

**From pattern to process:
Extracting ecology from time series**

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Forord

Denne hovedfagsoppgaven ble fullført med Nils Chr. Stenseth (UiO) som hovedveileder, og Tore M. Jonassen (HiO) som biveileder. Utgangspunktet for oppgaven var modellen som presenteres og et fokus på synkroni mellom atskilte populasjoner. På grunn av antallet parametere i modellen ble det etter hvert klart at det var vanskelig å si noe generelt om synkroni, og under prosessen har oppgaven derfor endret seg til mer å omhandle økologien som er ment å ligge i modellen.

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Abstract

Patterns in time series are observational records of past ecological processes, and identifying these processes remains a major challenge to population ecologists. Until recently, analysis of time series has concentrated on statistical description of density dependent structure of patterns, while the ecological factors that underlie the structure remain to a large part unknown. In this thesis, mechanistic properties of a model building on existing statistical framework are explored and discussed. By incorporating a two species trophic interaction and seasonality, the model may allow for direct ecological interpretation of density dependence. General model dynamics are explored and the biologically relevant parameter space identified. It is further shown that the relative length of summer/winter can have profound consequences for model dynamics, and very possibly force populations between regions of stable, cyclic and unstable dynamics. Supposing that the model can adequately describe the outcome of biological interactions, it is fitted to a large set of time series of voles from Hokkaido, Japan. From qualitative properties of six independent estimates of model coefficients, inferences are done about the parameter aggregates that constitute these coefficients. Inferences from two different ecological scenarios; predator-prey and grazer-vegetation, are then compared with the parameter space found appropriate from when studying the general model dynamics. Under specified assumptions, support is found for that signals in the time series are a result of an interaction between vole and its food resource.

Introduction

After almost a century of research, population ecologists have still not resolved what is frequently termed as the ‘enigma of cyclic populations’. Cyclic is here shorthand for multiannual periodic fluctuations in abundance, seen in classical examples such as e.g. small rodent cycles (Elton 1924) and the Canadian lynx cycle (Elton and Nicholson 1942). The enigma may be separated loosely into two parts. First, we have the (lack of) identification of mechanisms underlying the cycles on a local scale. These mechanisms can be of both exogenous (arising from outside the community) and endogenous origin (resulting from biological interactions), and when identified they must explain why some populations are cyclic and others are not, how populations may lose their cyclic behaviour, and of course the regularity and length of the cycle period. The second part refers to the synchrony occurring between seemingly distinct populations across large geographical areas (recently reviewed in Liebhold et al. 2004). Both exogenous and endogenous factors may play a role also here (Huitu et al. 2005), and again identified causes must explain how and why the synchrony arises or not.

Three more or less distinct research strategies have been used when studying population cycles: (i) experimental and observational studies that look directly at processes that might cause cycles, (ii) studying mathematical models that are explicitly biological and that contain the mechanisms or processes that are believed to generate the cycles, and (iii) time series analyses by statistical means with an emphasis on identifying density dependent structure. Although experimental/observational studies supply biological plausible causes of cycles, and is indeed the only way to test the hypotheses regarding these, the approach taken here will be a mixture of the two latter strategies. The idea is to take into account factors that are believed to be important in generating and synchronising cycles and model them within a statistical framework. These factors include self-limitation, a trophic interaction and alternation between seasons of varying length. This is, as far as I am aware of, the first attempt of deriving mechanistic properties from a model that connects directly to the statistical procedures used to study the patterns in time series. Once the model structure is given, its dynamical properties will obviously depend entirely on the values of parameters (or aggregates of these),

which in turn can be estimated statistically by fitting the model to data. Whenever estimated parameters give unrealistic model properties, we may question the appropriateness of the model and/or the factors that enter into it. Following several earlier studies (Bjørnstad et al. 1995; Stenseth et al. 1998*b*), the choice of framework here is an autoregressive (AR) model where interactions are assumed to be linear on a logarithmic scale. This sets limits to the structural complexity of the model and therefore also to the degree of biological realism, but has the advantage of being a widely used and well understood framework. Mechanistic interpretation of a model will then give explicit ecological interpretations of the statistically determined coefficients that result from fitting the model to data. In the following sections I discuss the limits to building a biological model within the framework, before presenting the full model. From there I will go on to investigate the general dynamics of the model with the aim of limiting the parameter space to a set appropriate for the model. Finally, I will confront statistical estimates of model coefficients (from real data) with predictions arising from this limited parameter space.

The Model

The Framework

Many single species models are available, but the one typically fitted to single species time series is an AR(p) model, i.e. of the form:

$$N_t = \alpha_0 + \alpha_1 N_{t-1} + \alpha_2 N_{t-2} + \dots + \alpha_p N_{t-p} + \varepsilon_t,$$

where N_t is the (often transformed) value of the observation at time t , the α_i are coefficients that are estimated from the time series, and ε_t is a white noise term. The number of lags (the order; here p) included in the model is determined on the basis of the partial autocorrelation function (Royama 1992; Chatfield 1999), or the partial rate autocorrelation function (Berryman and Turchin 2001). In biological literature the coefficient of the first lag (α_1) enters into what is often termed as (direct) density dependence (DD). DD is then equivalent to $[\alpha_1 - 1]$, and thereby reflects the dependency of growth on abundance. DD has previously been associated with processes such as intra- and interspecific competition (e.g. Stenseth et al. 1996a; Hansen et al. 1999) and generalist predation (e.g. Bjørnstad et al. 1995). The coefficients of larger lags are a direct measure of delayed density dependence (DDD); the effect of past time densities on current growth. DDD is necessary for a linear difference equation to display cyclic dynamics with a period larger than two (Royama 1992), and indeed, significant coefficients for larger lags have been found for many time series (Moran 1953a; Turchin 1990; Bjørnstad et al. 1995; Stenseth et al. 1996b; Murúa et al. 2003). For annual time series it is usually sufficient with two lags (Moran 1953a; Royama 1992; Bjørnstad et al. 1995; Stenseth et al. 1996b; Murúa et al. 2003) to describe the observed pattern, producing a second order model that is the foundation for the model to be presented.

Of all factors that are thought of as influencing population dynamics, three are explicit in the model to be presented. The first is self-limitation within the species, widely accepted as an important part of an organism's ecology, and has the effect of reducing population growth as density increases. This is an instantaneous process, meaning that its influence will affect the dynamics within a relatively short period of time, and with an AR model this is equivalent to a first order model. The second factor, and the one likely to produce the delay necessary for generating multiannual cycles, is a trophic interaction

(Stenseth 1986; Turchin 2003). This has effects working on both short and longer time scales, where the former is due to the direct action involved, and the latter through delayed feedback effects channelled through the other species. All populations are to some degree influenced by what it consumes and by what consume it, and these two levels of trophic interaction have both been suggested as the driving force behind cycles (e.g. Turchin et al. 2000; Hanski et al. 2001). Incorporating two trophic levels that both influence the growth of each other into one model gives a pair of coupled first order equations. These can then be reduced to the single species second order model needed to describe multiannual cycles. This will be shown in a later section. The third factor is seasonality, envisaged here as winter and summer. Although the species' growth function is structurally identical throughout the year, the parameters that enter it are season specific, and the time span (season length) over which each parameter set operates will affect the dynamics of the whole system. Different relative lengths of season may thereby put one of two, otherwise identical populations, into a cyclic region of dynamics and the other into a stable region. A trophic model consisting of two coupled first order equations is thereby extended to one of four equations, one for each trophic level for each season. Seasonality will as mentioned affect the populations on a local scale, but it is also related to the second part of the enigma by being a potential synchronising agent of geographically distant populations. The populations can then be thought of as connected through a correlation in an exogenous factor (similar season length) perhaps leading to a synchronisation of otherwise asynchronous populations. Such an effect has been shown to be true for additive correlated exogenous factors (Moran 1953*b*). This effect will not be addressed in this work, but it is worth noting that the extension is readily available within this framework.

Biology within the framework

The restriction of linearity on a logarithmic scale is decisive of how factors are incorporated into the model. Self-limitation in a single-species AR(1) model for log-abundances produces a discrete version of the model of Gompertz (1825). It may be expressed as $\left[N_{t+1}/N_t = e^{a_0} N_t^{-a_1} \right]$ (May et al. 1974, my notation), or rearranged on the logarithmic scale as $\left[n_{t+1} = a_0 + (1 - a_1)n_t \right]$, exposing the AR(1) structure. N_t is species

abundance, $n_t = \ln(N_t)$ and a_0 and a_1 is the maximum per capita rate of increase and the strength of self-limitation, respectively (Throughout the thesis uppercase letters will denote untransformed variables and lower case log-transformed variables).

