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Christian Jost

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Institut national agronomique Paris-Grignon

THÈSE

pour obtenir le grade de

Docteur de l'Institut national agronomique Paris-Grignon

présentée et soutenue publiquement par

Christian Jost

le 11 décembre 1998

**Comparaison qualitative et quantitative de modèles
proie-prédateur à des données chronologiques en
écologie**

**Comparing predator-prey models qualitatively and
quantitatively with ecological time-series data**

Jury :

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“Che voust far, cunter il vent nu poust pischar”

Old Rhaetian saying

“Steter Tropfen höhlt den Stein”

Old German saying

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Part I

General introduction and main
results of this thesis

Chapter 1

Predator dependence in the functional response and its implications in ecology

1.1 Some comments on mathematical population ecology

One of the first mathematical descriptions of population dynamics can be found by the end of the 18th century when Malthus (1798) introduced what is known today as Malthusian growth: a population increases exponentially as long as resources are unlimited. Defining $N(t)$ to be the population abundance at time t this growth can be described by the differential equation

$$\frac{dN(t)}{dt} = rN(t)$$

with growth rate r . But what happens if resources (e.g., space, food, essential nutrients) are limited? That limited resources can stop population growth was introduced empirically by Verhulst (1838) in what is called today logistic growth,

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right). \quad (1.1)$$

The carrying capacity K defines some population abundance limit beyond which the population growth rate becomes negative, while below it, this growth rate is positive. Thus, K is some equilibrium value towards which the population abundance tends to converge. K can also be interpreted as a measure of the available resources, the logistic growth is therefore a model with donor control (Pimm, 1982): the population is controlled by its resources.

There is another way how a population can be prevented from growing exponentially: there can be another population that consumes the first population at a rate exceeding this first populations' growth rate. Such a predator-prey interaction has first been described by two persons working independently, Lotka (1924) and Volterra (1926). With $P(t)$ being

the abundance of this second population, the predator, they described the interaction by the set of differential equations

$$\begin{aligned}\frac{dN}{dt} &= rN - aNP \\ \frac{dP}{dt} &= eaNP - \mu P\end{aligned}\tag{1.2}$$

with predator attack rate a , conversion efficiency e (percentage of consumed prey biomass that is converted into predator biomass) and predator mortality rate μ . Depending on the initial abundances of prey and predator they will cycle eternally, passing periodically through the initial values (neutral stability). The discovery of a cycling mathematical predator-prey system coincided with Elton's (1924) article on fluctuating animal populations. This initiated the hypotheses that such fluctuations are caused by predator-prey interactions. Hundreds of papers have investigated this hypotheses and still much is unknown (see review in Chitty 1996).

However, in this thesis I am not interested in cycling populations. Recall that in the logistic population growth model control is exercised from the bottom (donor control or bottom-up). Consider now the prey equilibrium in the Lotka-Volterra predator-prey system,

$$N^* = \frac{\mu}{ea}.$$

Not only is the predator preventing its prey from growing infinitely, its parameters μ , e and a also define the equilibrium state of the prey. This relation expresses mathematically what is often called top-down control.

There are no unique definitions in ecology (specifically in the context of trophic chains) for the terms top-down control/effect and bottom-up control/effect. In general, top-down control is used in the sense of Hairston et al. (1960), that is that every trophic level has the potential to control/repress its prey to a low level that is independent of the prey's resources, except if it is itself controlled by its own predator (the 'why the world is green hypotheses' in the case of three-level trophic chains, stating that herbivores do not graze plants down to low levels, thus creating a brown world, because they are controlled by carnivores). A generalisation of this to food chains of arbitrary length is the exploitation ecosystem hypotheses (EEH, Fretwell 1977; Oksanen et al. 1981) where trophic levels an odd number below the top trophic level are top-down controlled, while the others are bottom-up controlled. A special case are cascading effects (Carpenter et al., 1985; Carpenter & Kitchell, 1994) that study how changes in the top trophic level cascade several levels down the trophic chain. Bottom-up effects are the driving factor in donor-controlled food chains (Pimm, 1982; Berryman et al., 1995) where every trophic level is uniquely controlled by its resources and its mortality rate is independent of its predators density. For further information see the discussions in Hunter & Price (1992), Strong (1992), Power (1992) and Menge (1992) or the well written synthesis in chapter II of Ponsard (1998). In this thesis, I will talk of bottom-up control when the equilibrium abundance of a trophic level is positively correlated with the resources on the first trophic level in the studied system (e.g., increasing K in the case of logistic growth). Top-down control of a population refers to the case when a change in its predators abundance or

parameters induces a change in the prey population equilibrium abundance. As will be seen later, these definitions are not mutually exclusive, a population can be controlled both top-down and bottom-up.

The two views, top-down and bottom-up, are of general interest because they make very different predictions how trophic level equilibrium abundances change with increasing resources (see Table 1.1). For example, to reduce algal density in a eutrophic lake with four trophic levels (algae, herbivorous zooplankton, carnivorous zooplankton, planktivorous fish), the bottom-up control proposes that the unique way to do so is to reduce nutrient levels in the lake, while the top-down approach by Oksanen et al. (1981) suggests that, on the contrary, fertilizing the lake will reduce algal density by increasing herbivorous zooplankton density.

