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NONLINEARITY AND ENVIRONMENTAL STOCHASTICITY IN ECOLOGICAL INTERACTIONS

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Abstract: Individuals of natural populations interact with conspecifics, populations of other species and the surrounding physical environment. In addition to demographic stochasticity, these interactions cause the populations to fluctuate both in time and in space. This thesis focuses on modelling and analysing the effects of nonlinearity and environmental stochasticity in ecological interactions. This is done by exploring qualitatively the main characteristics of population abundances mainly by means of numerical simulations and time series analysis. Density-dependent, biotic factors, such as interactions with predators, are often incorporated in population models by using nonlinear functional forms. When more structure is added to one-dimensional difference equations characterizing the dynamics of single-species populations, there are additional possibilities to incorporate density dependence. These other forms of nonlinearities can dramatically change the properties of population dynamics, which is shown in this thesis in the analysis of spatially structured populations and the age-structure of the population. In addition, it is pointed out that nonlinearities, which are usually not taken into account in population models, can give new insight into more applied management questions, such as the causes of stunted growth in fish populations. Moreover, the way in which the interaction between the focal population and its resource is modelled is important. One-dimensional density-dependent population models, where this interaction is modelled only implicitly, cannot cause the other species to become extinct, but in host-parasitoid models, for example, this is a common phenomenon. Finally, we investigate how the dynamics of well-known discrete-time population models are modulated by external factors, e.g., environmental stochasticity. In particular, we focus on how temporal correlation structure of environmental noise influences the correlation structure of population dynamics.

Keywords: theoretical biology, population dynamics, bifurcation theory, age-structured models, spatial models

Academic dissertation

Systems Analysis Laboratory
Helsinki University of Technology

Nonlinearity and environmental stochasticity in ecological interactions

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Publications

The dissertation consists of the present summary article and the following papers:

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[II] Ylikarjula, J., Heino, M., Dieckmann, U. and Kaitala, V. 1999 Density-dependent individual growth simplifies dynamics in age-structured populations. International Institute for Applied Systems Analysis, Interim Report IR-99-51.

[III] Ylikarjula, J., Heino, M. and Dieckmann, U. 2000 Ecology and adaptation of stunted growth in fish. *Evolutionary Ecology*, accepted for publication.

[IV] Kaitala, V., Ylikarjula, J. and Heino, M. 1999 Dynamic complexities in host-parasitoid interaction. *Journal of Theoretical Biology* 197: 331–341.

[V] Kaitala, V., Ylikarjula, J., Ranta, E. and Lundberg, P. 1997 Population dynamics and the colour of environmental noise. *Proceedings of the Royal Society of London, Series* B 264: 943–948.

[VI] Kaitala, V., Lundberg, P., Ripa, J. and Ylikarjula, J. 1997 Red, blue and green: Dyeing population dynamics. *Annales Zoologici Fennici* 34: 217–228.

Preface

This thesis has been carried out in the Systems Analysis Laboratory, Helsinki University of Technology. I wish to thank Professor Raimo P. Hämäläinen, the Head of the Laboratory, for his positive attitude to my work and the opportunity to work in the Laboratory. I am indebted to my supervisor, Professor Veijo Kaitala, for familiarizing me with the field of population biology. I wish to thank him for his encouragement and many enlightening discussions concerning my work. Dr. Hanna Kokko and Dr. Graeme D. Ruxton kindly reviewed my thesis.

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Janica Ylikarjula

1 Introduction

Individuals of natural populations interact with conspecifics, populations of other species and the surrounding physical environment. The characterization of ecological interactions is one of the oldest application fields of mathematical biology. In addition to demographic stochasticity, these interactions cause natural populations to fluctuate both in time and in space. Traditionally, there has been a great controversy whether the population abundances are determined by density-dependent, biotic factors or mainly by the abiotic components of environment such as weather. A. J. Nicholson was one of the advocates of density-dependent processes. He studied species interactions especially host–parasitoid models (Nicholson 1933; Nicholson & Bailey 1935; see also **IV**) and showed with his contemporaries that, for example, cyclic fluctuations of population abundances can be linked to predator–prey or host–parasitoid interactions. Thus, the fluctuations in population numbers could be explained not just by physical factors but also by biotic influences. Andrewartha and Birch (1954) were opposing Nicholson's view and believed that density-dependent processes were of secondary importance. At present, there is an understanding that both density-dependent processes and environmental influences are important: no population is free from regulation and is thus affected by density-dependent factors, but also the surrounding environment of populations can be highly variable (Halley 1996).