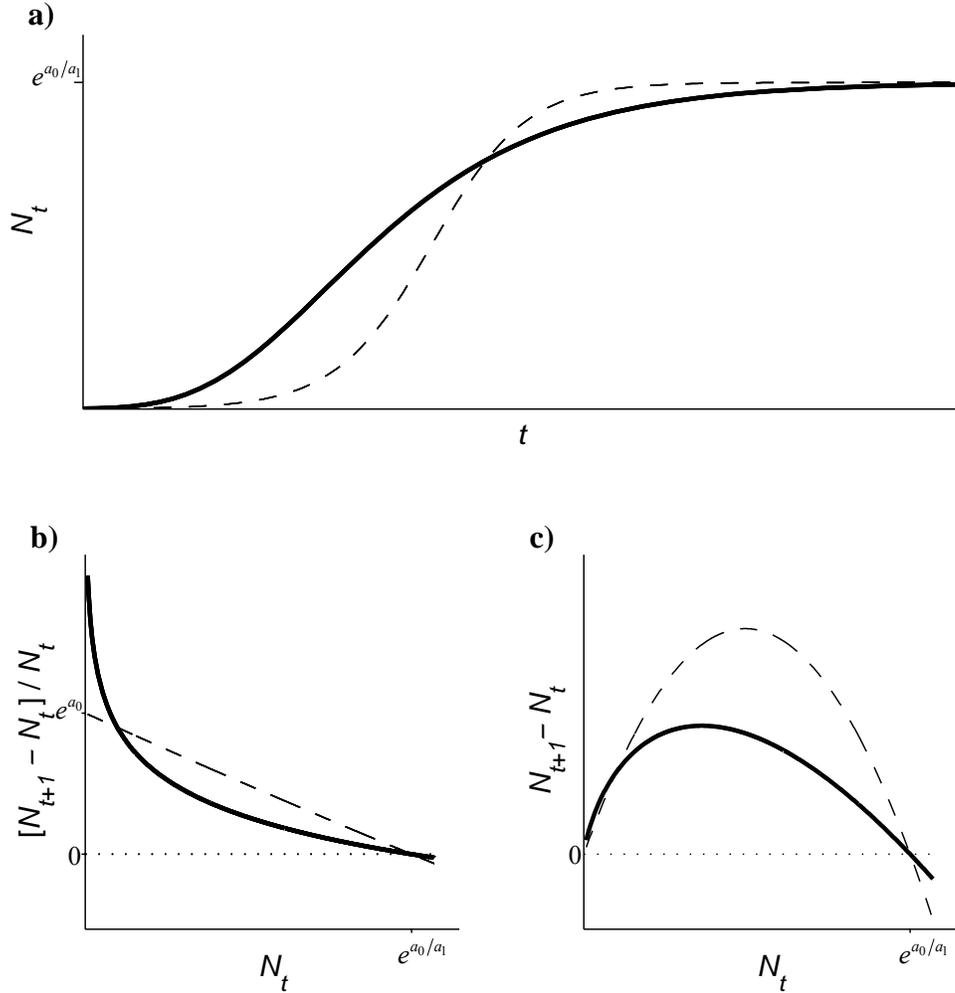


Figure 1: Some properties of the Gompertz growth function $[N_{t+1} = e^{a_0} N_t^{1-a_1}]$ (solid line) compared to the discrete logistic growth function $[N_{t+1} = N_t e^{a_0(1-N_t/K)}]$ (broken line). **a)** Population growth through time, **b)** Per-capita growth rate as a function of population size, and **c)** Population growth as a function of population size. Parameter values are chosen to facilitate comparison; $a_0 = 0.09$, $a_1 = 0.035$, $K = e^{a_0/a_1}$.

This model has previously been used to test for density dependent mortality (Morris 1959; Varley and Gradwell 1970), and stability conditions have been discussed by (May et al. 1974). I must emphasize that this self-limitation (through e.g. behaviour) is not due to interactions with the other species explicitly modelled, and will therefore have slightly

different ecological interpretations for the consumer and the resource (for the latter the self-limitation will include all resource competition). A summary of some properties of Gompertz growth is given in figure 1. In the single species situation, per-capita growth declines as a power function of density, i.e. growth is a decreasing, convex function of density (fig. 1b). This expresses more severe self-limitation at low densities than the traditional logistic models (e.g. the Ricker model (Ricker 1954)), and a more gradual decline in growth as saturation level is approached. Good empirical descriptions of growth versus density for experimentally manipulated populations are surprisingly rare in the literature, but convexly decreasing growth has been observed for voles (Turchin 1999; Aars and Ims 2002, their figure 2). Another conspicuous feature of the growth function is the unbounded per-capita growth as densities approach zero, indicating a lack of realistic descriptive properties at very low densities (Reddingius 1968; Hassell 1975). This feature will not necessarily seriously affect the population growth when the strength of self-limitation is sufficiently low (fig. 1c), but the biological soundness of the model will be sensitive to low values ($N \rightarrow 0$) in a data set.

The addition of the trophic interaction onto the Gompertz growth equation is done in a straightforward manner, which exemplified by the resource turns the growth function into $\left[N_{t+1}/N_t = e^{a_0} N_t^{-a_1} P_t^{-a_2} \right]$, or with the log-linear AR structure:

$\left[n_{t+1} = a_0 + (1 - a_1)n_t - a_2 p_t \right]$. P_t is consumer abundance, $p_t = \ln(P_t)$, and a_2 is a positive parameter controlling the strength of the trophic interaction. A similar model will apply for the consumer, but the sign in front of the trophic interaction parameter changes to positive as the resource will have positive effect on the consumer. Modelling consumption in this manner makes it hard to isolate the effect of a given number of consumers on the resource (and vice versa) due to the interaction with self-limitation. However, if we imagine populations that are not subject to self-limitation ($a_1 = 0$) and ignore growth, we may illustrate a consumer functional and numerical response. Figure 2a shows the former as the amount of resource that would be removed by different consumer densities between two time steps and the latter (fig. 2b) by means of resource density's effect on consumer per-capita growth. From the steady increasing linear functional response it is obvious that beyond some large resource density consumption will be exaggerated. In effect the model proposes that a given amount of consumers will

remove a given proportion of the resource irrespective of initial resource availability. This exaggeration may to some degree be counter balanced by noticing that individual consumers become less efficient as they become more abundant, i.e. per-capita consumption levels off as consumer density increases. The biological interpretation of this predator dependent response would be that consumption is not restricted by resource handling time, as in a ‘type 2’ functional response (see e.g. Begon et al. 1996), but by consumer interference or a response in the resource affecting its catchability (Abrams and Ginzburg 2000). Although consumer numerical response continues to increase for all resource densities, thereby giving no upper limit to consumer population growth potential, it quickly levels off, i.e. the additional gain to consumer growth at higher resource densities becomes smaller. Biological inconsistent model behaviour for very low abundances is also evident in the trophic interactions: the consumer will have a positive effect on resource (when $P < 1$), and the resource will have a negative effect on consumer growth (when $N < 1$).

From this assessment of the model’s ability to describe biology, it is clear that there is an inherent lack of realism for abundances close to zero. Disregarding this, the qualitative features of a consumer-resource interaction seem to be in place.

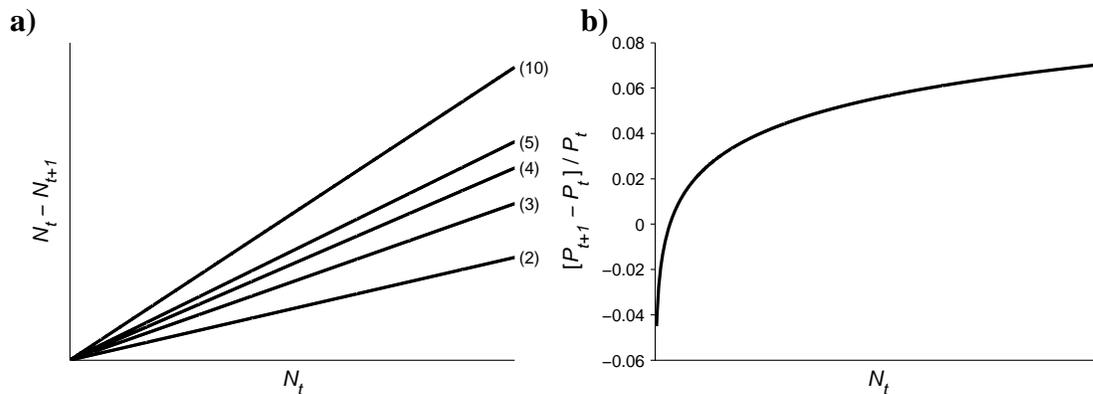


Figure 2: Model properties concerning the trophic interaction when self limitation and reproduction is taken out. **a)** The consumer functional response for different consumer densities (number in brackets), evaluated from $[N_{t+1} = N_t P_t^{-a_2}]$, **b)** The consumer numeric response, evaluated from $[P_{t+1} = P_t N_t^{b_2}]$. Parameter values are chosen so as to emphasize function properties; $a_2 = 0.2$, $b_2 = 0.02$.

The full model

Consider a year consisting of summer and winter, and let N and P be the abundances of the resource and the consumer respectively, at the transitions between the two seasons. The model may be presented as:

$$\begin{aligned}
 N_{f,t} &= N_{s,t} \exp \left\{ \left[a_{s0} - a_{s1} \ln(N_{s,t}) - a_{s2} \ln(P_{s,t}) + \varepsilon_{s,t}^n \right] \tau \right\} \\
 P_{f,t} &= P_{s,t} \exp \left\{ \left[b_{s0} - b_{s1} \ln(P_{s,t}) + b_{s2} \ln(N_{s,t}) + \varepsilon_{s,t}^p \right] \tau \right\} \\
 N_{s,t} &= N_{f,t-1} \exp \left\{ \left[a_{w0} - a_{w1} \ln(N_{f,t-1}) - a_{w2} \ln(P_{f,t-1}) + \varepsilon_{w,t}^n \right] (1-\tau) \right\} \\
 P_{s,t} &= P_{f,t-1} \exp \left\{ \left[b_{w0} - b_{w1} \ln(P_{f,t-1}) + b_{w2} \ln(N_{f,t-1}) + \varepsilon_{w,t}^p \right] (1-\tau) \right\}
 \end{aligned} \tag{1}$$

The first pair of equations describe the abundance of each of the interacting species at the end of the summer season (subscript f for fall) in year t , as the abundances at the start of summer of the same year (subscript s for spring) multiplied with the subsequent growth in summer (the exponential function). Likewise the second pair of equations describe abundances at the end of winter as a function of abundances in the preceding fall (year $t-1$). All the parameters in the equations are thereby season and species specific (a_{ij} affects resource growth, b_{ij} affects consumer growth, $i \in \{s \text{ (summer)}, w \text{ (winter)}\}$, $j \in \{0, 1, 2\}$). A diagram showing the relationships between the seasonal abundances and the parameters governing them is given in figure 3, and a table summarising all notation is included in Appendix A.

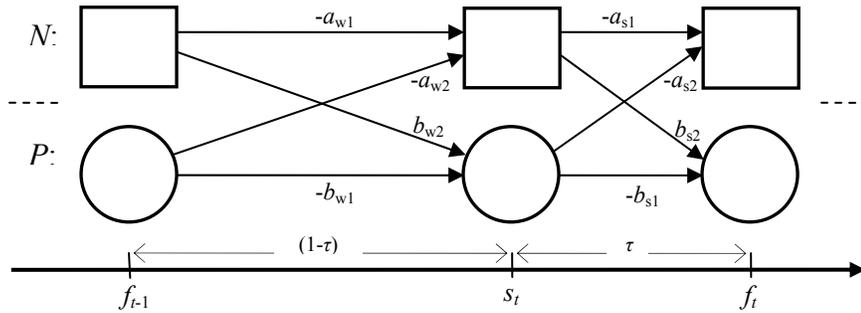


Figure 3: Diagram of an iteration through a full year (one winter and one summer) of inter- and intraspecific interactions included in the model (1). Noise terms and maximum rates of increase are not shown. Circles and rectangles represent consumer and resource respectively. See text for full information.