Coming now back to the Lotka-Volterra system: are all predator-prey systems of the top-down control type indicated by this system? Or do there also exist predator-prey systems that correspond better to bottom-up or mixed types of control? These questions are of a general interest, because all direct interactions between species at different trophic levels of a food web are of a predatory nature. The particular choice of the mathematical form describing the predator-prey interaction in such general food web models can have profound impacts on the predictions of these models to perturbations at the bottom (changing nutrient status) or the top (introduction or removal of top predators), see preceding paragraph. Such predictions are used when deciding about management policy of exploited natural populations or in conservation biology issues. There is still few known about the respective importance of top-down or bottom-up forces in natural systems (Menge, 1992; Power, 1992). In this situation, an ecologist should try to make predictions that are independent of the type of control, or at least, he should identify the predictions that are sensitive to the dominance of one of the forces. In the following, I will introduce a predator-prey model with bottom-up characteristics that can serve as an alternative to Lotka-Volterra types of predation. By confronting this model and Lotka-Volterra type models qualitatively and quantitatively with time-series data from observed predator-prey systems, I hope to gain some information about the controlling mechanisms in these systems.

1.1.1 A general predator-prey modelling framework

The predator-prey models that will be studied in this thesis follow two general principles. The first one is that population dynamics can be decomposed into birth and death processes,

$$\frac{dN}{dt} = \text{growth} - \text{death}.$$

The second one is the conservation of mass principle (Ginzburg, 1998), stating that predators can grow only as a function of what they have eaten. With these two principles we can write the canonical form of a predator-prey system as

$$\begin{aligned} \frac{dN}{dt} &= f(N)N - g(N, P)P - \mu_N(N)N \\ \frac{dP}{dt} &= e g(N, P)P - \mu_P(P)P \end{aligned} \tag{1.3}$$

with prey per capita growth rate $f(N)$, functional response $g(N, P)$ [prey eaten per predator per unit of time, Solomon 1949] and natural mortalities $\mu_N(N)$ and $\mu_P(P)$. The numerical response (predator per capita growth rate as a function of consumption) is considered in this framework to be proportional to the functional response. Note that the system (1.3) becomes the Lotka-Volterra system (1.2) when $f(N) = r$, $g(N, P) = aN$, $\mu_N(N) = 0$ and $\mu_P(P) = \mu$. Many other forms have been proposed in the literature for the functions f , g and μ_x ($x \in \{N, P\}$). See Appendix A for an (incomplete) collection of functions I found in the literature. In particular the functional response g has incited creative works, see Bastin & Dochain (1990) who list over 50 models.

Usually one considers consumption to be the major death cause for the prey. In this case $\mu_N(N)$ can be neglected and set to 0 (as long as the predator exists). I will follow this usage in the present thesis, replace the growth rate $f(N)$ by the standard logistic growth (Verhulst 1838, see Figure 2.3) and also consider predator mortality to be constant as in the Lotka-Volterra equations, giving the equations

$$\begin{aligned}\frac{dN}{dt} &= r \left(1 - \frac{N}{K}\right) N - g(N, P)P \\ \frac{dP}{dt} &= eg(N, P)P - \mu P.\end{aligned}\tag{1.4}$$

1.1.2 Top-down and bottom-up control in predator-prey models

Traditionally, the functional response in system (1.4) is assumed to be a function of prey abundance only, $g(N, P) = g(N)$, e.g.

$$g(N) = aN \quad (\text{Lotka 1924}) \tag{1.5}$$

$$g(N) = \frac{aN}{1 + ahN} \quad (\text{Holling 1959b}) \tag{1.6}$$

(see Table A.2 for further examples). I will call this case a prey-dependent functional response (Arditi & Ginzburg, 1989). In this case, the prey equilibrium density is of the form

$$N^* = g^{-1} \left(\frac{\mu}{e} \right).$$

Thus, as in the Lotka-Volterra case, it is entirely defined by the predator's parameters. Graphically, this is expressed in the vertical predator isocline in Figure 4.2a. Increasing carrying capacity K (enrichment) will only change the prey isocline and result in a destabilization of the equilibrium, the so-called paradox of enrichment (Rosenzweig, 1971). The traditional prey-dependent approach in the context of framework (1.4) will therefore always result in a top-down controlled predator-prey model that becomes destabilized under enrichment.

The previous analysis indicates where we have to change our system (1.4) to break this pattern: the functional response must also depend on predator abundance, $g = g(N, P)$. I will call this case predator dependence. Usually, higher predator density leads to more frequent encounters between predators. This can cause a loss in predating efficiency

either simply by time lost to detect that the encountered organism is not a prey (this time is thus not spent searching for other prey), or because of active interference between predators (Beddington, 1975; Hassell & Varley, 1969). Therefore, predator abundance should influence the functional response negatively,

$$\frac{dg(N, P)}{dP} < 0.$$

How this modification changes the top-down pattern will be discussed in more detail in the next section. There is a large literature on predator dependence of the functional response in both vertebrates and invertebrates (reviews in Hassell 1978 and in Sutherland 1996, Anholt & Werner 1998, Clark et al. 1999).

In behavioural ecology one finds also the inverse effect, predator facilitation. Cooperation between predators can pay off in increased reproductive success. Examples are lions hunting in pairs rather than alone (Krebs & Davies 1993, p. 278) or patellid limpets capturing drifting kelp and seaweed debris (Bustamante et al., 1995). However, this thesis will only consider detrimental predator dependence, which seems to be more frequent.

1.2 Introducing predator dependence

Predator dependence in the functional response has been introduced on many occasions. The first one that had some echo in the literature was by Hassell & Varley (1969), who proposed that the attack rate a should decrease with increasing predator density. They proposed an exponential decrease with rate m ,

$$a = \alpha P^{-m}. \quad (1.7)$$

Parameter m can be interpreted as an interference coefficient. The stronger predators interfere one with each other, the larger m should be. While used at first only to explain attack rates measured in the field, incorporating this attack rate into system (1.4) also showed a stabilising effect (Beddington, 1975; Beddington et al., 1978). There are two technical problems with this formulation. First, there is a minor dimensional problem (Beddington et al., 1978), which can be remedied by introducing a ‘dummy’ parameter u_P with dimension $[P]$ (representing one ‘unit’ predator) and rewriting (1.7) as

$$a = \alpha \left(\frac{P}{u_P} \right)^{-m}.$$

Usually, this ‘dummy’ parameter is not mentioned but tacitly assumed (Hassell 1978, p. 84). The second problem is more grave and concerns the mathematical analysis of systems using this type of attack rate: due to the exponent m it is often impossible to find the equilibria explicitly, thus rendering stability or other types of analyses much more tedious (requiring the use of implicit function theory or other more sophisticated techniques).