One way to analyse the variations in abundances of organisms is to use mathematical modelling. Traditionally, the focus has been on local stability analysis: finding the equilibria and determining the nature of their stability. However, this kind of examination is not enough when we study nonlinear equations because of their complex behaviour (e.g., long or chaotic transients; see Hastings & Higgins 1994). In order to make short-term forecasts of ecological systems, it may be very important to gather a lot of exact measurements and estimate the parameters of the model. Nevertheless, including all the relevant parameters in large simulation models to understand long-term changes in population sizes may be very difficult. Alternatively, the main characteristics of population dynamics can be studied qualitatively (Vandermeer 1993). This is the main method used in this thesis.

Different forms of basic ecological interactions are examined in this thesis in various contexts. Special attention has been paid to the effects of nonlinearities used for modelling density-dependent processes. Relation between individuals of the same species is studied in papers **I**, **II** and **III** and the interaction between two species is examined in paper **IV**. Both these forms of interaction as well as the interplay of the population and its surrounding environment is the focus in papers **V** and **VI**.

2 Intraspecific interactions

Since conspecifics have similar basic requirements, they compete for same limited resources. One characteristic of intraspecific competition is that its effects on the individuals are dependent on the population density. Discrete-time one-dimensional population models are often used to describe the dynamic behaviour of populations with intraspecific competition and non-overlapping generations. The dynamic properties of these mappings have been extensively studied and are well-known. A major breakthrough was achieved by Robert May, who examined simple nonlinear first-order difference equations and showed that they can produce bifurcations and complex dynamics (May 1974, 1976; May & Oster 1976). Thus, the internal dynamics may be an important component, in addition to environmental stochasticity, when we consider the fluctuations of natural time series.

Bellows (1981) examined seven one-dimensional discrete-time population models in order to study their flexibility to produce different forms of density dependence and also their ability to fit to thirty data sets on density-dependent mortality. The qualitative comparison of the models showed that all the one-parameter maps were able to produce only monotonically decreasing curves of proportionate survival against density. The most flexible forms were the Maynard Smith–Slatkin and the Bellows models (Maynard Smith & Slatkin 1973; Bellows 1981) but the Maynard Smith–Slatkin model, which is used in papers **V** and **VI**, fitted better to various data sets. In addition, in many commonly used functional forms for density-dependent growth rate density affects population abundance in an increasingly higher rate as population density approaches zero (Getz 1996). However, it is more realistic to assume that density has the most effect around some other characteristic density above the carrying capacity. This is valid, for example, for the generalized Ricker model and the Maynard Smith–Slatkin model (sometimes called the generalized Beverton–Holt model) (Getz 1996).

Density dependence is incorporated in one-dimensional models by including it to the intrinsic rate of increase or some other demographic parameter. When more structure is added to the models, for example, by including spatially separated populations or the age- or size-structure of population, there are more possibilities to incorporate density dependence. Regarding spatial structure, a population can use its environment in a density-dependent way, that is, exhibit density-dependent dispersal. In age- or size-structured models density dependence can be inserted, for example, to yearly growth increments. These are the focus of the next sections.

2.1 Spatial dimension

Due to human influence, many previously uniform habitats of a wide range of taxa have become fragmented. This process has aroused the attention of many theoretical ecologists, and during the recent decade the role of spatial structure in theoretical population models has been under intensive study.

Incorporating the spatial structure of populations has shifted the emphasis of theoretical ecology away from studies on pure temporal variations of population abundances. Models with spatial structure have been shown to produce complex temporal and spatial patterns which are not observed in one-dimensional discrete-time models. These phenomena include supertransients (Hastings & Higgins 1994), multiple attractors (Hastings 1993; Lloyd 1995) and spatial patterns such as spiral waves (Hassell *et al.* 1991).

Dispersal couples spatially scattered local populations. Hansson (1991) mentions three ultimate causes for dispersal. The first one is economic threshold: if certain resource, for example food, is below a critical level, then dispersal takes place. The second cause is intraspecific conflict over resources and the third one is inbreeding avoidance. The relative importance of these different categories is not evident and is very little studied. These causes may act density-independently or density-dependently. Nevertheless, the emphasis of most of the theoretical studies dealing with space has been on density-independent dispersal, and a common assumption is that a constant fraction of every subpopulation disperses each generation (e.g., Hastings 1993; Doebeli 1995; Lloyd 1995; Udwadia & Raju 1997).

In paper **I**, two forms of density-independent and three density-dependent dispersal strategies are under study. We examine their effects on population dynamics and also on the synchrony in fluctuations of local abundances for two and a larger number of local populations. The results are surprising: there do not seem to be any general differences between the effects of density-independent and density-dependent dispersal strategies neither on the type of dynamics nor on the level of synchrony. However, there are clear differences between different numbers of local populations.

Until recently, most of the theoretical research has concentrated on systems consisting of two local populations due to their simplicity and the possibility to obtain analytical results. However, we show that increasing the number of patches to 25 does not give similar results as two coupled local populations. When studying the case of four patches, we found that already this number of local populations is enough to produce qualitatively similar outcomes as the system consisting of 25 subpopulations. Thus, the applicability of the results obtained from a large number of theoretical papers dealing with only two local populations seems to be rather restricted.