For summer (and similarly for winter) their interpretation is as follows: a_{s0} is the maximum rate of increase of the resource, a_{s1} is the strength of self-limitation (intraspecific effects) including all competition, and a_{s2} is the strength of the regulation by the consumer (trophic effect). Combined with the abundances at the onset of summer these parameters determine growth rate during summer. The proportion of the year that this growth rate is working (i.e. proportionate length of summer) is controlled by τ which takes a value from 0 (winter all year) to 1 (summer all year). Each season is also associated with an additive, species specific white noise term ε (note that superscript of each ε is only meant to identify the trophic level to which the noise belongs). Interpretation of consumer parameters is slightly different to that of the resource as its resource is explicitly incorporated into the model: b_{s0} is the maximum rate of natural increase *when benefits due to the modelled resource are discarded*, b_{s1} is the degree of self-limitation *that is not due to availability of the modelled resource*, and b_{s2} is, as before, the strength of the trophic interaction. Interpretations and meaning of winter parameters are as for summer. The signs in front of all parameters in (1) are chosen so as to reflect the nature of the interaction between and within the species, and all parameters are therefore positive by definition. Throughout the paper I will refer to the a_{ij} and b_{ij} as the parameters of the model, τ as the season length, and for the different parameter aggregates introduced I will use the term coefficient.

General model dynamics

Logarithmic transformation of observed abundances is often done on time series to facilitate analysis and informative plots (Williamson 1972; Royama 1992; Chatfield 1999). The justification of this being that population growth is a multiplicative process, and if variance of per-capita number of offspring is constant it will increase with the mean. A log-transformation will then stabilize the variance (Chatfield 1999). Doing this on both sides of (1) gives four linear equations that fit straight into a multivariate AR(1) framework:

$$\begin{aligned} n_{f,t} &= n_{s,t} + (a_{s0} - a_{s1}n_{s,t} - a_{s2}p_{s,t} + \varepsilon_{s,t}^n) \tau \\ p_{f,t} &= p_{s,t} + (b_{s0} - b_{s1}p_{s,t} + b_{s2}n_{s,t} + \varepsilon_{s,t}^p) \tau \end{aligned} \quad (2)$$

$$\begin{aligned} n_{s,t} &= n_{f,t-1} + (a_{w0} - a_{w1}n_{f,t-1} - a_{w2}p_{f,t-1} + \varepsilon_{w,t}^n)(1 - \tau) \\ p_{s,t} &= p_{f,t-1} + (b_{w0} - b_{w1}p_{f,t-1} + b_{w2}n_{f,t-1} + \varepsilon_{w,t}^p)(1 - \tau) \end{aligned} .$$

Taking the logarithm of abundances excludes the possibility of zero-value observations, but this is in practice solved by adding a small constant to all observations (Framstad et al. 1997; Stenseth et al. 1998a), and is therefore not a problem in this context. The main challenge here is the amount of parameters present in the model.

Univariate second order annual model

Sadly, very few, if any, sufficiently long biannual time series of two tightly connected species from different trophic levels exist. On the contrary, time series often consist of annual observations of the one focal species. By solving (2) for one of the species in one of the seasons we get a model that can be fitted to such data, and the presumption of a second order AR process is made apparent. This is exemplified here by fall abundances of the resource (fig. 4):

$$n_{f,t} = \alpha_0 + \alpha_1 n_{f,t-1} + \alpha_2 n_{f,t-2} + Z_{f,t} \quad (3)$$

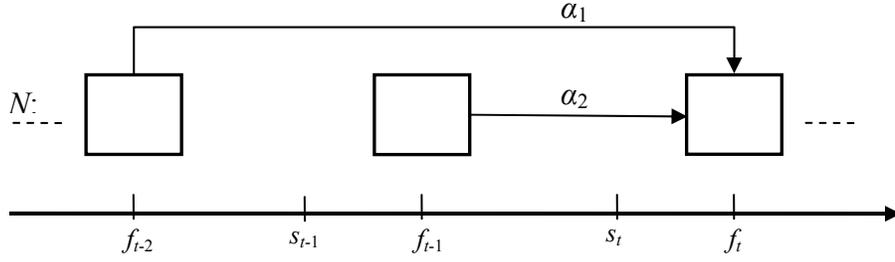


Figure 4: Diagram of one iteration of the second order univariate autoregressive model (3), showing how the density in one year depends on the densities the two preceding years. As in the text the fall resource densities are used as an example. Noise terms and constants are not shown. See text for full information.

Fitting this model to data will give estimates of the coefficients for which we now have expressions that incorporate ecological interactions:

$$\alpha_1 = (1 - \tau a_{s1})(1 - (1 - \tau)a_{w1}) + (1 - \tau b_{s1})(1 - (1 - \tau)b_{w1}) - \tau(1 - \tau)a_{w2}b_{s2} - \tau(1 - \tau)a_{s2}b_{w2}$$

$$\alpha_2 = -\left((1 - \tau a_{s1})(1 - \tau b_{s1}) + \tau^2 a_{s2}b_{s2}\right)\left((1 - (1 - \tau)a_{w1})(1 - (1 - \tau)b_{w1}) + (1 - \tau)^2 a_{w2}b_{w2}\right) .$$

From these expressions it is clear that there are potentially a lot of factors involved in the seemingly simple terms DD ($\alpha_1 - 1$) and DDD (α_2). Not only does consumption and intraspecific self-limitation enter DD, but also the self-limitation in the other species and various pair-wise interactions between parameters. The expression for DDD involves even more intricate parameter interactions, and α_0 , also a large expression, involves all interactions involving the maximum growth rates (see Appendix B). Although α_0 is decisive of absolute species abundance, it does not affect the dynamics of (3) (Royama 1992) and can be considered a constant. $Z_{f,t}$ is a noise term incorporating noise terms in (2) and the interactions between these and the model parameters (see Appendix C). It includes lags from both seasons and both species and strictly speaking (3) therefore contains moving average (MA) components (Chatfield 1999) in addition to the two autoregressive terms. The noise term is influential on model dynamics and is necessary for sustained cyclic dynamics (Stenseth 1999), but it can not tell us much about the parameters in the model, and will not be dealt with here. The above equation (3) could obviously be expressed in resource spring abundances or consumer spring/fall

abundances, but this will not affect the coefficient expressions as dynamics of the system remain the same (but it will affect the constant (α_0) and the noise term).

The dynamics of the deterministic version of (3) (i.e. ignoring the noise term) are determined solely by the coefficients of the two lags, and will according to these, be able to display a wide variety of patterns (Royama 1992; Bjørnstad et al. 1995). By ruling out types of patterns that are not observed in nature, and therefore should not be displayed by the model for any appropriate parameter combination, we will limit the parameter space. The most obvious requirement for the model with a given set of parameters, and a condition for most of the theory concerning time series analysis, is that of stationarity (the existence of a stable equilibrium). Biologically speaking this is the same as requiring long term persistence of bounded population sizes for both species. The boundaries for stationarity of (3) and qualitative dynamics within these are derived in Appendix D and shown in figure 5 (see also Royama 1992). These boundaries then define the widest set of parameter combinations that can enter the coefficients.

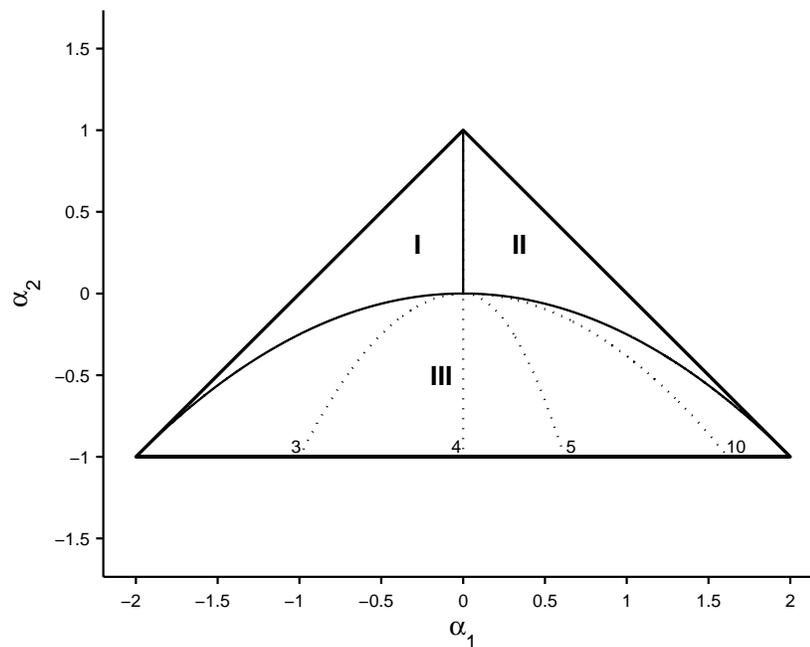


Figure 5: The figure shows the coefficient space of a second order autoregressive model and regions within this defining different dynamics. Within the triangle the model is stationary, and the bold lines thereby define the appropriate set of parameter combinations that enter into the coefficients. When coefficients are from the left side of the triangle, above the parabola, (region I) the model will show dampened two point cycles towards equilibrium. To the right (region II) a steady convergence towards equilibrium and below the parabola (region III) we have converging cycles with continuously increasing period as we move towards the right. Contour lines (dotted) define the borders for periods of length corresponding to the given number. See Appendix C for derivation and text for model details.

Examining the expressions for α_1 and α_2 reveals that they are second and fourth order polynomials in τ , respectively, and it is obvious that varying the season length variable will result in a change of the value of the coefficients (fig. 6). This can subsequently lead to a shift of the dynamics of a system with a given set of parameters, as the coefficients move within or across the borders defining stationarity (fig. 6c). In the α_1 -direction, variation of season length will give a path that tracks some part of the parabolic segment defined by α_1 for $\tau \in (0,1)$. The path will have at the most one turning point and the nature of this turning point, i.e. whether it is a maximum or minimum point, will follow from the sign of $\left[\frac{d^2}{d\tau^2}(\alpha_1) \right]$. The motion in α_2 -direction is more complicated as this follows some segment of a fourth order polynomial, having up to three turning points.