Both problems can be avoided by introducing predator dependence in the way proposed by Beddington (1975) and DeAngelis et al. (1975),

$$g(N, P) = \frac{aN}{1 + ahN + cP} \quad (1.8)$$

with prey handling time h (the same as in the usual Holling type II functional response (1.6)) and an empirical constant c . Beddington (1975) derived this model based on behavioural mechanisms, assuming that the predator spends its time either searching for prey, handling prey or handling other predators (recognition, maybe interference). c is in this context the product of predator encounter rate and predator handling time. The system (1.4) together with this functional response can be analysed in the usual way, solving for equilibria and testing stability (e.g., with the Routh-Hurwitz criteria, Edelstein-Keshet 1988). Doing this, DeAngelis et al. (1975) noted that in case of $1 + ahN \ll cP$ this system becomes donor controlled. Therefore, the functional response (1.8) provides a simple way to get bottom-up features in a predator-prey system. However, it has rarely been used either in mathematical studies or in applications to real ecological systems. Likely reasons are that the parameter c is difficult to estimate and the mathematical analysis is not as simple as for example with Lotka-Volterra or Holling type II functional responses because it is a function of two separate arguments, N and P , forcing the use of partial differentiation.

1.2.1 A novel approach: ratio-dependent functional responses

A simpler way to include predator dependence has been proposed by Arditi & Ginzburg (1989), modelling the functional response as a function of one argument only (as in the traditional way), but this argument being now the ratio prey per predator,

$$g(N, P) = g\left(\frac{N}{P}\right). \quad (1.9)$$

This is a special case of predator dependence, and models using this type of functional response are usually called ratio-dependent models (Arditi & Ginzburg, 1989). $g(x)$ is in general a continuous, increasing and bounded function of its argument x , just as in prey-dependent models. For example, a frequently used ratio-dependent functional response is based on an analogy with the Holling type II model (1.6),

$$g\left(\frac{N}{P}\right) = \frac{\alpha N/P}{1 + \alpha h N/P}. \quad (1.10)$$

The simplicity of the approach allowed Arditi & Ginzburg (1989) to analyse general food chains and to compare how the equilibria of the different trophic levels change with changing primary productivity $F := f(N)N$. The results are summarised in Table 1.1. It can be seen that in ratio-dependent models equilibria of all trophic levels increase with higher productivity (independently of the food chain length), while prey-dependent food chains show an alternating pattern with increase, no change and decrease. In particular, the second highest trophic level is always top-down controlled, while trophic levels that are an even number below the top level are bottom-up controlled. The prey-dependent pattern has been observed in a three-level microbial laboratory food chain (Kaunzinger & Morin, 1998), although a slight (unexplained) increase of the second trophic level with enrichment was observed. Oksanen et al. (1981), who analysed prey-dependent food chains in general, thought to find the pattern predicted by prey-dependent theory in

Table 1.1: Trends of equilibria of basal prey (N^*) and predatory trophic levels (P_1^* , P_2^* , etc.) with increasing primary productivity F in either prey-dependent or ratio-dependent food chains. Arrows indicate the direction of change. Table adapted from Arditi & Ginzburg (1989).

Trophic level	Prey-dependence				Ratio-dependence			
	2	3	4	5	2	3	4	5
P_4^*				↗				↗
P_3^*			↗	→			↗	↗
P_2^*		↗	→	↗		↗	↗	↗
P_1^*	↗	→	↗	↘	↗	↗	↗	↗
N^*	→	↗	↘	↗	↗	↗	↗	↗

data of ecosystems of arctic-subarctic plant communities (Oksanen, 1983). In the field, the best data are available from freshwater lakes along a gradient of nutrient content. Extensive studies have shown that the biomasses of all trophic levels (phytoplankton, herbivorous zooplankton, carnivorous zooplankton, planktivorous fish) increase along a gradient of enrichment (McCauley et al., 1988; Mazumder, 1994; Mazumder & Lean, 1994; McCarthy et al., 1995; Harris, 1996; Sarnelle et al., 1998). Thus, the observations conform qualitatively with the predictions of the ratio-dependent model. A number of explanations have been advanced to explain this pattern (McCauley et al., 1988; Abrams, 1993), predator dependence in the functional response is just one possibility. However, ratio dependence offers one of the most parsimonious ways to model the observed patterns. Note that the use of a ratio-dependent functional response in system (1.4) also influences the link between stability and enrichment (see chapter 5 for details): a change in carrying capacity K only influences the amplitude of trajectories, but not the stability behaviour of the equilibrium. This signifies that the paradox of enrichment is closely linked to the vertical predator isocline and any variation from this will make other responses than destabilization possible.

Modelling food webs rather than food chains is mathematically more complex. Michalski & Arditi (1995a) and Arditi & Michalski (1995) developed mathematical food webs with Holling type II, DeAngelis-Beddington and ratio-dependent functional responses. With the latter a distinctive feature emerged that was not present with the other functional responses: while the dynamics are in a transient state (before reaching equilibrium), trophic links appeared and disappeared frequently (Michalski & Arditi, 1995b). Once at equilibrium, there are few links in the food web, but if the food web is observed continuously during transient dynamics, the links accumulate and give very complex looking food webs such as the cod food web in Lavigne (1996) (reproduction in Yodzis (1995)).