According to our results, the synchrony in dynamics of local populations is very much dependent on dispersal rule, the number of local populations and the intensity of dispersal. The level of synchrony differs also among density-independent and density-dependent dispersal rules.

2.2 Density-dependent individual growth and stunted growth in fish

If demographic properties, such as fecundity or survival, vary with age, it is not advisable to treat all individuals identical but to use age-classified matrix models. These models are a special case of stage-classified models, size-classified models being another example. In this section, age-structured population models are used to describe individuals with indeterminate growth.

One outcome of competition for resources is density-dependent individual growth. Because resource limitation provides less energy for growth, it results in decreased individual growth. Growth increments are usually density-dependent, since higher density of the population leads to a more severe shortage of food. Density-dependent individual growth is especially common in size-structured populations, where differences in size strongly determine the result of competition for resources (Post *et al.* 1999).

What kind of effects does density-dependent individual growth have on population dynamics? This question is addressed in paper **II**. The parameter values are selected to describe Eurasian perch populations. The model, which is used in this study, is developed from the energy allocation model by Roff (1983). The maintenance requirements are assumed to have the first priority. The energy in excess of maintenance is used for somatic growth for immature individuals. For mature individuals a part of this energy is used for reproduction, and the allocation of energy between somatic growth and reproduction is determined by assuming that the gonadosomatic index (ratio between the weight of gonads and somatic weight) is constant. This assumption is valid for many fish species including perch (Roff 1983). A similar model has previously been used by Perrin and Rubin (1990) when studying the age-to-size reaction norms and by Heino and Kaitala (1997a, 1997b) when dealing with optimal maturity in freshwater clams. In our model, a density-dependent individual growth is modelled by using the Beverton–Holt-type functional response (Beverton & Holt 1957).

We study three characteristics of fish populations which produce non-equilibrium dynamics: newborn survival regulation, cannibalism of newborns and cannibalism which is dependent on the relative lengths of fishes. Cannibalism is another intrinsic regulating factor of the population in addition to competition. Cannibalism denotes that larger individuals are preying upon smaller ones of the same species. This is a frequent phenomenon, for example, among many insects (e.g., Costantino *et al.* 1998) and fish (e.g., Thorpe 1974; FitzGerald 1992). The variations caused by the first two characteristics are inherent but the third one produces fluctuations, because some environmental stochasticity is incorporated in juvenile and adult survival probabilities. Adding density-dependent individual growth to these three cases has similar effects on all of them: increasing the severity of the growth limitation decreases the total biomass and also decreases the variation in biomass. In the two cases where the fluctuations are inherent strong density-dependent individual growth can even eradicate the variations in total biomass and produce equilibrium dynamics. Thus, incorporating a density-dependent growth increment to an age-structured model can strongly affect the population dynamics.

A phenomenon related to density-dependent individual growth, stunted growth in fish, is systematically investigated in paper **III**. Stunted growth indicates that individual growth is lower than the potential of the species. This is a phenomenon which is observed in many freshwater fish species (e.g., Burrough & Kennedy 1979; Bodaly *et al.* 1991; Ridgway & Chapleau 1994). Naturally, stunted growth has significant economical effects due to the smaller sizes of the individual fish forming the catch. Still, theoretical investigations of the causes of stunting have been scarce. The phenomenon of stunted growth is studied by using a similar model as in paper **II**. When none of the three factors producing fluctuations in paper **II** is included in the model, the population shows equilibrium dynamics.

Our hypothesis is that the ultimate cause of stunting is resource limitation but that also changes in survival probabilites can affect the length of the fish. The results presented in paper **III** show that density-dependent individual growth produces such lengths of perch which are in good accordance with the empirical findings of normal and stunted perch populations (see Figure 2 in **III** and Figure 7 in Roff 1986). The changes in survival probabilities also affect the length of the fish and can lead to dwarf individuals. One example of this phenomenon is increased survival of larger fish which can be due to decreased fishing pressure. However, stunting does not occur because of these factors alone but requires that individual growth is density-dependent. A better survival of larger fish also increases the total biomass although the lengths of fish are considerably smaller. Hence, the increased survival more than compensates for the decrease in the lengths of fish.

In addition to the immediate ecological effects, the possible adaptive responses to the changes in growth conditions are studied. The evolutionary optimal age at maturity is calculated for different states of growth conditions by using the invasion fitness measure (Metz *et al.* 1992). The simulations show that changes in survival probabilities can indeed alter the age at maturity. Changing the fishing pressure can produce adaptive responses in age at maturity which also have pronounced effects on the length of fish and on total biomass (Figure 3 in **III**). Although pure ecological factors would predict normal-sized fish to be observed, due to evolutionary responses stunted fish individuals would be found. Thus, this study shows that when examining the causes of stunting pure ecological factors may give misleading results.

