SARA a 9076-SP1, an IBM parallel system with 8 RISC-processors, is operating. UvA, VU and CWI take part in the joint study agreement which makes this machine available for the Amsterdam scientific institutes. All groups involved are hence part of this agreement and will put forward proposals to exploit this system for their research. It is planned to also use the Parsytec PowerXplorer as target platform. The necessary parallel computing facilities for this project will be made available by the IC^3A. Cooperation with Prof.L.O.Hertzberger from the Interdisciplinary Center for Complex Computer Facilities Amsterdam ($\mathrm{IC}^3\mathrm{A}$) is essential for the accessibility to the parallel computing facilities and expertise in Parsytec and IBM technology. The software package PVM runs on all the target computer systems. For comparison purposes we can also use the vector supercomputer Cray C98 at SARA and CWI is connected to the Cray T3D in Lausanne with 512 processors.

Genericiteit

The application of natural solvers can advance research on DCS in biology significantly. It is expected that this project will yield several generic techniques which can be applied in modelling and simulation of other examples of DCS from biology and physics and will promote the transfer of expertise in parallel computing to research in biology.

The numerical analysis of physiologicaly structured population models will be of importance for the theory of numerical bifurcation analysis for high dimensional systems of equations in general. The developed techniques in this part of the research will be directly applicable in other fields of science as well.

Cooperation among the groups
Three of the four research groups involved in this joint application have a long history in cooperation, among others in the context of the NWO priority program on non–linear systems. Joint projects (both for PhD–students and Post–docs) are testimony for this cooperation. Moreover, all members of these groups have been involved with the developments of the theory of structured population models, either from the individual (VUA) or population (RUL,UVA) perspective or from a mathematical and theoretical point of view (RUL, CWI).

It has been made clear that the discreteness–continuity dichotomy cannot be resolved without the input of the different approaches, yielding the necessary contrasts. The coherence, mutual benefits and cross–fertilization between the different research topics is therefore obvious. The existing collaboration with respect to mathematical modelling of population dynamics between the groups A, B and C will be continued. The Numerical Mathematics group of the CWI will deliver the necessary support the other groups and will bring in the expertise in numerical analysis, the construction of parallel algorithms and the use of parallel computers solving large-scale problems. The just started collaboration between groups B and C with respect to the numerical analysis of phsyiologically structured population models will be continued and strenghned.

Group D will bring in expertise in parallel programming environments and the parallel natural solvers (Lattice Boltzmann method). For this purpose the results from the MPR project "Portable parallel simulation of crystal nucleation and growth" will be used. The results of a previous research project: "Modelling growth and form of marine sessile organisms and the influence of the physical environment", in cooperation with the Faculty of Biology of the University of Amsterdam, will be used in this project.

10. Relevance for other fields of science and society

Possible applications of the theory on structured population dynamics are abundant. The treatment of sewage water is one example, which at present focus of research of the group at the VUA.

The class of "natural solvers" that will be investigated will have a wide range of application in other fields as well. One of the biological fields of application concerns the research that is funded with European Artifical Reef Research network (EARRN). In this context initiatives for cooperation exist at present between group D and the Rijks Instituut Kust en Zee (RIKZ, Rijkswaterstaat).

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Ondertekening

Aanvrager: Datum: