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News Letter

A newsletter for the project 'Population dynamics, including epidemiology' being part of the NWO priority program 'Nonlinear Systems'.

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This newsletter will appear once every three months during the course of the project. Its content will mainly consist of announcements of activities, such as seminars and workshops. Moreover, information about foreign visitors being in the Netherlands as part of the program will be given.

To make this newsletter as informative as possible we ask you to let us know about activities that are planned and the date visitors are coming and give lectures. Also addresses of persons (in the Netherlands or abroad) who might be interested in receiving this newsletter are welcome.

Contributions to this newsletter were made by: Chris Klok, Mark Peletier, Marten Scheffer.

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1 Report of visit Prof. S. Rinaldi

by Marten Scheffer, `Marten.Scheffer@Aqec.WKAO.WAU.NL` and Bob Kooi `kooi@bio.vu.nl`

Prof. S. Rinaldi had informal discussions with Marten Scheffer, he was a speaker at the symposium held Tuesday 27 June 2000 VU Amsterdam and he asked questions on the defence by Martin Boer of the thesis entitled "Tritrophic food chain dynamics". The program of this symposium was given in the previous issue of the Newsletter, dated May 18, 2000.

Martin Boer was the first speaker and for an abstract of his talk the reader is referred to the summary of his PhD thesis given in the May 18 issue. At the website `http://www.bio.vu.nl//thb/deb/deblab/art.html` you will find a number of figures presented by Martin during his contribution One figure shows a 3-D plot of the domain of attraction for a chaotic attractor of a tri-trophic food chain consisting of a nutrient, prey, predator and a top-predator in the chemostat. Other figures show a homoclinic orbit of a saddle cycle and a heteroclinic orbit between a saddle equilibrium and a saddle cycle

Abstracts of the talks by Sergio Rinaldi (Milaan) and Marten Scheffer (Wageningen UR) are:

Sergio Rinaldi, Politecnico di Milano, Italy, `rinaldi@elet.polimi.it`.

Peak–to–Peak Dynamics in food chains

Dynamical systems with chaotic behavior sometimes enjoy a remarkable property, called peak–to–peak dynamics (PPD). Such PPD can be either simple or complex. When a simple PPD exists in a chaotic system, the next maximum (peak) of any relevant variable can be predicted from the last maximum through a 1-dimensional map. The same is true for the time of occurrence of the peak. The existence of PPD is critically related with the fractal dimension of the strange attractor. Simple PPD have been discovered in various fields of science, in particular in electrochemistry, both through laboratory experiments and modelling exercises. By contrast, in population dynamics only a few convincing examples have been discovered until now. Examples of PPD in ecology are presented by discussing some models, among which a forest–pest model, a forest–fire model and a plankton–fish model. This means that it is virtually possible to forecast pest-outbreaks in forest ecosystems, fires in Mediterranean forests, and plankton blooms in lakes: a quite remarkable result. The sensitivity of PPD to measurement and environmental noise is also discussed, together with the possibility of using PPD for solving management problems.

Marten Scheffer, Wageningen UR, `Marten.Scheffer@Aqec.WKAO.WAU.NL`

Between models and reality

Although the merits of combining modeling and empirical research are broadly recognized the approaches remain quite segregated in practice. Also, within the modeling world there is a distinct separation between theoreticians working with abstract minimal models and groups working on more applied quantitative simulation models. Meanwhile, in empirical aquatic ecology many experimentalists disguise whole lake manipulations as uninterpretable, whereas lake manipulators argue that the approach of controlled 'bottle experiments' has revealed little about how the real world works. Obviously, the different approaches may produce different fragments of the complex image of how aquatic ecosystems work. Whole lake experiments help to identify the main regulatory mechanisms, but the conditions are difficult to control and there are usually no replicates. As a result it is often difficult to understand what happened for what reason in the hindsight. Small scale replicated and controlled experiments, on the other hand, are necessarily conducted under rather unnatural conditions and do not reveal how the mechanism addressed interacts with other mechanisms in the field. Elaborate simulation models can help putting different processes into quantitative perspective but are difficult to study due to their mere complexity. Very simple "minimal" models are easier to understand but do not help to reveal the relative importance of the addressed mechanism in the field. Obviously, linking these approaches could boost our insight. This leads one to wonder what are the main causes of the separatism between approaches and how it could be overcome. It seems likely that the high cost–benefit ratio of integration of approaches is a major limitation. Focusing on the problem of relating models to reality, it takes a major investment from a modeller to publish outside the relatively protected environment of purely theoretically oriented journals. Not only are reviewers likely to eliminate descriptions of many technical aspects, they also tend to question the value of the model for enhancing insight and point out numerous omissions in discussing empirical literature. Indeed, the effort of linking a model to reality is generally much larger than the effort required to formulate and analyze the model. I argue that, nonetheless, at this stage true advancement of insight in the functioning of aquatic ecosystems may well benefit more from such laborious linking than from digging deeper along separate tracks.