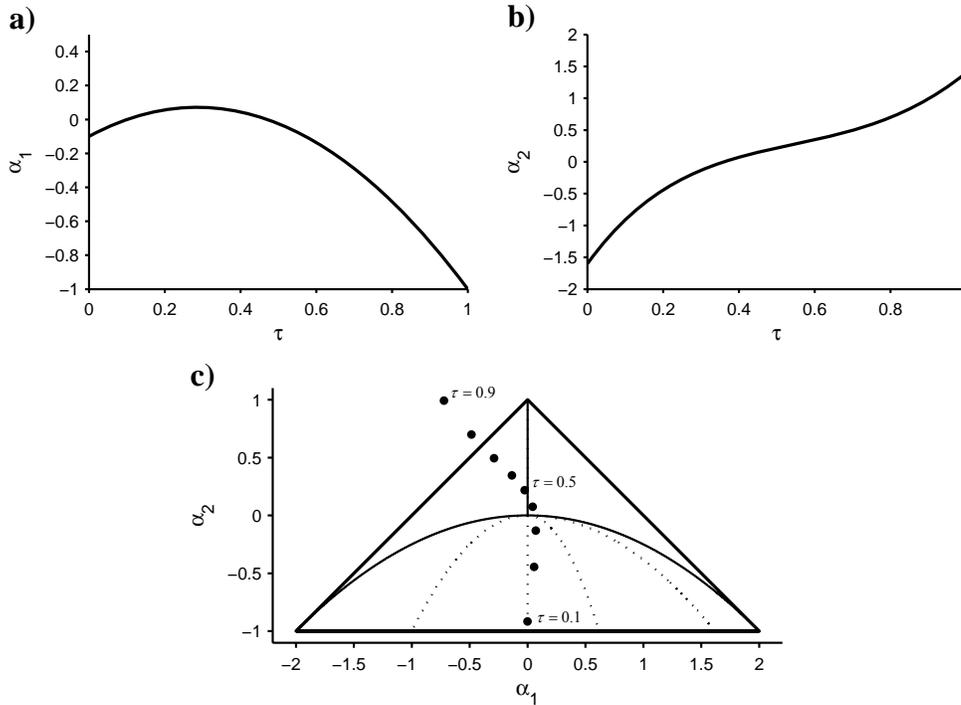


Figure 6: Changes in values taken by the coefficients of the second order model with change in season length. **a)** The parabolic change of α_1 with τ , in a case where the turning point is a maximum, **b)** The change in α_2 in a case where it increases for the whole interval $\tau \in (0,1)$, **c)** The path resulting from the combined change in coefficients with season length overlain on the borders defining model dynamics (see fig. 5). We see that the deterministic system passes through all major types of qualitative dynamics as τ increases. Model parameters are the same in the three figures, and values were chosen so as to emphasize function properties.

Tracking the coefficients in the deterministic model as they alter with season length and predicting the changes in dynamics would be unproblematic if we had reliable estimates of the model parameters. Going the other way, we could attempt to study a specific change in dynamics (pathway in $\alpha_1\alpha_2$ -coordinates) with a given change in season length, and search for parameter combinations that could result in that specific pattern. Unfortunately the amount of parameters, their interactions, and the interdependencies of the coefficients through the parameters make this approach close to, if not impossible.

Bivariate first order annual model

By eliminating the consumer in the preceding section some detail of information was lost, and as annual data from both trophic levels would require the model to be expressed accordingly, I bring them back into the model. Again, a bit of algebra can change the appearance of (2), this time into a pair of coupled, first order bivariate equations (fig. 7):

$$\begin{aligned} n_{f,t} &= \beta_{10} + \beta_{11}n_{f,t-1} + \beta_{12}p_{f,t-1} + Z_{f,t}^n \\ p_{f,t} &= \beta_{20} + \beta_{21}n_{f,t-1} + \beta_{22}p_{f,t-1} + Z_{f,t}^p \end{aligned} \quad (4)$$

where the coefficients of the lagged abundances are:

$$\begin{aligned} \beta_{11} &= (1 - \tau a_{s1})(1 - (1 - \tau)a_{w1}) - \tau(1 - \tau)a_{s2}b_{w2} \\ \beta_{12} &= -(a_{w2}(1 - \tau)(1 - \tau a_{s1}) + \tau a_{s2}(1 - (1 - \tau)b_{w1})) \\ \beta_{21} &= b_{w2}(1 - \tau)(1 - \tau b_{s1}) + \tau b_{s2}(1 - (1 - \tau)a_{w1}) \\ \beta_{22} &= (1 - \tau b_{s1})(1 - (1 - \tau)b_{w1}) - \tau(1 - \tau)a_{w2}b_{s2} \end{aligned}$$

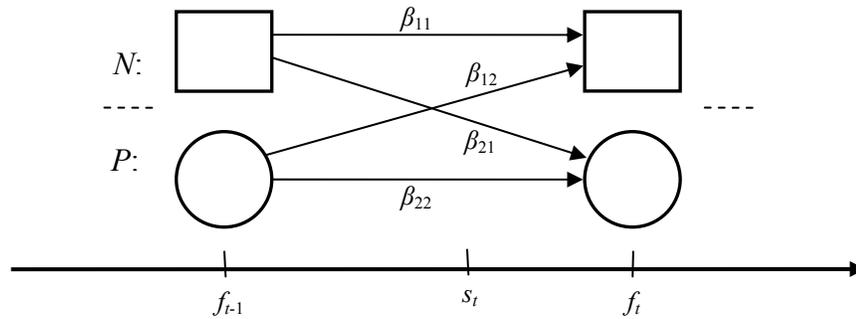


Figure 7: Diagram of one iteration of the first order bivariate autoregressive model (4), showing how the density of both species in one year depend on densities the preceding year. As in the text the fall densities are used as an example. Noise terms and constants are not shown. See text for full information.

Again, β_{10} and β_{20} are constants (Appendix B) that do not affect dynamics, and the noise terms consist of noise from both seasons and species (Appendix C), but the focus will still be on the coefficients of the lags. By solving (4) for one of the species it can easily be shown that the connection between the coefficients of (3) and (4) is:

$$\begin{aligned}\alpha_1 &= \beta_{11} + \beta_{22} \\ \alpha_2 &= -(\beta_{11}\beta_{22} - \beta_{12}\beta_{21}),\end{aligned}$$

and the stability boundaries that apply to (3), with respect to α_1 and α_2 , must therefore apply to the respective combinations of the coefficients of (4). Due to the nature of a trophic interaction, we can additionally state that $[\beta_{12} < 0]$ and $[\beta_{21} > 0]$ (the consumer has negative impact on resource and vice versa), and by this we put further restrictions on suitable parameter combinations. We see for example that if $[\tau b_{s1} > 1]$ and $[(1 - \tau)a_{w1} > 1]$ we have a contradiction of $[\beta_{21} > 0]$, giving an upper bound for the combination of parameters governing the strength of self-limitation in the two species.

Having a model with equations for both resource and consumer also allows us to study the zero growth isoclines (ZGI) predicted by the model. These describe the

abundances at which each of the populations are stable, i.e. $\frac{N_{f,t}}{N_{f,t-1}} = 1$ and $\frac{P_{f,t}}{P_{f,t-1}} = 1$. On

the logarithmic scale the ZGI are straight lines. For the consumer we can very reasonably require that the size at which the population is stable will increase with increasing resource availability, i.e. ZGI_P increases with resource abundance (subscript indicating trophic level). Similarly, for the resource we may require that the fewer consumers present, the larger the stable population size, i.e. ZGI_N decreases with increasing consumer abundance. For these requirements to be met by the coefficients we need $[\beta_{22} < 1]$ and $[\beta_{11} < 1]$ (see Appendix E for derivation). We may further define a required shape of the ZGI, although this information is partly concealed by the straight lines within logarithmic axes (fig. 8). In the case of the consumer it may be argued that at increasingly high resource densities, a given amount of additional resources will have less affect on the size of the stable consumer population. Accepting that negative crowding effects must take place within the consumer population would see to such an

effect, i.e. we can require a concave ZGI_P . In Appendix E the consequences of this requirement is shown to imply the criterion $[\beta_{21} + \beta_{22} < 1]$. Similar reasoning for the resource isocline will not supply any new criteria, as the curvature is given when the constraint of negative slope is established.

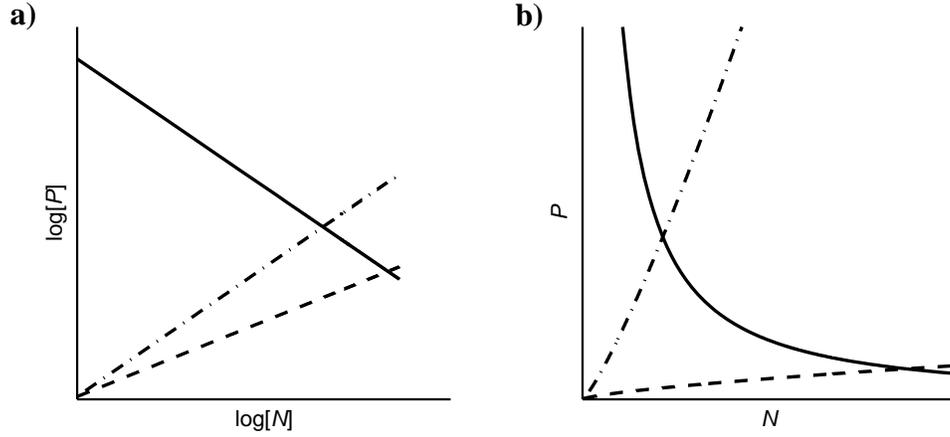


Figure 8: The zero growth isoclines (ZGI) of the resource (N , solid line), and the consumer (P , broken lines). **a)** On a logarithmic scale we see the decreasing nature of ZGI_N and the increasing nature of ZGI_P . **b)** The same ZGI in normal axes. Information on curvature is obscured in the former as can be seen by comparing the two ZGI_P in the two plots; a sufficient increase in slope will also alter the curvature of ZGI_P from concave to convex. The dashed line applies for $[\beta_{21} + \beta_{22} < 1]$, and the dash-dot line for $[\beta_{21} + \beta_{22} > 1]$.