1.2.2 Experimental evidence for ratio dependence

Besides the cited plankton abundances that are correlated with the trophic state of lakes there is also experimental evidence. There has been a series of experiments with two cladoceran predator species, *Daphnia magna* and *Simocephalus vetulus*, feeding on the algae *Chlorella vulgaris* (Arditi et al., 1991b; Arditi & Saïah, 1992). Algae were raised in

a separate vessel and added at a constant rate to a first vessel with the predator. Outflow from this vessel (with algae only, predators prevented from migration to the next vessel) went to a second vessel with predators and so on. The hypothesis was that in case of a vertical predator isocline (prey dependence) the predator should subsist only in the first vessel, grazing algae down to a fixed level that cannot sustain predator populations in the following vessels. On the other side, if the predator isocline is slanted, predators are likely to survive also in consecutive vessels (see Figure 1.1). The predators chosen for the experiment had a particular spatial behaviour, *Daphnia* swimming homogeneously in the medium while *Simocephalus* keeps close to the vessel walls. *Daphnia* followed the pattern predicted by a vertical predator isocline, while *Simocephalus* persisted in several consecutive vessels. In a next step *Daphnia* were prevented from moving in the whole vessel while *Simocephalus* were distributed homogeneously by frequent stirring. With this setup, *Daphnia* persisted in several vessels, while *Simocephalus* only persisted in the first one. These experiments clearly demonstrate that spatial heterogeneity can cause a slanted predator isocline. However, they do not show that the predator isocline goes through the origin, as predicted by ratio-dependent models (Ruxton & Gurney, 1992; Holmgren et al., 1996). Figure 1.1 illustrates this point for the example of three consecutive vessels. Both the ratio-dependent model and a DeAngelis-Beddington type model predict qualitatively the same pattern, namely that predator abundance at equilibrium decreases geometrically from one vessel to the next.

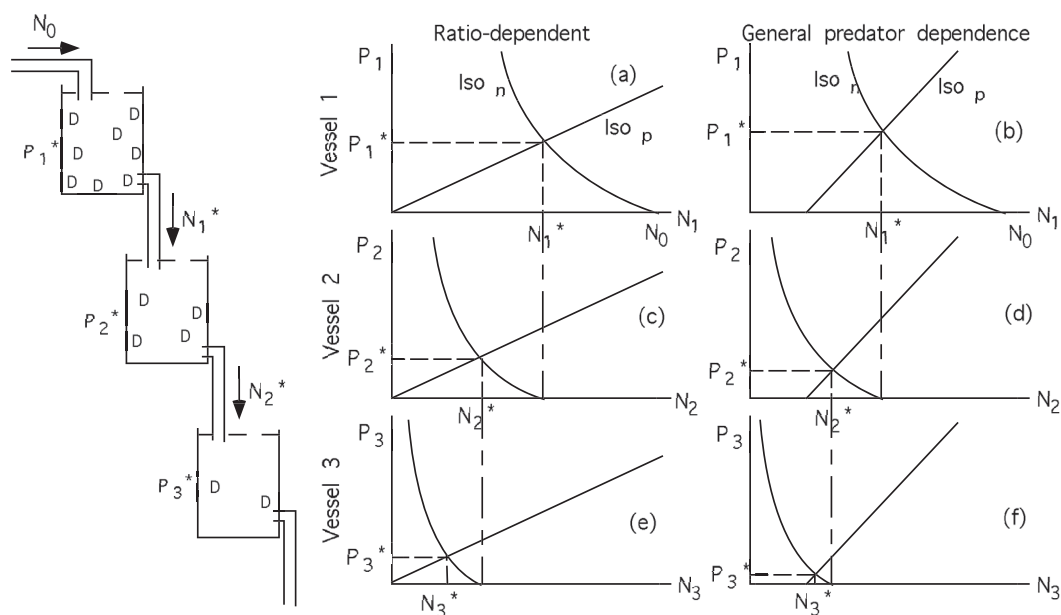


Figure 1.1: Predictions of the predator equilibrium abundances in the chained vessel experiments described in Arditi et al. (1991b), for a ratio-dependent model (left) and a DeAngelis-Beddington type model (right). N is the algae concentration and P the number of cladoceres. Iso_n and Iso_p are prey-isocline and predator-isocline respectively. D represent cladocere individuals. The first vessel equilibrates as indicated in (a) and (b), letting N_1^* flow into the second vessel (c) and (d) and so on. With both models P_i^* decreases in a geometrical way.

In another study, Arditi & Akçakaya (1990) reanalyzed data of functional response

experiments found in the literature (predator-prey and host-parasitoid systems). In all these experiments both prey and predator abundances were varied and the functional response was measured as a function of both variables. Arditi & Akçakaya fitted a model based on the Hassell & Varley (1969) function (1.7),

$$g(N, P) = g\left(\frac{N}{P^m}\right) = \frac{\alpha P^{-m} N}{1 + \alpha P^{-m} h N}. \quad (1.11)$$

Note that this Hassell-Varley-Holling functional response is prey-dependent for $m = 0$ while ratio-dependent for $m = 1$. Actual estimation was done in two steps, first estimating for each predator density the attack rate $a = \alpha P^{-m}$ by regressing the usual Holling type II model (nonlinear regression, taking prey depletion into account by use of the random predator equation, Rogers 1972),

$$g(N|P) = \frac{aN}{1 + ahN},$$

then estimating m by linear regression on log-scale using the relation (1.7). These measurements yielded estimates of m that are mostly closer to 1 than to 0, thus indicating that the predator isoclines should not only be slanted, but that ratio dependence is closer to real dynamics than prey dependence.