2 Report of visit Prof. James Keener

by Mark Peletier, CWI Amsterdam, `Mark.Peletier@cwi.nl`

During the month of June, Professor James Keener (University of Utah)`http://www.math.utah.edu/~keener/` was an honorary visitor of the Centre for Mathematics and Computer Science (CWI) in Amsterdam.

Professor Keener is a specialist on mathematical aspects of physiology (see e.g. his book, in collaboration with James Sneyd, *Mathematical Physiology*, Springer, 1998). During his stay in Amsterdam he was actively involved in a variety of current research projects at the CWI (see `http://dbs.cwi.nl:8080/cwwwi/owa/cwwwi.print_projects?ID=5`), and also spawned a couple of new ones. As an example, a conversation with Frank Bruggeman (VU-Amsterdam) sparked a new research project on the relation between ultra-sensitivity, scaffolding, and diffusion in signal-transduction processes. As another example, combination of work that

Professor Keener had started earlier, and interests present at the CWI, led to a collaborative project on mechanical aspects of biofilm growth.

In addition to these informal activities, Professor Keener presented a series of lectures entitled *Cardiac Electrophysiology and Arrhythmias* in which he gave a basic introduction to wave propagation in cardiac tissue, and analysed both the normal function and a number of well-known arrhythmias in terms of the spatial properties of the associated wave patterns. He was also a speaker at the first MAS Crossroads Colloquium *Modelling and Analysis in the Life Sciences* (June 7 2000, at the CWI-Amsterdam).

3 Summary of PhD-thesis by Chris Klok

Summary of the PhD-thesis by **Chris Klok**, Wednesday 27th September 2000, Email: `T.C.Klok@Alterra.wag-ur.nl`

A Quest for the Role of Habitat Quality in Nature Conservation

In this thesis the importance of habitat quality for the persistence and conservation of endangered species is discussed. The studies presented incorporate several aspects of habitat quality that have a major impact on the population dynamics of the species under consideration.

In chapter 2 the importance of habitat quality and size on the persistence of populations is analysed, given stochasticity in demographic processes. In this chapter habitat quality is expressed in terms of R_0 (the lifetime reproductive output of an individual), and habitat size is described by K (the number of territories in the population). The results show that for the common shrew *Sorex araneus* the population density is mainly influenced by the habitat size. The population extinction time, on the other hand, depends more on the habitat quality than on habitat size. In the common shrew the expected extinction time increases exponentially with the number of territories and more than exponentially with the lifetime reproductive output. Moreover, the expected extinction time is always more than twice as sensitive to changes in habitat quality than to changes in habitat size. These results are derived for (1) a uniform and contiguous habitat area, (2) no restrictions on settlement (occupation of territories by juveniles is random) and (3) habitat quality (R_0) not correlated with its size (K). In the context of (1) a discontinuous area (heterogeneous or fragmented habitat), (2) non-random settlement (e.g. in a metapopulation context), and (3) correlation between R_0 and K, the sensitivity of the expected extinction time to habitat quality even increases. In a more general setting, chapter 2 shows that irrespective of the species under consideration, the likelihood of extinction as a consequence of demographic stochasticity can be more effectively countered by enhancing the reproductive opportunities of its individuals, if this is feasible, than by increasing population size.

Chapter 3 shows that a permanent reduction in habitat quality, such as induced by copper, can have a strong impact on population performance. In this chapter the effects of sublethal levels of copper on the population growth rate of earthworms is assessed. Copper influences the energy budget of the individuals which results in a decline in their growth and reproduction, leading to a decrease in the population growth rate. Especially reduction of individual growth has a large impact on the population growth rate because it delays the maturation. The population dynamical model used to assess the impact of Cu predicts population extinction to occur in the range of 200 to 300 mg copper per kg soil. This result, applied to earthworms living in sandy loam soil, is in reasonable agreement with field data. To assess the actual state of a population under field conditions the model is also used to study the effects of copper on the composition of the population in terms of juveniles, subadults and adults. These effects on the population structure reveal that toxicants, that reduce the individual growth, induce change in the population structure only close to the point where the population goes extinct. Therefore, to inspect the viability of earthworm populations in field situations the population structure is not a good statistic.