3 Interspecific interactions

In one-dimensional density-dependent population models the focal population is implicitly assumed to interact with its resource. In a more realistic manner, the dynamics of the other species can be incorporated in the model explicitly. An important difference between single-species and multi-species models is that including the other species explicitly to the model can cause one of the species to become extinct for some parameter values or it can produce such complex dynamics which cannot occur when the resource is modelled only implicitly (**IV**).

The main categories of interactions between species are competition, predation and mutualism. Predation is a classical form of population interactions and the main part of ecological communities (Vandermeer 1993). Here we concentrate on one type of predator–prey interactions, namely, host–parasitoid interactions. There have been many studies dealing with parasitoids due to their economic importance in controlling insect pests. They also provide a simple system where the dynamics common to many consumer–resource interactions can be examined (Godfray & Hassell 1997).

3.1 Host–parasitoid interactions

Parasitoids are a group of insects which are free-living as adults, but they lay their eggs on or in other insects, which makes their reproduction closely dependent on the number of hosts parasitized. The larvae eventually almost totally consume the host and therefore kill it (Hassell 1978). The arthropod host–parasitoid systems have quite distinctive generations, which makes the difference equations suited for describing them.

A widely used general host–parasitoid model (Hassell 1978) has the following form:

$$\begin{aligned} N_{t+1} &= \lambda N_t f(N_t, P_t), & (1) \\ P_{t+1} &= q N_t [1 - f(N_t, P_t)], & (2) \end{aligned}$$

where N_t and P_t are host and parasitoid population sizes in generation t, respectively, λ is the net rate of increase of the host per generation, q is the average number of female parasitoids emerging from each host attacked and function f is the fraction of hosts that survive from parasitism.

Beddington *et al.* (1975) studied the dynamics of a discrete-time host–parasitoid model and observed that it can produce high-period cycles and chaos — more complex behaviour than those detected in continuous-time models. This work was based on the Nicholson–Bailey model (Nicholson 1933; Nicholson & Bailey 1935)

$$\begin{aligned} N_{t+1} &= N_t e^{-AP_t}, & (3) \\ P_{t+1} &= N_t (1 - e^{-AP_t}). & (4) \end{aligned}$$

Parameter A, sometimes called the "area of discovery", is the probability that a certain predator will encounter a given prey during its searching lifetime. Beddington and his co-authors modified the model by introducing a self-regulation of the host in the absence of predators (Beddington *et al.* 1975). Thus, host population size does not grow exponentially without parasitism but, more realistically, it has some other regulating factors. Equations (3)–(4) assume that the functional response (the numbers of hosts eaten per a parasitoid as a function of host density) is of Holling type 1 (Holling 1959) and that encounters between hosts and parasitoids are randomly distributed among the available hosts. Type 1 functional response is, however, not common and insect predator–prey systems exhibit type 2 responses (e.g., Hassell 1978). Random search is a valid assumption especially if we consider a population of parasitoids during longer periods. Otherwise, during a shorter time period a single parasitoid might search regions of high host density (Rogers 1972). The original Nicholson–Bailey model is unstable for all the parameter values — a deviation from a steady state causes the populations of host and parasitoid to oscillate around an equilibrium with increasing amplitude (Hassell & May 1973). Thus, the additional nonlinearity (i.e., the self-regulation of host) has a pronounced effect on the stability and the dynamics of the populations.

Another aspect which can provide the persistence of host and parasitoid populations produced by the Nicholson–Bailey model is the subdivision of environment and the movement of individuals to neighbouring patches (Hassell *et al.* 1991; Comins *et al.* 1992; Solé & Valls 1992). Even a deterministic process where a constant fraction of hosts and parasitoids disperses to adjacent patches may exhibit spatial patterns such as spiral waves and crystal lattices. This pattern formation depends on the dispersing fraction and the number of local populations. The importance of space in host–parasitoid interactions has got support from empiricists reporting that habitat change can affect host–parasitoid population dynamics and that parasitoids influence both the extinctions and the dynamics of host metapopulations (Lei & Hanski 1997; Maron & Harrison 1997; Roland & Taylor 1997).

The host–parasitoid model (Holling 1959; Royama 1971; Rogers 1972) considered in this thesis (**IV**) has the same assumptions as in Beddington *et al.* (1975) apart from the form of functional response, which is now assumed to be of Holling type 2. In this modification of the model, we have also assumed that the net rate of increase of the host per generation is not constant but exhibits dynamics according to the Ricker model (Ricker 1954). The average number of parasitoids emerging from each host is assumed to be one, which is common for insects (e.g., Hassell 1978). One aspect not considered in this model is the mutual interference between parasitoids, which increases with parasitoid density and reduces the searching efficiency. The other factors not examined here are a search-limited encounter rate (e.g., Nicholson & Bailey 1935; Hassell & May 1988) and an egg-limited encounter rate (Thompson 1924; Getz & Mills 1996). A search-limited encounter rate takes into account that the encounter and attack rates of parasitoids are limited by their efficiency to search hosts and an egg-limited encounter rate considers also the limitation of parasitoids to produce eggs when the host is very abundant. It has been reported that spatial heterogeneity promotes the stability of host–parasitoid interactions in search-limited encounter rate models without the self-regulation of host (e.g., Pacala *et al.* 1990). However, if also the egg-limited encounter rate is included, some additional restrictions are needed on the growth rates of host and parasitoid populations for the stability of the interaction (Getz & Mills 1996).