1.2.3 Mechanistic derivations of ratio dependence

One of the most frequent criticisms of ratio-dependent theory concerns its introduction as a phenomenological model (Murdoch et al., 1998; Abrams, 1994). Originally, Arditi & Ginzburg (1989) gave several possible mechanisms that can lead to ratio dependence (different time scales of feeding and population dynamics, predator interference, refuge for prey, non-random search, general aspects of heterogeneity) but without elaborating on them. Some of these hypothetical causes have recently been analysed mathematically and it has been shown that they can indeed lead to ratio dependence. Michalski et al. (1997) and Poggiale et al. (1998) studied systems where the prey have a refuge patch and migration of prey between the refuge and the patch with the predator occur at a slower time scale than the population dynamics in the mixed patch (where predation is assumed to occur in a prey-dependent way). This model can be aggregated mathematically to a one-patch predator-prey model and results in a linear ratio-dependent functional response. Cosner et al. (1999) studied different ways of spatial organisation of predators during feeding activity. Depending on the geometry of the predator distribution (evenly distributed, patchy, aligned), functional responses of several types, including ratio-dependent, can result.

We can derive ratio dependence also by taking directly the original functional response proposed by Beddington (1975),

$$g(N, P) = \frac{aN}{1 + ahN + cP'}, \quad (1.12)$$

where c is the product of predator encounter rate and interference time and $P' = P - u_P$ is one unit predator (u_P) less than the total predator abundance. Beddington derived this

form by letting the predator either search for prey, meet a prey and consume (handle) it or meet a predator and engage in interference (during some constant interference time). Although there are some problems in his reasoning (Ruxton et al., 1992), this functional response is often cited in the literature, usually replacing P' by P for simplicity. However, keeping P' and rearranging (1.12) gives

$$g(N, P) = \frac{aN}{(1 - cu_P) + ahN + cP}.$$

For $c = 0$ this becomes the usual Holling type II functional response, while for $c = 1/u_P$ we obtain a ratio-dependent functional response. The Beddington-DeAngelis model is thus a true intermediate model like the Hassell-Varley-Holling model (1.11).

Additional mechanistic derivations in the microbiological context are mentioned in chapter 6: Fujimoto (1963) derived ratio dependence based on enzyme kinetics, while Characklis (1978) based his reasoning on saturation kinetics applied to mass transfer limited growth.

1.2.4 Alternatives to predator dependence

Before concluding this section, I should discuss possible alternatives to predator dependence in the functional response. Going back to the general predator-prey system (1.3), we see that slanted predator isoclines, as they are suggested by the empirical evidence of correlated equilibria along a gradient of enrichment, could also be explained by density-dependent predator mortality rates $\mu(P)$ (Gatto, 1991; Gleeson, 1994). The idea of such a density dependence has been introduced many times in predator-prey or more general models (DeAngelis et al., 1975; Steele & Henderson, 1981, 1992; Edwards & Brindley, 1996), see also Table A.4. While in predator-prey models this idea indeed gives the desired correlation between equilibrium abundances, in 3-level food chains with density-dependent mortality at the highest level there can be negative or positive correlation between the lower two trophic levels (see section 4.B). More complex patterns are to be expected with longer food chains. Predator dependence in the functional response thus offers a more ‘natural’ explanation since this feature yields correlated equilibrium abundances of all trophic levels independently of the specific parameter values. Furthermore, the functional response data analysed in Arditi & Akçakaya (1990) demonstrate directly predator dependence of the functional response, while I could not find such experimental evidence for a density-dependent mortality rate.

Another alternative is to abandon the general framework (1.3), in particular the conservation of mass principle. A prominent predator-prey model of this type goes back to Leslie (1948). This predator-prey model conserved the functional response in the prey equation, but used a logistic type form in the predator equation,

$$\begin{aligned} \frac{dN}{dt} &= r_1 \left(1 - \frac{N}{K}\right) - g(N)P \\ \frac{dP}{dt} &= \left(r_2 - b \frac{P}{N}\right)N \\ g(N) &= aN \quad (\text{standard Lotka-Volterra interaction}). \end{aligned} \tag{1.13}$$

An extension is to use a Holling type II functional response (1.6), giving a predator-prey system analysed by May (1975) and by Tanner (1975) and therefore called in the literature either the Leslie-May model or the Holling-Tanner model. Two features render this system interesting: First, the existence of limit cycles where the populations do not come close to extinction, and second, a more varied link between system stability and enrichment. The idea of density dependence based on the ratio predator by prey has been generalised to food webs and is quite prominent under the name logistic food web theory (Berryman et al., 1995). In the literature these approaches are also often referred to as ratio-dependent models (Freedman & Mathsen, 1993; Hsu & Huang, 1995), but referring here to the ratio predator per prey. However, Ginzburg (1998) argues that conservation of mass is an important feature of food web models and I will discuss in this thesis only models that comply with this principle.