The sensitivity analysis in chapter 4 shows that in earthworms the time spent in the adult stage has the highest impact on the population growth rate. This implies that stress factors delaying maturation of juveniles, and thus reducing the duration of the adult stage, given a maximum life span, can have a large impact on the population. The result contrasts with the commonly held view in risk assessment that reproduction is considered the most important life history aspect.

The results of chapter 5 demonstrate that persistence and population density in the barn owl, a resident predator that responds numerically to temporal variations in its prey abundance (voles), are more sensitive to years with low vole densities than to peak prey years. Although peak vole years increase the number of owls in the population, the lows bring their number down to such levels that the population cannot benefit from the ensuing peak year. This result is irrespective of the period of the fluctuations and whether the fluctuations are periodic or random. This conclusion also holds for open populations since voles fluctuate in synchrony over extensive areas. Therefore, conservation in the barn owl should be directed at improving the food conditions in the years with low vole densities. Also for other raptor species, that show a numerical response to their prey, it is expected that especially the bad years, with respect to food, determine the population performance. In chapter 6 the contributions of soil pollution, acidification and fragmentation on survival of the badger are explored since the species seems to be threatened by the combination of these factors in The Netherlands. Soil pollution with cadmium can result in a direct effect (kidney lesion), whereas copper induces an indirect effect (food shortage). Badgers are confronted with these risks by feeding on earthworms. Earthworms accumulate cadmium to high levels, which badgers deposit in internal organs such as the kidney. Copper induces decline in development and reproduction in earthworms leading to reduction in their population growth rate and population density. This decrease in earthworm density reduces the amount of food available to the badger. Soil acidification enhances the risks of kidney lesion and food shortage on the badger, because it increases the availability of these pollutants.

The results in chapter 6 show that the risk on kidney lesion and food shortage are substantial; kidney lesion occurs within two to four years, and food levels are reduced up to 10%. This implies that next to fragmentation also soil pollution and acidification can interact with fragmentation to increase traffic mortality since both intoxication (that increases energy requirements for detoxification) and food shortage can force the badger to roam larger areas in search of food.

Practical perspectives

Conservation

This thesis emphasises the importance of habitat quality for the conservation of endangered species. As shown in chapter 2, the likelihood of extinction as a consequence of demographic stochasticity can best be countered by improvement of habitat quality. Also an enlargement of the habitat size increases the population persistence. However, increases in habitat size always have a lesser effect than a similar improvement in habitat quality. Populations of endangered species are often restricted to highly fragmented habitats of marginal quality. Management options aiming at the preservation of these populations should therefore include strategies to improve both habitat quality and habitat size. Compared to enlargement of the habitat area improvement in quality is more difficult to achieve. Habitat quality comprises many factors such as physical conditions, the abundance of resources, breeding sites etc. and its assessment requires thorough knowledge of the ecology of the species under consideration. Common practice in conservation is to classify habitat quality into categories like marginal, central, good, medium and bad (Gilpin & Soulé 1986). It is not always possible to improve both the quality and the size of the habitat. Hence it is important to understand in how far these habitat aspects can be interchanged with respect to their effect on population persistence. The fact that habitat quality always has a higher impact on the population persistence than size, suggests that these aspects are not equivalent and therefore not directly interchangeable. This implies that for example a management strategy that enlarges the area of an endangered population with habitat categorised as bad, may not lower the risk of extinction, but, on the contrary, enhance this risk. Conservation strategies should therefore focus especially on improvement of the habitat quality; if this is not feasible, alternatives must be chosen with caution. In The Netherlands a large number of rural areas are of marginal quality resulting from pollution with toxicants. There is a tendency to use these areas of questionable habitat quality for nature conservation (e.g. Ilperveld and Volgermeer in the province of Noord-Holland, De Venen in the western part of The Netherlands). Given the importance of habitat quality for the persistence of species, addition of these areas to existing reserves may be an erroneous strategy. Common practice in conservation is to assess the viability of field populations by monitoring population density. As shown in chapter 2 the population persistence can decrease drastically with decline in habitat quality whereas the population density remains more or less stable. This implies that the viability of populations is not reflected in the population density by definition. The viability of populations depends on both the number of individuals in the population and their probabilities to reproduce and survive. Chapter 2 emphasises that the likelihood of extinction is even more dependent on these probabilities to reproduce and survive, which can be summarised in the lifetime reproductive output (R_0), than on the population number per se. As a measure of the viability of field populations these processes therefore are more informative than the population density. Moreover, the population density is a resultant of the reproduction and survival of the individuals, and strongly influenced by the dynamic interaction of the individuals with their environment (Hengeveld & Walter 1999). For example in a territorial species such as the common shrew, social interaction within the species for a limited number of territories restricts the number of individuals in the population. The common shrew is an annual species with a high reproductive output. As long as the individuals can replace themselves ($R_0 \geq 1$) all territories remain occupied. Only if the outcome of reproduction and survival leads to values of $R_0 < 1$ the population density is expected to decline. Given the fact that the viability of populations is not unambiguously reflected in the population abundance it follows that monitoring based on species density alone can be misleading. Therefore, the processes that determine the life time reproductive output R_0, that is survival and reproduction of individuals, should be measured in addition to density (van Horne 1983).