Without the self-regulation of host population the model presented in paper **IV** is always less stable than the Nicholson–Bailey model (Hassell & May 1973). The Nicholson–Bailey model is a special case of this model and can be obtained if the parasitoid's handling time is set to zero. In paper **IV**, a two-dimensional bifurcation analysis is conducted by using the instantaneous search rate of parasitoids and the intrinsic rate of increase of hosts as bifurcation parameters (for a detailed review of bifurcations, see Kuznetsov 1994). For a rather large range of parameter values (see Figure 1 in **IV**), the coexistence of host and parasitoid is not possible but the parasitoid goes extinct. This occurs, for example, for low instantaneous search rates of parasitoids. Increasing the intrinsic growth rate first produces stable dynamics and with higher values more complex dynamics: periodic, quasiperiodic or chaotic attractors. Other complexities displayed by the model include, for example, multiple attractors, fractal basins of attraction, intermittency, supertransients and chaotic transients. The complexity of the dynamics of final attractors, the non-uniqueness of these attractors, the complexity of transient behaviour and the sensitivity to changes in parameter values call for awareness and caution when studying even basic interspecific interactions. These phenomena have previously been detected in models from various disciplines. However, here we show that this wide range of dynamics may occur in basic predator–prey models. This implies that they have to be taken into account when we examine the dynamic behaviour of ecological systems.

4 Effects of environmental stochasticity

In addition to density-dependent processes and demographic stochasticity, environmental variations affect population abundances. Environmental stochasticity refers to the random temporal variations of the surrounding physical environment, such as fluctuations in weather conditions. Environmental stochasticity affects the population, for example, through changes in the dynamics of its resources. Due to simplicity, in many theoretical models this is incorporated by adding random variation to one parameter of the model.

Robert May (1973) studied the relation between models where parameters are either constants or fluctuate randomly about some mean value. He showed that if the stabilizing influence of the interactions is strong compared to the effects of random environmental variations, for many practical purposes, the population dynamics are indistinguishable from the deterministic model. However, he noted that there are cases where even the smallest environmental fluctuations produce results which are qualitatively different from the corresponding deterministic system. Schaffer *et al.* (1986) added stochasticity to one-dimensional maps as well as to finite dimensional flows and investigated their effects on the population dynamics. They showed that including noise to systems exhibiting high-period cycles or chaos did not hidden the underlying deterministic system. However, this was the case for equilibrium dynamics.

Many discrete-time population models which have more than one dimension show fractal basin boundaries (see e.g., Kaitala & Heino 1996; **IV**). An important question is whether a part of this structure persists when environmental stochasticity is added. Hastings (1993) studied this question and showed that even after including some environmental fluctuations there still existed a sensitive dependence on initial conditions. Naturally, increasing the variance of environmental stochasticity would probably erase the fractal structure of basin boundaries. The temporal structure of environmental stochasticity is studied in Section 5.

5 Ecological colour problem

The importance of basic ecological interactions and environmental stochasticity is observed in this section dealing with so-called ecological colour problem. This problem addresses the discrepancy between the patterns of temporal autocorrelation of one-dimensional population models and many ecological time series. Different forms of interactions studied in this summary are used to shed light on this question. First, in the next subsection some concepts and tools, which are used in this context, are presented.

5.1 Time and frequency domain

One way to characterize the variations in ecological time series is to study the temporal autocorrelation function of the population fluctuations. Autocorrelation function shows how much temporal correlation there is between the adjacent data points. Positive autocorrelation indicates that the neighbouring values are more matching than expected merely by chance (Fig. 1a), whereas negative autocorrelation exhibits more zigzag fluctuations (Fig. 1b). There are also other ways to characterize the variations in ecological time series. These include the Hurst exponent (for details, see Ariño & Pimm 1995), the iterated function system (for details, see Miramontes & Rohani 1998) and the power spectrum through Fourier transform (Cohen 1995).

Since power spectra are used in most of the studies mentioned in this section and in papers **V** and **VI**, it is explained here in more detail. The standard Fourier transform expresses the time series as a sum of multiples of simple periodic functions, sines and cosines, at the fundamental frequency and its harmonics (Hastings & Sugihara 1993). The set of the coefficients in a Fourier transform is called its spectrum. The discrete Fourier transform (DFT) is a discrete-time analogue to the standard Fourier transform and can be expressed as complex exponential functions. DFT requires only a finite number of data points and, thus, is more suited for analysing the time series of population abundances.