1.2.5 Ratio dependence: state of the art

The results reviewed in the preceding pages show that predator dependence in the functional response is a frequent feature of laboratory and natural predator-prey populations, both for theoretical and experimental reasons. Or, the vertical predator isocline predicted by prey-dependent functional responses in framework (1.4) has experimentally been proven wrong in many cases. However, many alternatives exist (Hassell & Varley, 1969; Hassell & Rogers, 1972; Beddington, 1975; DeAngelis et al., 1975; Gatto, 1991), and ratio-dependence is only one possibility, although admittedly a very parsimonious one that can easily be generalised to food chains and food webs while remaining mathematically tractable. This latter argument is in fact a very strong one, since modelling as a tool in applied ecology (natural resource management, conservation biology, environmental impact assessment, etc.) should be simple to apply with few parameters that need to be estimated, otherwise the proposed models won't be used by practitioners. Two parameters for the functional response represent in this context already an upper limit, I am not aware of any study in applied ecology using more complex functional responses. Nevertheless, while the reported experiments (Arditi et al., 1991b; Arditi & Saïah, 1992) and the correlated plankton abundances along a gradient of richness demonstrate that the predator isocline is not vertical in many cases and that spatial heterogeneity increases the slope of the predator isocline, both results do not allow to distinguish between general slanted predator isoclines (Hassell & Varley, 1969; DeAngelis et al., 1975) and a predator isocline going through the origin as predicted by the ratio-dependent model (see also Figure 1.1). Arditi & Akçakaya (1990) and McCarthy et al. (1995) are the only papers with indications that ratio-dependent models are in many systems closer to reality than prey-dependent models (estimates of the interference parameter m being mostly closer to 1 than to 0). However, since this parameter m appears in a nonlinear context, being closer to 1 than to 0 does not mean necessarily that the predator isocline in the range of observed abundances is better approximated by a diagonal rather than by a vertical line (see Figure 1.2 and 4.2).

Despite all the empirical and theoretical evidence against prey-dependent predator-prey models, ratio dependence is still far from being accepted as a valid theoretical framework for modelling predator-prey systems or more complicated food chains and food webs.

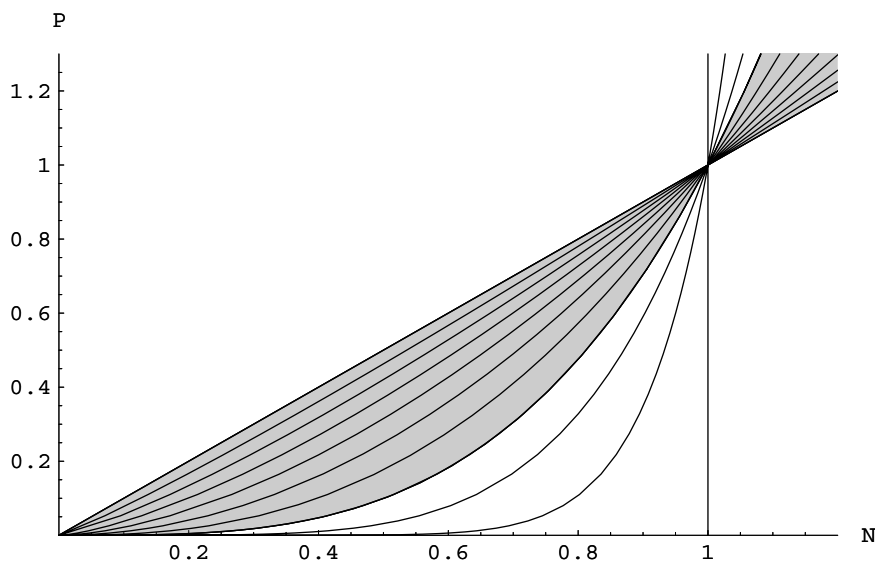


Figure 1.2: The predator isocline for different values of m in system (1.11). The grey shaded area indicates the range of values of m found by Arditi & Akçakaya (1990). For lower values of m the vertical predator isocline might be a better approximation than the diagonal predator isocline.

While some scientists regard it as complete nonsense (Abrams, 1994, 1997) others are afraid that it might deflect attention from more general forms of predator dependence (Murdoch et al., 1998). Still others criticise that predators can potentially persist at arbitrary low resource levels (Yodzis, 1994). However, this last argument also applies to logistic growth models, but nobody would argue that logistic growth (1.1) must be abandoned, e.g., in favour of its counterpart with Allee effect (Allee, 1931) (see section 2.3.1). Furthermore, there is no experimental evidence that disappearance of predators with decreasing resources is a deterministic rather than a stochastic result. Demographic stochasticity or mutational meltdown (accumulation of deleterious mutations in small populations due to the weaker power of selection in comparison to genetic drift, Lynch et al. 1995) will also show this disappearance of predators at low resource levels. Actually, the reasoning behind Yodzis' criticism has best been developed by Oksanen et al. (1981) and leads to the prediction that richer environments permit the existence of longer food chains. However, Pimm (1991, p. 224) shows that there is no evidence for such a correlation between primary productivity and food chain length.

In sum, there remains work on several levels to be done. First, prey-dependent and ratio-dependent models have to be compared to data on an equal footing, e.g., by statistical comparison tools (nonlinear regression in a likelihood framework) or by developing experiments that can disprove both types of isoclines, vertical ones and those that go through the origin. Second, there are still some features in ratio-dependent models that are mathematically poorly understood (dynamic behaviour at the origin where the models are not defined). A thorough mathematical understanding of a model can indicate both weaknesses and potentially strong features. Third, other possibilities of including predator dependence in an equally simple way as in ratio dependence have to be studied and confronted with the ratio-dependent approach. The interference parameter m proposed

by Hassell & Varley (1969) is such a candidate, the functional response proposed by Ashby (1976) (see Table A.3) another one. In this thesis, I will contribute mainly to the first and to the second task. Other possibilities of predator dependence are not analysed because they require more model parameters to have the same range of dynamic behaviours (see section 2.3.1 and chapter 8).