Populations of endangered species often consist of small numbers. As a result of their low number, they are trapped in what is called the extinction vortex. This indicates that the combination of inbreeding depression, demographic stochasticity and genetic drift lead to positive feedback loops that make small populations even smaller (Caughley 1994). Management practice directed at conservation of these populations is confronted with the question how large the population size must be to escape the risk of extinction inherent in small numbers. The concept of the minimum viable population (MVP) size aims at resolving this question. The MVP size corresponds to the threshold number of individuals at which the population will exist in a viable state for a given interval of time under the risk of extinction as a result of demographic, environmental and genetic stochasticity, or catastrophes (Shaffer 1981). The MVP size is species-specific since the life history of a species can have a large impact on the outcome of the abovementioned stochastic events (Franklin 1980; Soulé 1980). Moreover, the MVP size will also depend on the temporal and spatial distribution of the habitat (Gilpin & Soulé 1986), and its quality. Since habitat quality has a drastic non-linear effect on the risk of extinction (see chapter 2) this factor has a large impact on the MVP size. As a consequence, the size of MVPs in areas of inferior habitat should be non-proportionally greater than those in good habitat (van Horne 1983). In case of temporal fluctuations in habitat quality, when populations are restricted to island-like habitats (Gilpin & Soulé 1986) or if the habitat quality fluctuates in synchrony over extensive areas (chapter 5), the MVP size should be based on the lowest habitat quality The above considerations on MVP size indicate that a single species-specific MVP size is of little practical use. To overcome this problem species-specific MVP size distributions seem to be a solution. However, the concept of MVP based on size fails since the likelihood of population extinction is more sensitive to the processes of reproduction and survival than to the population number. A better alternative would be to develop a statistic based on both the lifetime reproductive output and the population number.

Risk assessment

The objective in risk assessment is to protect ecosystems from detrimental effects of pollution. In The Netherlands, current methods in ecotoxicological risk assessment are mainly based on laboratory tests at the individual level using a limited number of species. From these single species tests critical toxicant concentrations are derived, beneath which the ecosystem is considered to be protected. The applied derivation method (Aldenberg & Slob 1993) assumes that the species-specific sensitivities to a certain pollutant of the species composing an ecosystem can be expressed by a log-logistic distribution. This log-logistic distribution is constructed if at least four No Observed Effect Concentrations (NOECs) are available, derived from single species tests of different taxonomic groups. From the distribution a Maximum Permissible Concentration (MPC) is derived at the toxicant level where less than a certain percentage (usually 5%) of the species are affected by the pollutant. This method has some serious restrictions since it implicitly assumes that (1) the sensitivity of the populations of each species correlates linearly with the sensitivity of its individuals, that (2) the sensitivity of organisms to toxicants measured under laboratory conditions, in which all circumstances are optimal with the exception of the toxicant, represents the sensitivity under field conditions, and (3) interactions among species are totally ignored.