To summarise findings from studying the model as expressed in (4), we have an appropriate model if:

$$[\beta_{12} < 0], [\beta_{21} > 0], [\beta_{11} < 1], [\beta_{22} < 1], [\beta_{21} + \beta_{22} < 1].$$

These conditions combined with the general conditions for stationarity can be illustrated as the boundaries within cross sections of the four dimensional coefficient space of (4) shown in figure 9.

As with the univariate second order model (3), this bivariate model may also be expressed in spring densities, this time leading to slightly different parameter combinations in the coefficients of the lags. Indexed in the same manner as in (4) we get:

$$\begin{aligned} \gamma_{11} &= (1 - \tau a_{s1})(1 - (1 - \tau)a_{w1}) - \tau(1 - \tau)a_{w2}b_{s2} \\ \gamma_{12} &= -(a_{w2}(1 - \tau)(1 - \tau b_{s1}) + \tau a_{s2}(1 - (1 - \tau)a_{w1})) \\ \gamma_{21} &= (1 - \tau)b_{w2}(1 - \tau a_{s1}) + \tau b_{s2}(1 - (1 - \tau)b_{w1}) \\ \gamma_{22} &= (1 - \tau b_{s1})(1 - (1 - \tau)b_{w1}) - \tau(1 - \tau)a_{s2}b_{w2} \end{aligned}$$

Arguments, identical to those used above, regarding the nature of a consumer-resource interaction and biological reasonable ZGI, will have to apply for these coefficients too, giving:

$$[\gamma_{12} < 0], [\gamma_{21} > 0], [\gamma_{11} < 1], [\gamma_{22} < 1], [\gamma_{21} + \gamma_{22} < 1].$$

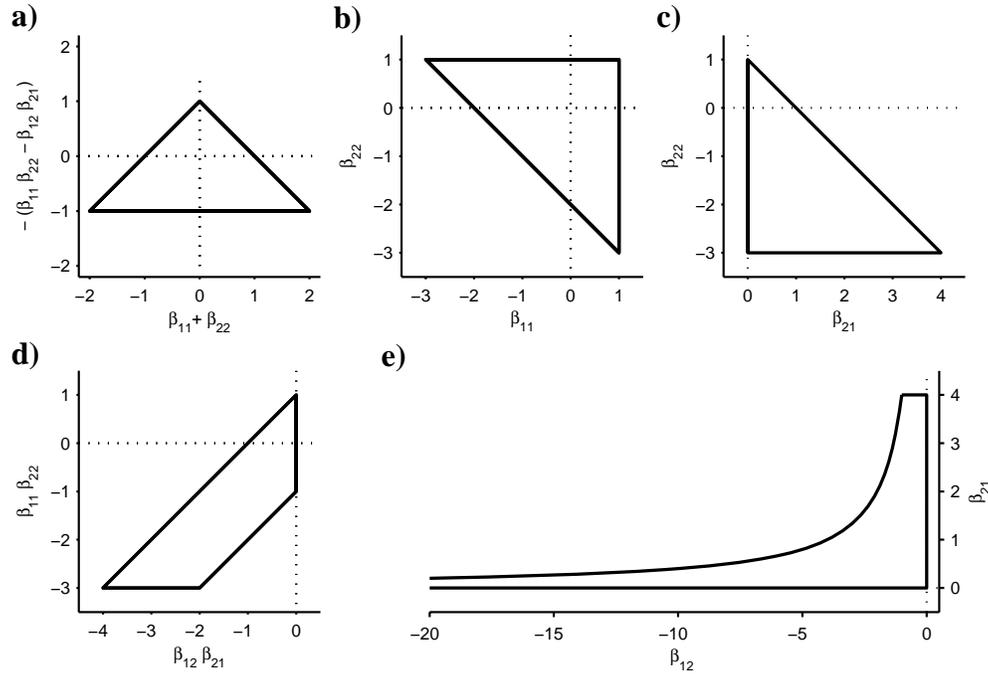


Figure 9: Boundaries that together define the appropriate coefficient space for the consumer resource model. **a)** The general conditions for stationarity found when studying the second order univariate model (see fig. 5). **b, c, d, e)** Additional conditions found by studying the first order bivariate model. Notice that in figure e) for sufficiently small β_{21}, β_{12} is unbounded to the left. The same boundaries apply for the model coefficients when expressed in spring abundances (γ_{ij} , see text). For derivations of the boundaries see Appendix E.

Together with the criteria for stationarity found in the preceding section, the criteria concerning the β_{ij} and γ_{ij} then give necessary conditions for the parameter combinations to give a biological feasible consumer-resource model. After fitting (4) to data presumed to be connected by a trophic interaction, it should be checked whether the estimated values for coefficients comply with these conditions.

The second and fourth order polynomials (in τ) constituting the coefficients of (3) have in (4) been split up into combinations of respectively two and four second order polynomials (the expressions of the β_{ij} or γ_{ij}). The different coefficients will respond

differently to a change in τ , depending on the parameters that enter into them. It may then be pictured that a change in season length that leads to change in dynamics is channelled mainly through a change in one of these coefficients, and with more exact knowledge about parameter values this could be predicted.

Model with estimates from data

With the limits of the parameter space found in the above section, the model will now be fitted to data. The data used is part of an extensive collection of time series on the vole *Clethrionomys rufocanus*, from Hokkaido; an island in northern Japan (see Stenseth et al. 1996b, for a detailed description of geography and sampling). The time series exhibit varying dynamics, including periodic cycles and seemingly random fluctuations. A total of 84 of these time series, covering 30 years of spring and autumn observations of vole densities, were grouped into six groups according to topographic characteristics (see Stenseth et al. 2003, for description of groups). The grouping gives six independent estimates of the coefficients, but has no additional significance in this thesis. Although the timing of observations does not necessarily coincide with the exact timing of the winter-summer/summer-winter transitions, I assume that the data points adequately represent the transition densities. At the same time I assume that the difference in season length between the groups is negligible (season length for all groups was estimated to lie in the interval 0.382-0.421 by Stenseth et al. 2003). With these data at hand the model was expressed as a bivariate second order model of one species; bivariate in the sense that spring and fall densities are expressed separately and second order because abundance relies on the densities in two preceding time steps.

$$\begin{aligned} x_t &= s_0 + (1 + s_1)y_t + s_2x_{t-1} + Z_{x,t} \\ y_t &= w_0 + (1 + w_1)x_{t-1} + w_2y_{t-1} + Z_{y,t} \end{aligned} \quad (5)$$

x and y now denote the log-abundance of the same species (consumer or resource) in fall and spring, respectively. A schematic presentation of the model is given in figure 10. The link between the coefficients in (5) and the coefficients in (3) is

$[1 + s_1 + s_2 + w_1 + w_2 + s_1w_1 = \alpha_1]$ and $[-s_2w_2 = \alpha_2]$, as can easily be seen by solving the first equation for y and substituting into the second. The exact combination of parameters that enter into the coefficients will depend on whether the model is solved for consumers or resource. Although the noise terms in (5) incorporate noise from both voles and mustelids, and dates several time steps back (Appendix C), they were treated as white

noise when fitting the model.

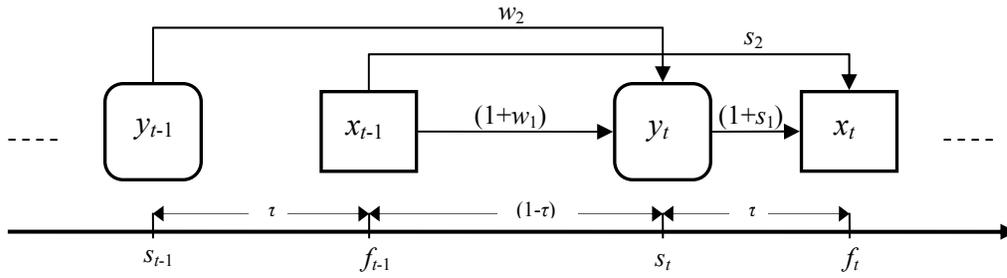


Figure 10: Diagram of one iteration of the seasonal autoregressive model (5), showing how the density of a species (consumer or resource) in one season depends on densities in the preceding two seasons. Noise terms and constants are not shown. See text for full information.

The model coefficients were estimated within a Bayesian framework (H. Viljugrein, unpubl. results; see Stenseth et al. 2003, for description of methods), and the results are presented in table 1. Again, the model constants are not focused on, but full expressions are included in Appendix B. The general pattern seen in table 1 is that negative DD in the winter is larger than that in summer, while DDD is small and in several instances not significant. It is also noteworthy that the model does not place any of the groups in a cyclic regime, although a direct fitting of a second order univariate model would do so for groups 2 and 5 (Stenseth et al. 2003). In an attempt to avoid erroneous conclusions when using these results, I focus on qualitative rather than quantitative properties, in the following discussion of parameter values.

Table 1: Estimates of coefficients of the seasonal model (H. Viljugrein, unpubl. results). Numbering of groups follow Stenseth et al. (2003), and number in brackets specifies number of time series within each group. σ_i is the mean standard deviation of the noise for each season within each group. The coefficient values of the univariate annual model are calculated by using the link between the two models' coefficients (see text). Only the signs in the last column are used for the inferences done in this thesis.

Season	Coefficient	Group						Mean ^{***}	Sign
		1S (15)	1N (15)	2S (14)	2N (16)	5S (12)	5N (12)		
Winter	w_1	-0.81	-0.89 ^{**}	-0.85	-0.75	-0.65	-0.87	-0.79	-
	w_2	0.125 [*]	0.16	0.09 [*]	0.00 [*]	-0.12 [*]	0.19	0.17	+
	σ_w	0.76	0.75	0.93	0.81	0.95	1.03	0.87	
Summer	s_1	-0.25	-0.47	-0.24	-0.24	-0.23	-0.30	-0.29	-
	s_2	-0.04 [*]	0.18	-0.12	-0.20	-0.06 [*]	-0.09 [*]	-0.05	nc
	σ_s	0.91	0.92	1.13	1.09	1.19	1.02	1.04	
Annual	α_1	0.23	0.39	0.09	-0.01	0.09	0.19		
	α_2	0.01	-0.03	0.01	0.00	-0.01	0.02		

* = not sign. from 0, ** = not sign. from (-1), *** = only sign. estimates included, nc = not conclusive

Until now the model has been treated as a general consumer-resource model, and applying it on a specific system may allow for specific assumptions concerning some of parameters. As we presumably do not know whether the dynamics of the system are due to the vole interacting with its environment as a consumer or as a resource we have to envision two scenarios, and these are treated separately in the following sections.