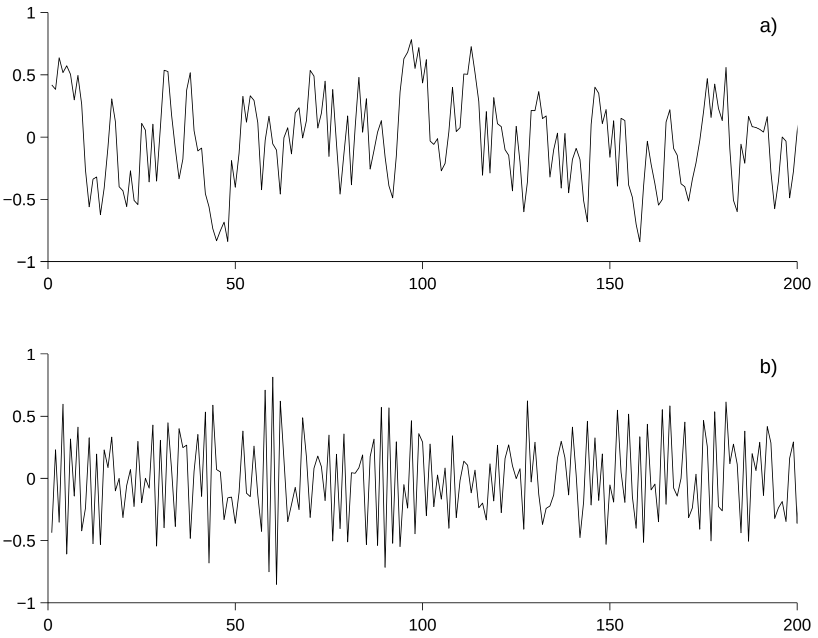

Figure 1: Simulation of a first-order autoregressive process (AR(1)), $d_{t+1} = cd_t + w_t$, where w_t is uniformly distributed between [-0.5,0.5]. a) Positive autocorrelation ($c = 0.5$) and b) negative autocorrelation ($c = -0.5$).

Let $x(t)$ be the time series studied, where $t = 0, 1, 2, ..., N-1$. In population biology, $x(t)$ is usually the population size or density in generation t. The DFT of $x(t)$, $X(f_k)$, is defined as

$$X(f_k) = \sum_{t=0}^{N-1} x(t) e^{-i2\Pi f_k t}, \tag{5}$$

where $f_k = \frac{k}{N}$, $k = 0, 1, ..., N-1$.

The power spectrum of Fourier transform is $P_x(f_k) = \frac{1}{N}|X(f_k)|^2$, which is essentially the sequence of squares of the amplitudes of the spectrum. Thus, power spectra reveals the proportional "intensity" of different frequences by decomposing the time series into spectral frequences.

By analogy with the wavelength composition in light, if the time series is dominated by low-frequency variations, that is, the amplitudes of long wavelenghts are more prominent than the amplitudes of shorter wavelenghts (positive temporal autocorrelation), it is called red. Similarly, if it is dominated by high-frequency fluctuations (negative temporal autocorrelation), it is called blue and if there are no particular frequencies that dominate, the time series is said to be white.

5.2 Red data

Several data on natural animal populations show dominance of low-frequency fluctuations (Ma 1958; Diamond & May 1977; Pimm & Redfearn 1988; Ariño & Pimm 1995; Sugihara 1995; Halley 1996). Also three classic laboratory time series exhibit red spectra (Miramontes & Rohani 1998). What is the cause behind this? Several suggestions have been put forward to explain the redness of the animal populations. These include both external and internal factors. The effect of external forcing means that abiotic physical variables of the environment can tinge the population abundances with red (Steele 1985; Pimm & Redfearn 1988; Ariño & Pimm 1995; **V**, **VI**). Also the spatial structure of the populations (White *et al.* 1996a; 1996b) may affect the frequency distribution of the population densities. Internal effects include, for example, population-level (McArdle 1989) and community-level explanations (Pimm & Redfearn 1989; Kaitala & Ranta 1996, Ripa *et al.* 1998; **VI**).

Steele (1985) examined the records of both terrestrial and marine physical variables, such as temperature, and observed that marine environment shows red dynamics and terrestrial environment white up to several decades and after that red spectrum. For example, the temperature capacity of the ocean is better than the capacity of air and, thus, the fluctuations of marine temperature are "slower" than the ones exhibited by air temperature. Also geophysical records show reddened spectra (Mandelbrot & Wallis 1969).