An obvious, intermediate step to remedy these shortcomings is to evaluate toxic effects at the population level. Population dynamic models as illustrated in this thesis can integrate laboratory results on individuals and assess their population level consequences. Moreover, these models can approximate effects under field conditions by evaluating the effects on the population under different suboptimal environmental conditions. Also the impact of toxicants on interacting species can be assessed to arrive at the consequences at the community level. Models that interpret the effects of toxicants at the population level should be firmly based on the ecology of the species under consideration. Such models should exist of a submodel at the individual level and a submodel at the population level. The first model assesses the effects of toxicants on the individual life history parameters, i.e. growth, development, reproduction and survival. The second submodel at the population level performs a bookkeeping operation to track changes in life history of all individuals composing the population. At the individual level, the energy allocation in organisms changes when they are confronted with toxicants. These changes result from e.g. detoxification or decreased food intake (Kooijman & Metz 1984) and can become apparent in the individual life history as retarded growth and development, or reduced reproduction and survival. To analyse these reductions in a consistent way energy budget models such as the Dynamic Energy Budget model (DEB) (Kooijman & Metz 1984; Kooijman 1993; Kooijman & Bedaux 1996) are essential instruments. The DEB model makes it possible to correlate in a mechanistic way negative effects such as reduced individual growth and reproduction since they are likely to result from the same mode of action of the toxicant on the energy allocation in the individual (see chapters 3, 4 and 6). Given such changes in the individual life history, the impact of toxicants on the population performance can be assessed with discrete- or continuous-time structured models. These population dynamical models can be extended to incorporate the impact of toxicants in a food chain (e.g. chapters 5 and 6) and the impact of toxicants in combination with other stress factors (e.g. chapter 6). In The Netherlands many rural areas are polluted resulting from dumps of industrial and household waste and application of harbour sediments. Given the pollutant levels of these sites high ecotoxicological risks are expected which makes their use for agriculture, recreation or nature doubtful. Insight is needed in the actual risk posed by the pollutants on the local ecosystem. To assess site-specific risks of soil pollution, the model PODYRAS (Population Dynamical Risk Assessment) has been developed which is based on the earthworm models described in chapters 3, 4 and 6. Earthworms are central in the model since they play an important role in the soil ecosystems; they readily accumulate various chemical substances from the soil, constitute one of the central nodes in the food web, and have a large influence on soil processes (Edwards & Lofty 1977; Lawton 1994). The model is parameterised with data from laboratory bioassays on growth and reproduction of earthworms living in the polluted soils of the site. The model can be extended to assess effects in food chains (earthworm-badger, earthworm-godwit) and in the functioning of the soil by assessing the contribution of earthworms in soil processes like decomposition.

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4 Calendar

June 3-8, 2001

6th Int. Conference on Mathematical Population Dynamics, Marrakech, Morocco, June 3-8, 2001
Organized by: The Department of Mathematics, Chalmers University of Technology and the University of Göteborg, Göteborg, Sweden
and Le Centre Internationale de Formation et de Recherche: Systemes Dynamiques Marrakech, Morocco
Call for papers: Research papers on different aspects of population dynamics are solicited from researchers in a very wide range of areas in biology and applied mathematics.
Scope: The purpose of the conference is to serve as an interdisciplinary meeting where biologists and mathematicians discuss issues of mutual interest. Among the invited and keynote speakers, we expect to have the names of some of the most prominent researchers in the area.
Topics: Examples of theme are Cell- and Molecular Biology, Mathematical Ecology, Molecular Population Genetics, Epidemiology and Theory of Epidemics, Mathematical Methods of Population Dynamics, Control Theory, Public Health Issues, Urban Dynamics, Mathematical Demography, Stochastic Models, Biostatistics and Bioinformatics, Spatial Dynamics and any other themes were deterministic or stochastic population modelling is involved.
Location: The conference will take place in a pleasant resort in the beautiful city of Marrakech, Morocco.
Organizing Committee: M. Alexandersson (Berkeley), O. Arino (Paris), E. Aitdads (Marrakech), H. Bouslous (Marrakech), R. Bravo de la Parra (Alcala), H. Hbid (Marrakech), M. Khaladi (Marrakech), B. Kimmel (Houston), U. Olofsson (Göteborg), Z. Taib (Göteborg), M. Yahiaoui (Rabat).
Deadlines: The deadline for pre-registration is January 15 2001. Abstracts must be submitted before January 30 2001.
Information:
Conference secretaries: Marina Alexandersson, Ulrica Olofsson, Ziad Taib,
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