1.2.6 A short digression: to what density does ‘density dependence’ refer in the functional response?

There is some confusion in the literature about the use of the term density dependence in the context of predator-prey models since density may refer to prey or predator abundance. A reasonable approach has been used by Ruxton and coworkers who call the case of predator-dependence a ‘density-dependent’ functional response (Ruxton & Gurney, 1992; Ruxton, 1995), because the functional response is intrinsically bound to the predator (no functional response without predator) and also because density dependence indicates in its original sense a detrimental character concerning growth of an organism. However, other authors refer to prey density when using the term ‘density-dependent predation’ (Sih, 1984; Trexler, 1988; Moore, 1988; Mansour & Lipcius, 1991; Possingham et al., 1994; Anholt & Werner, 1998). This usage goes actually back to the founder of the terms functional and numerical response, Solomon (1949, p.16): “To be density-dependent, the enemy must take a greater proportion of the population as the host density increases”. Solomon himself refers to Varley (1947) and Nicholson (1933) for this usage. Despite the historical primacy I consider this to be wrong usage of the term. To avoid any confusion one might call a functional response that only depends on prey density a prey-dependent functional response. When this function also depends on predator density one can refer to a predator-dependent functional response.

Chapter 2

A case of model selection

To compare prey-dependent models to ratio-dependent models in the full generality included in these two classes of models is a difficult, if not an impossible task. A possible approach is to take a parametric representative of each class, both of the same complexity (in the sense of having the same number of parameters and of having the same range of possible dynamic behaviours), and then confront these two predator-prey models qualitatively (stability analysis, reaction to parameter changes, temporal dynamics) and quantitatively (nonlinear regression, likelihood) to ecological data. A better agreement between one of the models and the data can then be interpreted that the strength of predator dependence in the functional response is smaller or larger. The data are either qualitative temporal dynamics of a predator-prey system (plankton dynamics in freshwater lakes, section 2.2) or time-series data from simple protozoan predator-prey systems, structurally more complex arthropod systems and complex freshwater plankton systems (section 2.5).

2.1 The candidate predator-prey models

I will analyse two models. Both have logistic growth of the prey (in the absence of a predator) and a constant predator mortality rate. The prey-dependent functional response is of the Holling type II form (1.6), while the ratio-dependent model is also of this form, but with the ratio N/P (prey per predator) as its argument,

$$\begin{aligned}\frac{dN}{dt} &= r\left(1 - \frac{N}{K}\right)N - g(N, P)P \\ \frac{dP}{dt} &= eg(N, P)P - \mu P\end{aligned}\tag{2.1}$$
$$\frac{aN}{1 + ahN} \longleftarrow g(N, P) \longrightarrow \frac{\alpha N/P}{1 + \alpha hN/P}.$$

Both models have six parameters. As will be shown in chapter 4 they have both three possible equilibria and the dynamics can be either stable coexistence, unstable coexistence (limit cycle), extinction of the predator only or extinction of both populations (the latter

exists in the prey-dependent model only approximatively, i.e., large amplitude limit-cycle oscillations bringing the dynamics very close to extinction). These dynamics are also found in the ecological time-series with which I will confront the models.

Density dependence in the prey growth function is required for two reasons, first, that the prey population does not explode in the absence of predators, second, because malthusian growth combined with a bounded functional response would always yield an unstable non-trivial equilibrium. There are alternative growth functions (Gompertz, 1825; Rosenzweig, 1971) and we chose the logistic one simply because of its general acceptance. Both functional responses are bounded (saturation of the consumption), an ecologically uncontested feature. There are prey-dependent alternatives to the Holling type II functional response that have also two parameters (Ivlev, 1961; Watt, 1959) and we choose the Holling type II function simply because it is the most widely used and best understood function. There exist also predator-dependent alternatives to the ratio-dependent functional response, such as the linear Hassell-Varley type functional response,

$$g(N, P) = \alpha P^{-m} N,$$

or the form proposed by Ashby (1976) or Hassell & Rogers (1972),

$$g(N, P) = \frac{aN}{1 + ahN} \frac{1}{P}.$$

While both have only two parameters like the ratio-dependent model, they both have the drawback that the functional response is unbounded for $P \rightarrow 0$ and that in the framework (2.1) they cannot have an unstable non-trivial equilibrium or stable limit cycles. We can therefore safely argue that the Holling type II like ratio-dependent functional response is the only simple predator-dependent functional response whose dynamic behaviours are comparable to the ones with a Holling type II (prey-dependent) function.

2.1.1 Note on discrete versus continuous models

The two candidate models developed in the preceding section are both continuous time models (differential equations). Such models apply to large populations that have complete overlap between generations. The opposite extreme to this are populations that are made up of a single generation, with no overlap between generations (e.g., annual plants). Such populations should evolve in discrete steps,

$$\begin{aligned} N_{t+1} &= F(N_t, P_t) \\ P_{t+1} &= G(N_t, P_t) \end{aligned}$$

(see comments to such models in May (1976a) or in Begon et al. (1996a)). The ratio-dependent approach has rarely been used in discrete models, the only example to my knowledge is Carpenter et al. (1993) and Carpenter et al. (1994) (they used discrete models for technical reasons in their time-series analysis). The real data used in this thesis for model comparison can all be characterised by overlapping generations with large populations, they therefore conform better to continuous time models. For this reason I only used and compared differential equations, which is numerically more demanding but easier for the theoretical aspects. The usefulness of ratio-dependent approaches in discrete models remains so far unexplored.

2.2 Qualitative comparison of models

This section will summarise the ideas and results of the analysis developed in chapter 4.

The best known temporal dynamics from non-laboratory systems probably come from plankton in freshwater lakes of the temperate zone. Studying the detailed dynamics of phyto- and zooplankton in 24 lakes of the temperate zone Sommer et al. (1986) developed a verbal model (PEG-model, PEG standing for Plankton Ecology Group) of these dynamics in 24 statements that can be grossly summarised as in Figure 4.1. In early spring both phytoplankton and zooplankton start growing from the low overwintering levels. Phytoplankton reaches a very high spring peak, followed by a strong decline to very low levels due to overgrazing by herbivorous zooplankton and nutrient depletion. This decline is called the clear water phase (CWP) because the water appears very clear due to the low phytoplankton levels. After this decline phytoplankton increases again to the spring peak levels, dominated mostly by inedible species (filamentous, with defence structures, toxic), and remains at these levels during the summer until decreasing temperature and light engender a population decline in autumn. Zooplankton dynamics follow these dynamics with some lag with less distinct maxima and minima. The observed dynamics are quite independent of the trophic state of the lake, only the amplitudes increase and the spring peak is reached earlier with increasing nutrient status.