Many marine ecosystems show stronger reddening than terrestrial ecosystems in a similar fashion as the physical environment itself (Ariño & Pimm 1995). This implies that the environment of the population might affect the temporal correlation structure of the population abundances (Ariño & Pimm 1995; Sugihara 1995). However, the fact that also laboratory populations show red spectra (Miramontes & Rohani 1998) indicates that it might not only be environmental variability but some intrinsic factor which causes the redness of the animal time series. McArdle (1989) gave another explanation for the redness of the population time series by pointing out that the same animals may be present for adjacent censuses and, thus, may increase the positive temporal correlation of the time series. Of course, there might be several causes which bring about the observed temporal autocorrelation of population abundances.

5.3 Blue models

Joel Cohen (1995) examined eight nonlinear, deterministic, discrete-time population models and studied their power spectra for parameter values producing chaotic dynamics. He found that they all produce blue spectra, that is, short-term fluctuations are more prominent. The discrepancy between ecological time series having red spectra and simple models producing blue spectra has aroused a lot of attention. This so-called ecological colour problem is reviewed in paper **VI**. Several explanations have been suggested to cause this difference. Blarer and Doebeli (1996) pointed out that the results of Cohen were shown only for a limited choice of parameter values and that red spectra can be observed especially for intense competition. Sugihara (1995) gave three possible causes to the problem: natural populations are not chaotic, the models used by Cohen (1995) are flawed or environmental forcing needs to be considered.

Also ecosystem structure can affect the temporal autocorrelation. For example, delayed density dependence, which is often used to describe the interaction with other members of the community, reddens the otherwise blue spectra (Kaitala & Ranta 1996). This is also the case for adding explicit spatial structure to the models (White *et al.* 1996a, 1996b).

As suggested by several authors, environmental forcing may strongly influence the colour of the population dynamics (Steele 1985; Ariño & Pimm 1995; Sugihara 1995). We examine the effect of coloured environmental noise on the colour of population dynamics for the Ricker and the Maynard Smith–Slatkin models (**V**, **VI**). The basic Ricker model cannot produce red spectra unlike the Maynard Smith–Slatkin model (White *et al.* 1996a). The effect of the coloured environmental noise on the colour of population dynamics depends strongly on the system parameters such as the intrinsic rate of increase and the strength of competition. For the Ricker model and for the Maynard Smith–Slatkin model with higher growth rates, the effects of differently coloured environmental noises are notably distinct for parameter values which produce stable or periodic dynamics without environmental noise. Population dynamics subjected to red or blue noise show redder or bluer spectra, respectively. However, the differences diminish as the intrinsic growth rate or the strength of competition increases and the dynamics show chaotic fluctuations in the basic model. For the Maynard Smith–Slatkin model with lower growth rates, the spectra is always red irrespective of the strength of competition or noise colour. Because the deterministic Maynard Smith–Slatkin model can exhibit blue spectra with low growth rates, blue dynamics may become red due to environmental noise but the opposite, red becoming blue, was never observed. Especially, the colour of the environmental noise does not have to have red spectra to tinge the population dynamics with red (Balmforth *et al.* 1999; **V**, **VI**). White *et al.* (1996b) showed that some of the models used by Cohen cannot produce red dynamics. However, we have shown that introducing environmental noise to the system may redden or at least whiten the spectrum of population dynamics.

5.4 Effects of noise colour

No matter what is the cause for the redness of animal data there is a rather convincing evidence that the spectrum of many physical variables is red as mentioned in Section 5.2. However, in population biology environmental stochasticity is most often modelled as white noise with no temporal autocorrelation. How do the effects of red environmental noise differ from the ones produced by white noise? One factor which makes the comparison between white and red noise difficult is that the variance of different coloured time series is similar only at certain time scale (Heino *et al.* 2000).

Coloured environmental noise is mostly modelled as a first-order autoregressive process (e.g., Ripa & Lundberg 1996; Johst & Wissel 1997; Petchey *et al.* 1997; Heino *et al.* 2000; **V**, **VI**). However, pink $1/f$-noise has been suggested to best describe environmental stochasticity (Lawton 1988; Halley 1996; Miramontes & Rohani 1998). The variance of pink noise increases with increasing the length of time series. In an autoregressive process the temporal correlation declines exponentially between two events with their separation in time but in $1/f$-noise it falls off as a power law (Halley 1996).