The vole as a resource

The specialist predation hypothesis is perhaps the most studied and most popular hypothesis sought to explain the observed multi-annual cycles in small mammals (Hanski et al. 1991; Hanski et al. 1993; Korpimäki and Norrdahl 1998; Klemola et al. 2000; Gilg et al. 2003; Klemola et al. 2003). More specifically, it is thought that a delayed numerical response by the resident predator imposes a delayed density dependent increase in mortality of the resource species. With respect to rodent systems in the boreal and arctic regions, mustelid predators have been pointed out as a potential mediator of this delayed density dependent mortality (Korpimäki et al. 1991; Hanski et al. 1993; Korpimäki 1993), three of which are present and considered important predators of small rodents in Hokkaido (Kaneko et al. 1998). So, in this setting the voles in Hokkaido are a resource for a resident specialist mustelid predator.

Before I go on to make inferences about the various parameters that constitute the coefficients, I will make two simplifying assumptions. First, I will assume that effects of intraspecific effects on the vole population growth (self-limitation) is working in winter only, and that during summer they are negligible, i.e. $[a_{s1} = 0]$. Limitation of food in winter, when primary production is low, is in agreement with earlier studies on small rodents (Hansson 2002; Aars and Ims 2002; Huitu et al. 2003). Limited available space due to snow cover may further add to self-limitation through increased intraspecific interference. Setting summer self-limitation to zero is then justified by the large increase in space and food supply, the latter supported by the small amount of available plant material removed by voles (Krebs and Myers 1974). Second, I assume that the mustelids are specialists in winter only, and that abundance of voles in spring has a negligible effect on mustelid abundance in fall, i.e. $[b_{s2} = 0]$. The rationale being that during summer

alternative prey become available (Järvinen 1985; Korpimäki et al. 1991), causing a decoupling of the tight relationship with voles that exists during winter. With these assumptions we get the following expressions for the coefficients:

$$\begin{aligned}
 w_1 &= -(1-\tau) \left(a_{w1} + \frac{a_{w2}}{a_{s2}} \left(b_{s1} - \frac{1}{\tau} \right) \right) \\
 w_2 &= (1-\tau) \left(\frac{a_{w2}}{a_{s2}} \left(b_{s1} - \frac{1}{\tau} \right) \right) \\
 s_1 &= -\tau \left(\frac{a_{s2}}{a_{w2}} \left(b_{w1} - \frac{1}{(1-\tau)} \right) \right) \\
 s_2 &= \tau \left(\frac{a_{s2}}{a_{w2}} \left(b_{w1} - \frac{1}{(1-\tau)} \right) (1 - (1-\tau)a_{w1}) - (1-\tau)a_{s2}b_{w2} \right) .
 \end{aligned}$$

Viewing the coefficients as functions of τ and using information from the estimates, we may check what predictions they make about parameters in the expressions. Starting with the w_i , we see that when summed they give a direct prediction for the strength of self-

regulation of voles in winter, i.e. $\left[a_{w1} = -\frac{1}{(1-\tau)}(w_1 + w_2) \approx 1 \right]$. A positive w_2

implies $\left[b_{s1} > \frac{1}{\tau} \right]$, which also guarantees a negative w_1 , in accordance with its estimate.

This indicates that self-limitation working within the mustelid population in summer is considerably larger than that working on the voles in winter. The negative estimate of s_1 points to considerable self-limitation in the mustelids in winter too, as the sign can only

be obtained if $\left[b_{w1} > \frac{1}{(1-\tau)} \right]$. The complexity and the ambiguous estimate of s_2 make it

hard to infer any predictions concerning parameters in it. The next step is then to take these predictions and assumptions and confront them with the criteria found from studying the general dynamics of the model. If we accept the assumptions done above regarding the parameters and the qualitative results from fitting the model to the data, any inconsistencies would suggest that the dynamics may not be a result of a predator-prey interaction. And indeed, we have a contradiction of $[\beta_{21} > 0]$. Under the given

assumptions the expression for this coefficient is $\left[\beta_{21} = b_{w2}(1-\tau)(1-\tau b_{s1}) \right]$, and clearly

this becomes negative with the lower limit inferred for b_{s1} , implying that the voles have a negative impact on the predator. This result then suggests that the summer self-limitation parameter for predators that is consistent with the empirical estimate is too great for a model consistent with a predator-prey interaction.

The vole as a consumer

The other hypothesis compatible with the model presented here is that an interaction between the voles and the vegetation is the main factor driving dynamics. The recovery time of the plants serving as food source for the voles then creates the time lag necessary for cyclic dynamics (Agrell et al. 1995). This recovery may be in terms of quantity and/or quality of food for the voles. The grey sided vole is a folivorous species, and in Hokkaido the diet is dominated by leaves and shoots of bamboo grass (*Sasa* spp.)(Kaneko et al. 1998; Saitoh et al. 1999). In winter density independent (climatic) factors limit growth of bamboo, and although competition for light and/or nutrients may affect individual bamboo stands in summer, I assume that this does not have population level effects. This is consistent with the 'Law of Constant Yield', stating that productivity in terms of biomass is independent of plant density (see e.g. Begon et al. 1996). This allows for simplification of coefficient expressions by setting [$a_{s1} = 0$, $a_{w1} = 0$], and no assumptions concerning vole parameters are done. The expressions for the estimated coefficients are then:

$$w_1 = -(1-\tau) \left(b_{w1} - \frac{1}{\tau} \frac{b_{w2}}{b_{s2}} \right)$$

$$w_2 = (1-\tau) \left(\frac{b_{w2}}{b_{s2}} \left(b_{s1} - \frac{1}{\tau} \right) - \tau b_{w2} a_{s2} \right)$$

$$s_1 = -\tau \left(b_{s1} - \frac{1}{(1-\tau)} \frac{b_{s2}}{b_{w2}} \right)$$

$$s_2 = -\tau \left(\frac{1}{(1-\tau)} \frac{b_{s2}}{b_{w2}} (1 - (1-\tau)b_{w1}) + (1-\tau)b_{s2}a_{w2} \right).$$

Proceeding as before, we see from w_1 that $\left[b_{w1} > \frac{1}{\tau} \frac{b_{w2}}{b_{s2}} \right]$, indicating either strong vole self-limitation in winter, or strong impact of food availability in summer compared to

winter. The limitation of food in winter seen in earlier studies (Hansson 2002; Huitu et al. 2003) would suggest the former. Strong self-limitation in summer must be the case, as a positive estimate of w_2 can only be achieved if $\left[b_{s1} > \frac{1}{\tau} + \tau a_{s2} b_{s2} \right]$. s_1 sets demands to the same parameter by $\left[b_{s1} > \frac{1}{(1-\tau)} \frac{b_{s2}}{b_{w2}} \right]$. None of these predictions contradict the criteria set when considering the general dynamics of the model, and a conclusion would then be that the dynamics, as captured by the bivariate seasonal model, indicate that we are dealing with a system driven in large by herbivore-plant interactions.

Discussion

The preliminary conclusion reached when comparing the coefficients from the statistical analysis with the results from analysis of dynamics, is that support is found for that a vole-vegetation interaction is dominating the vole dynamics. The specialist predation hypothesis is, in contrast, contradicted by an analogous comparison where statistical estimates implied predator self-limitation too great for it to benefit from the voles.

The predator-prey inconsistency, however, rests entirely on the assumption that the predator has no benefit of the explicitly modelled prey during summer, which of course is not strictly true, and only a slight benefit would prevent the contradiction. Discarding the possibility of predator-prey interactions driving the observed dynamics on this basis would be an overstatement and a mistake. On the other hand, no inconsistencies were found in the grazer-plant scenario, which certainly emphasises that this is a possible alternative. This is valid even if the assumption of no effect of competition on plant biomass is false. The focus in the thesis though, has been to assess the *possibility* of drawing conclusions about ecology from time series data. It is shown that if we construct hypotheses regarding the system in question (e.g. important predators), we can incorporate them into AR models that can be fitted to data. The connection between ecology and the statistical coefficients follow directly from the interactions included in the model. Including other interactions (such as adding a trophic level) will not only give coefficients with different ecological interpretations, but may also give a different number of predicted lags. By combining models encompassing different ecological scenarios (hypotheses) with available experimental and observational knowledge regarding their interactions (i.e. information on parameters), and comparing model predictions from each of the scenarios with statistical estimates, one may get an indication of which of the scenarios is the most likely. This is true also when time series exist only for one of the species in the model.

A crucial feature that has only briefly been mentioned so far is the noise structure of the model. At the starting point, noise terms are assumed to be white and additive on a logarithmic scale, and to result from factors that are not affected by the species'

abundances. As we reduce the model for it to be applicable to the type of data usually at hand (one species and/or one season), we see that the originally white noise accumulates into aggregates of noise terms that no longer can be viewed as time-independent (see Appendix C for full expressions for all noise terms presented). The full model therefore predicts a mixed ARMA process, while the model that was fitted to the data was (out of simplicity) a pure AR model. It has previously been demonstrated that when AR models are fitted to ARMA processes this may cause erroneous conclusions regarding the density dependent structure of the process (Williams and Liebhold 1995). Although general statements concerning the effects of ignoring correlated noise are difficult to make, there is all reason to believe that not including the MA components when fitting the model will give erroneous estimates of the AR coefficients. The fact that the second order coefficients from the annual model listed in table 1, deviate from previous direct estimates (Stenseth et al. 2003), may result from ignoring the different MA components in each case. Another noise related indication that the model fitted to the data may not be the appropriate one, is the relatively large standard deviation of the noise (prediction errors, see table 1). Several factors could contribute to this. The model may include the wrong type or the wrong number of lags, the former discussed above and the latter a possibility supported by the finding of up to four significant lags by Stenseth et al. (2003) in the same data. Also, the ability of the model to pick up relevant signals in the data will at least partly rely on the how the supposed processes behind the signals are incorporated into the statistical model. Fitting linear models to data from non-linear processes and vice-versa could very well increase noise. This underlines the importance of at least qualitative knowledge of the ecological processes going on. Questions that need to be answered in the scenarios studied here are: can per-capita growth as a function of density be described with a convex curve for the density range of the data? Can functional response be assumed to be linear for the data range? The questions may be answered through an experimental/observational approach, and probably the necessary data already exist. I have, however, not succeeded in finding studies that empirically evaluate other functional forms than those traditional to ecological theory (e.g. logistic growth, ‘type 2’ response etc.).

The difficulties in evaluating the exact dynamical effects of varying season length are entirely due to the uncertainties regarding parameter values. If reliable values were at

hand this could be done through analysis of the first and second derivatives of the coefficient expressions. It is generally shown here that the effects can be substantial, and considering the entirely different conditions that seasons provide for species in areas with boreal and temperate climate, it would seem reasonable that the relative length of seasons would affect dynamics. Relevance of this aspect is especially highlighted by the current debate on climate change.

Concluding remarks

An ecological interpretation of the signals picked up by time series analysis was facilitated by deriving a well-known statistical model from a mechanistic basis. Under certain assumptions, inconsistencies were found when confronting a mustelid-vole scenario with output from statistical analysis, while no inconsistencies were found for the vole-vegetation scenario. Any clear conclusion of which of the factors engage in driving vole dynamics; vegetation or predators, was not achieved here due to sensitivity to the simplifying assumptions done in the mustelid-vole scenario. Still, if we accept the model (1) as an ecological model it is shown that certain expectations can be set to statistical estimates. By confronting expectations resulting from alternative hypotheses with such estimates one may get an indication of which is the most likely. More knowledge about how biological accurate/inaccurate the simple functional forms in the model actually are, would contribute to the confidence in the model predictions. Paying more attention to the predicted noise structure when fitting the model, would perhaps increase the accuracy of coefficient estimates. The relative length of seasons has a potential large effect on dynamics, and uncovering the sensitivity of dynamics to a change in season length is crucial when trying to unravel the consequences of climate change. For the time being the enigma of cyclic vole dynamics remains unresolved.

Appendix

A. Notation

The table summarises all notation used for variables, parameters and coefficients that are discussed in the thesis, and gives a short description of their interpretations. The number in brackets included in the first column refers to numbers given to model expressions in the text.

Model	Variable, Parameter or Coefficient	Description
Full model (1)(2)	$N_{f,t}, N_{s,t}$	resource abundance at time t in fall and spring, respectively
	$n_{f,t}, n_{s,t}$	$\ln(N_{f,t}), \ln(N_{s,t})$
	$P_{f,t}, P_{s,t}$	consumer abundance at time t in fall and spring
	$p_{f,t}, p_{s,t}$	$\ln(P_{f,t}), \ln(P_{s,t})$
	a_{s0}, a_{w0}	resource maximum rate of increase in summer and winter, respectively
	a_{s1}, a_{w1}	controls resource self limitation in summer and winter
	a_{s2}, a_{w2}	controls detrimental effect of consumer on resource in summer and winter
	b_{s0}, b_{w0}	consumer maximum rate of increase in summer and winter in absence of the modelled resource
	b_{s1}, b_{w1}	controls consumer self limitation in summer and winter
	b_{s2}, b_{w2}	controls benefit of resource to consumer in summer and winter
	τ	proportionate length of summer, $\in (0,1)$
	$\mathcal{E}_{s,t}^n, \mathcal{E}_{w,t}^n, \mathcal{E}_{s,t}^p, \mathcal{E}_{w,t}^p$	white noise terms with season and species specific variance
Univariate second order model (3)	α_0	constant affecting mean abundance of focal species
	α_1	direct annual density dependence of focal species
	α_2	delayed annual density dependence of focal species
Bivariate first order model (4)	β_{10}, γ_{10}	constants affecting mean fall and spring abundances of resource, respectively
	β_{11}, γ_{11}	annual effect of resource on own fall and spring abundances
	β_{12}, γ_{12}	annual effect of consumer on resource fall and spring abundances
	β_{20}, γ_{20}	constants affecting mean fall and spring abundances of consumer
	β_{21}, γ_{21}	annual effect of resource on consumer fall and spring abundances
	β_{22}, γ_{22}	annual effect of consumer on own fall and spring abundances
Bivariate second order model (5)	x_t	fall abundance of focal species
	y_t	spring abundance of focal species
	s_0, w_0	constants affecting mean abundances in fall and spring, respectively
	s_1, s_2	respective effect of abundances in spring and previous fall on summer growth
	w_1, w_2	respective effect of abundances in fall and previous spring on winter growth

B. Model constants

The following are the full expressions for all the model constants referred to in the text. The number in parenthesis corresponds to numbers given to the models when presented in the in the text.

Univariate second order annual model of resource fall abundance (3):

$$\begin{aligned}\alpha_0 = & (1-\tau)a_{w2} \left(\tau^2 a_{s0} b_{s2} - (1-\tau a_{s1}) \left((1-\tau)b_{w0} (1-\tau b_{s1}) + \tau b_{s0} \right) \right) \\ & + \left(\tau a_{s0} + (1-\tau)a_{w0} (1-\tau a_{s1}) \right) \left(1 - (1 - (1-\tau)b_{w1}) (1-\tau b_{s1}) \right) \\ & - \tau a_{s2} \left(\tau (1 - (1-\tau)b_{w1}) \left((1-\tau)a_{w0} b_{s2} + b_{s0} \right) + (1-\tau)b_{w0} (1 + \tau(1-\tau)a_{w2} b_{s2}) \right)\end{aligned}$$

Bivariate first order annual model of fall abundance (4):

$$\begin{aligned}\beta_{10} = & \tau a_{s0} + (1-\tau)a_{w0} (1-\tau a_{s1}) - \tau(1-\tau)a_{s2} b_{w0} \\ \beta_{20} = & \tau b_{s0} + (1-\tau)b_{w0} (1-\tau b_{s1}) + \tau(1-\tau)a_{w0} b_{s2}\end{aligned}$$

Bivariate second order seasonal model (5):

Resource:

$$\begin{aligned}s_0 = & \tau \left(a_{s0} - (1-\tau)a_{s2} b_{w0} - a_{w0} \frac{a_{s2}}{a_{w2}} (1 - (1-\tau)b_{w1}) \right) \\ w_0 = & (1-\tau) \left(a_{w0} - \tau a_{w2} b_{s0} - a_{s0} \frac{a_{w2}}{a_{s2}} (1 - \tau b_{s1}) \right)\end{aligned}$$

Consumer:

$$\begin{aligned}s_0 = & \tau \left(b_{s0} - (1-\tau)a_{w0} b_{s2} - b_{w0} \frac{b_{s2}}{b_{w2}} (1 - (1-\tau)a_{w1}) \right) \\ w_0 = & (1-\tau) \left(b_{w0} + \tau a_{s0} b_{w2} - b_{s0} \frac{b_{w2}}{b_{s2}} (1 - \tau a_{s1}) \right)\end{aligned}$$

C. Noise terms

The following includes full expressions for all noise terms referred to in the text. The number in parenthesis corresponds to numbers given to the models when they were presented.

Univariate second order annual model of resource (3):

$$\begin{aligned}
Z_{f,t} = & \tau \varepsilon_{s,t}^n \\
& + (1-\tau) \left[(1-\tau a_{s1}) \left(1 - (1-(1-\tau)b_{w1})(1-\tau b_{s1}) \right) - \tau^2 a_{s2} b_{s2} (1-(1-\tau)b_{w1}) \right] \varepsilon_{w,t}^n \\
& - (1-\tau) \left[(1-\tau) a_{w2} \left((1-\tau a_{s1})(1-\tau b_{s1}) + \tau^2 a_{s2} b_{s2} \right) + \tau a_{s2} \right] \varepsilon_{w,t}^p \\
& + \tau \left[2 - (1-(1-\tau)b_{w1})(1-\tau b_{s1}) + \tau(1-\tau) a_{w2} b_{s2} \right] \varepsilon_{s,t-1}^n \\
& - \tau \left[\tau a_{s2} (1-(1-\tau)b_{w1}) + (1-\tau) a_{w2} (1-\tau a_{s1}) \right] \varepsilon_{s,t-1}^p
\end{aligned}$$

Bivariate first order annual model of fall abundance (4):

$$\begin{aligned}
Z_{f,t}^n &= \tau \varepsilon_{s,t}^n + (1-\tau)(1-\tau a_{s1}) \varepsilon_{w,t}^n - (1-\tau) \tau a_{s2} \varepsilon_{w,t}^p \\
Z_{f,t}^p &= \tau \varepsilon_{s,t}^p + (1-\tau) \tau b_{s2} \varepsilon_{w,t}^n + (1-\tau)(1-\tau b_{s1}) \varepsilon_{w,t}^p
\end{aligned}$$

Bivariate second order seasonal model (5):

Resource:

$$\begin{aligned}
Z_{x,t} &= \tau \varepsilon_{s,t}^n - \frac{a_{s2}}{a_{w2}} \tau (1-(1-\tau)b_{w1}) \varepsilon_{w,t}^n - \tau(1-\tau) a_{s2} \varepsilon_{w,t}^p \\
Z_{y,t} &= (1-\tau) \varepsilon_{w,t}^n - \frac{a_{w2}}{a_{s2}} (1-\tau) (1-\tau b_{s1}) \varepsilon_{s,t-1}^n - \tau(1-\tau) a_{w2} \varepsilon_{s,t-1}^p
\end{aligned}$$

Consumer:

$$\begin{aligned}
Z_{x,t} &= \tau \varepsilon_{s,t}^p - \frac{b_{s2}}{b_{w2}} \tau (1-(1-\tau) a_{w1}) \varepsilon_{w,t}^p + \tau(1-\tau) b_{s2} \varepsilon_{w,t}^n \\
Z_{y,t} &= (1-\tau) \varepsilon_{w,t}^p - \frac{b_{w2}}{b_{s2}} (1-\tau) (1-\tau a_{s1}) \varepsilon_{s,t-1}^p + \tau(1-\tau) b_{w2} \varepsilon_{s,t-1}^n
\end{aligned}$$

D. Stability conditions

The solution to the deterministic part of (3) is equivalent to the solution of the linear homogenous second order difference equation (the constant α_0 does not affect dynamics and is therefore put to zero):

$$n_{t+2} - \alpha_1 n_{t+1} - \alpha_2 n_t = 0 \quad (\text{A1})$$

Supposing the solution is of the form λ^t , where λ may be a complex number, and substituting into (A1) we obtain the characteristic equation (or auxiliary equation):

$$\lambda^2 - \alpha_1 \lambda - \alpha_2 = 0,$$

$$\text{whose two roots are } \lambda_1 = \frac{\alpha_1 + \sqrt{\alpha_1^2 + 4\alpha_2}}{2}, \lambda_2 = \frac{\alpha_1 - \sqrt{\alpha_1^2 + 4\alpha_2}}{2}.$$

These are the characteristic roots and give the general solution to (A1) (Elaydi 1996).