As mentioned in Section 5.3, noise colour can affect the colour of the spectrum of population abundances (**V**, **VI**). Several papers have also dealt with an important conservational question: what are the effects of coloured noise on extinction risk (e.g., Ripa & Lundberg 1996; Johst & Wissel 1997; Petchey *et al.* 1997; Heino 1998; Heino *et al.* 2000; **VI**). Intuitively, one would expect that the risk of extinction is too optimistic when white noise is used because with red spectra a bad year is likely to be followed by another bad year (Lawton 1988; Pimm & Redfearn 1988; Halley 1996). These intuitive reasonings are supported by Johst and Wissel (1997) and Petchey *et al.* (1997). However, Ripa and Lundberg (1996) showed that red environmental noise produces a lower risk of extinction and that the route to extinction occurs very often through high population abundances. Similar results were shown earlier by Roughgarden (1975). Petchey *et al.* (1997) came to the conclusion that spatial structure and undercompensatory dynamics are factors which increase the extinction risk under red noise. However, Heino *et al.* (2000) showed that this is not a general result but depends on the scaling of the expected variance of noise — increasing the autocorrelation of the environmental noise may increase or decrease the risk of extinction. The effects of also $1/f^{\beta}$ noises, where $\beta > 1.5$, on population persistence are studied by Cuddington and Yodzis (1999). The extinction risks in spatially structured populations have been reported by Heino (1998). He found that red-shifted noise increases the global extinction risk but the effects on population synchrony are dependent on how the environmental noise is incorporated in the model.

The colour of environmental noise can also affect population dynamics (Steele & Henderson 1984). Many pelagic fish stocks show strong fluctuations in size with intervening periods of rather constant abundances. One explanation put forward is that these fluctuations are shifts between alternative equilibrium states. Steele and Henderson simulated a simple population model which describes fish populations and studied the effects of white and red environmental noise on population dynamics. If the environmental variations were modelled as white noise, population adundance fluctuated around a point which was between the two equilibria produced by the deterministic model. For red noise, the fish stock varied between the two equilibria in a qualitatively similar way as suggested by the observations. Thus, the noise colour affects significantly the qualitative properties of the dynamics. Caswell and

Cohen (1995) observed that red spectrum also reduces local diversity by diminishing the possibilities for species coexistence.

There is a great need for the empirical testing of the hypotheses put forward by theoretical studies. Laboratory conditions provide an important opportunity, for example, to control environmental conditions and, thus, to test the effects of environmental noise on population dynamics. A novel apparatus has already been proposed (Cohen *et al.* 1998).

6 Concluding remarks

This thesis consists of studies which deal with ecological interactions and how density-dependent factors and environmental stochasticity could be incorporated in population models and which are their effects on population dynamics. Different modelling approaches can have important consequences. For example, including density dependence in individual growth increments (**II**) and the self-regulation of host population in host–parasitoid interactions (**IV**) can dramatically change the dynamics of the system. Also nonlinear effects, which are usually not taken into account in population models, can give new insight into more applied management questions, such as the causes of stunted growth in fish populations (**III**). Moreover, the manner in which the interaction of the focal population and its resource is modelled is significant. For example, modelling this interaction explicitly can produce complex dynamics and the extinction of one species (e.g., **IV**), which cannot occur if the interaction is modelled only implicitly.

The relevance of complex dynamics predicted by simple models has been a major challenge in population ecology ever since Robert May published his seminal paper on chaotic dynamics (1976). In nature many populations are surprisingly stable, but there are also many indications of more complicated dynamics. For example, northern populations of grouse (e.g., Bergerud 1970; Lindén 1988, 1989) and voles (e.g., Hanski *et al.* 1993; Turchin 1993) as well as Hudson Bay Company's classical data on lynx fur returns (Elton & Nicholson 1942) show regular cycles. Existence of more complex dynamics in wild populations has been controversial. The very influential work concerning the possible existence of chaos in natural ecosystems was done by Hassell *et al.* (1976). Their analysis dealt with data of four laboratory and 24 wild insect populations. The main result of the paper was that most wild populations have densities that return to equilibrium following a disturbance, that is, these populations are stable. Only one wild insect population showed cycles and none was chaotic. Among laboratory insect populations one exhibited chaotic dynamics, two of them cycles and one dampened oscillations. However, some defects were found from the model Hassell *et al.* used. For example, it incorporated only direct density dependence (Prout & McChesney 1985; Turchin 1990). Turchin examined population dynamics of 14 forest insects and deduced that eight data sets indicated a clear evidence of delayed density dependence.

The laboratory experiments with flour beetle (*Tribolium castaneum*) done by R. F. Costantino and his co-workers have given a new insight into the question of the complexity of natural and laboratory populations (Costantino *et al.* 1995, 1997, 1998; Dennis *et al.* 1995; Desharnais *et al.* 1997). The authors showed experimentally that changes in demographic parameters (e.g., fecundity and survival) may cause qualitative changes in the behaviour of the population in a similar manner as predicted by a simple nonlinear age-structured model. This has given an insuring evidence of the importance of nonlinear mathematics in population biology and the ability of feasible mathematical models to predict changes in the dynamics of ecological systems (Rohani & Miramontes 1996; Rohani & Earn 1997). However, there are caveats relating to modelling population dynamics as shown in this thesis. Basic models of ecological interactions can exhibit complex dynamics of transient phase and final attractor, sensitivity to changes in initial conditions and parameter values as well as temporal autocorrelation which is not in accordance with the correlation structure of ecological time series. These phenomena require caution when investigating and using these models.

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