There are two relevant cases:

$$\alpha_1^2 + 4\alpha_2 > 0 \Rightarrow \text{Real distinct roots: } n_t = C_1 \lambda_1^t + C_2 \lambda_2^t,$$

$$\alpha_1^2 + 4\alpha_2 < 0 \Rightarrow \text{Complex conjugated roots, (in polar coordinates):}$$

$$n_t = C_1 r^t \cos(t\theta - C_2),$$

$$\text{where } r \equiv |\lambda| = \sqrt{\left(\frac{\alpha_1}{2}\right)^2 + \left(\frac{\sqrt{-(\alpha_1^2 + 4\alpha_2)}}{2}\right)^2} = \sqrt{-\alpha_2}, \theta = \tan^{-1}\left(\frac{\sqrt{-(\alpha_1^2 + 4\alpha_2)}}{\alpha_1}\right), \text{ and } C_1$$

and C_2 are constants that depend on initial conditions.

It follows from the general solutions in both cases that they are stable for $t \rightarrow \infty$ iff

$|\lambda| < 1$ for both roots, i.e. they both fall within the unit circle. This condition is fulfilled

when:

$$\begin{aligned} (i) \quad \left| \frac{\alpha_1 \pm \sqrt{\alpha_1^2 + 4\alpha_2}}{2} \right| < 1 &\Rightarrow \left| \sqrt{\alpha_1^2 + 4\alpha_2} \right| < 2 - |\alpha_1| \\ &\Rightarrow \left(\left| \sqrt{\alpha_1^2 + 4\alpha_2} \right| \right)^2 < (2 - |\alpha_1|)^2 \\ &\Rightarrow |\alpha_1| < 1 - \alpha_2 \end{aligned}$$

and

$$(ii) \quad \sqrt{-\alpha_2} < 1 \Rightarrow \alpha_2 > -1$$

Combining (i) and (ii) provides the triangle in figure 5:

$$\begin{cases} \alpha_2 < 1 - \alpha_1 & , \forall \alpha_1 > 0 \\ \alpha_2 < 1 + \alpha_1 & , \forall \alpha_1 < 0 \\ -1 < \alpha_2 < 1 \end{cases}$$

The border between regions of real and complex roots is defined by:

$$\alpha_1^2 + 4\alpha_2 = 0 \Rightarrow \alpha_2 = -\left(\frac{\alpha_1^2}{4}\right).$$

With the general solutions to (A1) given above, it is clear that the qualitative dynamics are also given by the characteristic roots.

In the case of real roots, the root that is largest in magnitude will dominate.

For $\alpha_1 > 0$ (region II), λ_1 will be dominant and positive, and n_t will steadily approach equilibrium as $t \rightarrow \infty$. The number of time steps needed to reach some close proximity to the equilibrium will depend on the actual magnitude of the root; for dominant roots closer to 1 the more time steps are needed and convergence is slower. The magnitude increases as we approach the outer boundary, and decreases towards the centre and the complex border.

For $\alpha_1 < 0$ (region I), λ_2 will be dominant and negative, and λ_2^t will alternate between positive and negative values for even and odd t , respectively. This will give a dampened two point cycle towards the equilibrium, and both the number of time steps needed and the amplitude of the cycle, increase as we approach the outer boundary, and decrease towards the centre.

When roots are complex conjugated (region III), the rate of convergence is also dependent on the (now equal) magnitude (r) of the roots, giving slower convergence and larger amplitude as we approach the base of the triangle, where $r = 1$; resulting in stable limit cycles. As we see from the general solution, the period depends on θ . The cosine function has a cycle length of 2π , and the number of time steps needed to complete one cycle (i.e. the period) is given by $t\theta = 2\pi \Rightarrow t = \frac{2\pi}{\theta}$. The period increases with

decreasing θ , and solving for different t gives the period contour lines in figure 5. With the following properties of the (multivalued) inverse tangent function:

$$\tan^{-1}(0^-) = \pi, \quad \tan^{-1}(\infty) = \frac{\pi}{2}, \quad \tan^{-1}(0^+) = 0,$$

we see that as we move (below the parabola and within the triangle) from left to right, θ decreases from π for $\alpha_1 = -2\sqrt{-\alpha_2}$ (\Rightarrow period = 2), through $\frac{\pi}{2}$ for $\alpha_1 = 0$ (\Rightarrow period = 4), and towards 0 for $\alpha_1 = 2\sqrt{-\alpha_2}$ (\Rightarrow period = ∞).

E. Zero growth isoclines

The following is solved with equations in untransformed variables (anti-log transformation of (4)) due to information of curvature (see ‘Bivariate first order annual model’). Ignoring constants (as they become positive) and noise, the ZGI are then described by the conditions:

$$\text{ZGI}_N: \frac{N_{f,t}}{N_{f,t-1}} = 1 \Rightarrow (N_{f,t-1})^{\beta_{11}-1} (P_{f,t-1})^{\beta_{12}} = 1$$

$$\text{ZGI}_P: \frac{P_{f,t}}{P_{f,t-1}} = 1 \Rightarrow (N_{f,t-1})^{\beta_{21}} (P_{f,t-1})^{\beta_{22}-1} = 1.$$

Dropping subscripts and solving these equations for P we get both ZGI as functions of N :

$$\text{ZGI}_N: P = (N)^{\frac{1-\beta_{11}}{\beta_{12}}} \quad \text{and} \quad \text{ZGI}_P: P = (N)^{\frac{\beta_{21}}{1-\beta_{22}}}. \quad (\text{Since } \{N, P\} > 0)$$

For ZGI_N we have required a decrease with increasing P , equivalent to a decrease of P with increasing N , giving:

$$\frac{\partial}{\partial N}(\text{ZGI}_N) < 0 \Rightarrow \left(\frac{1-\beta_{11}}{\beta_{12}} \right) (N)^{\frac{1-\beta_{11}}{\beta_{12}}-1} < 0 \Rightarrow \left(\frac{1-\beta_{11}}{\beta_{12}} \right) < 0,$$

and knowing $[\beta_{12} < 0]$, this is true iff $[\beta_{11} < 1]$.

An increasing ZGI_P is equivalent to

$$\frac{\partial}{\partial N}(\text{ZGI}_P) > 0 \Rightarrow \left(\frac{\beta_{21}}{1-\beta_{22}} \right) (N)^{\frac{\beta_{21}}{1-\beta_{22}}-1} > 0 \Rightarrow \left(\frac{\beta_{21}}{1-\beta_{22}} \right) > 0,$$

and with $[\beta_{21} > 0]$, this is true only iff $[\beta_{22} < 1]$.

The curvature is given by the sign of the second derivatives:

For the resource we have:

$$\frac{\partial^2}{\partial N^2}(\text{ZGI}_N) = \left(\frac{1-\beta_{11}}{\beta_{12}} - 1 \right) \left(\frac{1-\beta_{11}}{\beta_{12}} \right) (N_{f,t})^{\frac{1-\beta_{11}}{\beta_{12}}-2}, \text{ which with the above conditions is}$$

always positive, guaranteeing a convex ZGI_N .

For the resource we have:

$$\frac{\partial^2}{\partial N^2}(\text{ZGI}_P) = \left(\frac{\beta_{21}}{1-\beta_{22}} - 1 \right) \left(\frac{\beta_{21}}{1-\beta_{22}} \right) (N_{f,t})^{\frac{\beta_{21}}{1-\beta_{22}}-2}, \text{ which with the above conditions is}$$

negative and thereby concave iff $\left(\frac{\beta_{21}}{1-\beta_{22}} - 1 \right) < 0 \Rightarrow \frac{\beta_{21}}{1-\beta_{22}} < 1 \Rightarrow \beta_{21} + \beta_{22} < 1$.

F. Coefficient boundaries

Following is the derivation of coefficient boundaries depicted in figure 9. This is done by combining the conditions found when studying the general model dynamics. The alphabetical listing corresponds to the indexing in figure 9.

a) follows directly from the stability criteria (fig. 5 and Appendix D) and the link between the coefficients.

b) follows from combining $[\beta_{11} < 1]$, $[\beta_{22} < 1]$, and the lower boundary in $[-2 < \beta_{11} + \beta_{22} < 2]$. This implies $[-3 < \beta_{11}]$, $[-3 < \beta_{22}]$, and $[-3 < \beta_{11}\beta_{22} < 1]$.

c) follows from $[\beta_{21} > 0]$, $[\beta_{21} + \beta_{22} < 1]$, and implication from b): $[-3 < \beta_{22}]$.

This implies $[0 < \beta_{21} < 4]$.

d) follows from $[\beta_{21} > 0 \vee \beta_{12} < 0 \Rightarrow \beta_{21}\beta_{12} < 0]$, $[-1 < (\beta_{11}\beta_{22} - \beta_{11}\beta_{22}) < 1]$, and implication from b): $[-3 < \beta_{11}\beta_{22} < 1]$. This implies $[-4 < \beta_{21}\beta_{12} < 0]$.

e) follows from $[\beta_{12} < 0]$ combined with implications from c): $[0 < \beta_{21} < 4]$, and d): $[-4 < \beta_{21}\beta_{12} < 0]$.

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