2.2.1 Interpretation in the predator-prey context

These dynamics from spring to autumn are interpreted in the PEG-model as the result of trophic interactions. The simplest possible way is to consider phytoplankton as prey and zooplankton (mostly *Daphnia sp.*) as predators and the temporal dynamics correspond to transient dynamics starting with low initial conditions and reaching the equilibrium state during summer after some strong oscillations. Chapter 4 explores whether the two models under consideration in this thesis (2.1) can explain these dynamics and if there are differences between their predictive power.

In a first step the global dynamics of the two predator-prey systems are analysed. A first observation concerns the prey equilibrium and how it changes with enrichment (eutrophication, modelled by carrying capacity K): in the prey-dependent model the prey-equilibrium is independent of carrying capacity, while the ratio-dependent model predicts a proportional relationship. Observations of natural lakes show a strong correlation between nutrient status and average phytoplankton abundance (McCauley et al., 1988; Mazumder & Lean, 1994), thus being in accordance with the ratio-dependent model. To study the transient dynamics we first construct the isoclines. Both models have a humped prey isocline and a straight predator isocline, the difference being that the prey-dependent model has a vertical predator isocline and the ratio-dependent model a diagonal one (Figure 4.2). There are maximally three equilibria: the origin $(0, 0)$, the system without predators $(K, 0)$ and a non-trivial equilibrium. This section focuses on the last (non-trivial) equilibrium which should be locally stable and reached with oscillations to conform to the dynamics of the PEG-model. After non-dimensionalisation the regions in parameter space that permit such dynamics are identified, see Figure 4.3. The main

difference between the models is, again, the reaction to enrichment (increasing K): destabilization in the prey-dependent model, only increasing amplitudes in the ratio-dependent model. This makes the ratio-dependent model conform better with the observed dynamics that did not show any sign of destabilization in more eutrophic lakes. However, the ratio-dependent model can explain the observed earlier attaining of the spring peak in eutrophic lakes (as described in the PEG-model) only if with eutrophication the growth rate r also increases.

Despite this slight advantage of the ratio-dependent model, neither model can reproduce the PEG-model dynamics: either there is a strong initial oscillation (causing the CWP), but then the system continues oscillating during the summer, or the system stabilises in early summer but then there is no CWP (Figure 4.5). Apparently, the two predator-prey systems are too simple to explain the dynamics.

McCauley et al. (1988) suggested that several parameters change during the season:

- growth rate r increases due to higher water temperatures,
- attack rate a (α) decreases due to an increasing proportion of inedible algae,
- predator mortality μ increases due to higher predation (fish larvae) in the later season.

These potential parameter changes suffice in both models to generate the desired dynamics (see Figure 4.6 for an example).

We can conclude that both models are too simple to explain the dynamics of the PEG-model if parameters are fixed, but that both models can explain them if one or more parameters are allowed to change during the season. The only distinguishable feature in the models is the reaction to enrichment (if we translate this enrichment as only increasing carrying capacity K). In this case both models contain predictions that are incompatible with the PEG-model: the prey-dependent model cannot explain the increasing phytoplankton equilibrium while the ratio-dependent model cannot explain the earlier spring peak (or generally the changing period in the oscillations). However, if enrichment also increases r then both models agree with the PEG-model.

2.2.2 Adding a trophic level

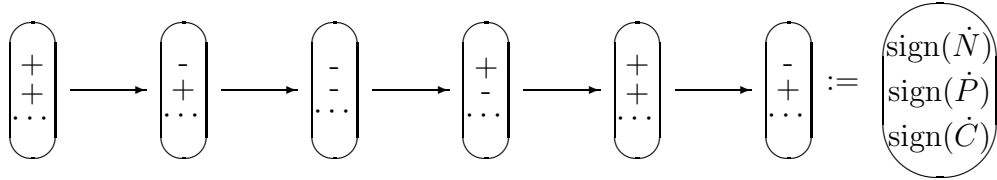
The results mentioned in this subsection are not part of the article in chapter 4. They form a preliminary assessment how the work of chapter 4 could be continued.

The suggested seasonal parameter changes in the previous paragraph are mostly due to changes in the influence of another trophic level on the phytoplankton-zooplankton system (a top predator eating *Daphnia*, increasing abundance of inedible algae). Instead of changing the parameter we can also directly model this trophic level. Adding a top

predator C gives the system

$$\begin{aligned}\frac{dN}{dt} &= f(N)N - g_1(N, P)P \\ \frac{dP}{dt} &= e_1g_1(N, P)P - g_2(P, C)C \\ \frac{dC}{dt} &= e_2g_2(P, C)C - \mu C.\end{aligned}\tag{2.2}$$

Bernard & Gouzé (1995) developed a method to study the possible succession of extrema for this type of food chain models. Following the dynamics of the PEG-model and marking each trophic level with a $+$ if it increases and with a $-$ if it decreases then we can depict the PEG-model dynamics in the following succession of \pm -vectors (see Appendix D for details),



Using the method by Bernard & Gouzé (1995) we can analyse prey- and ratio-dependent food chains if they can show this succession of events. This analysis shows that both food chains have exactly the same succession of extrema and can predict the above depicted succession (see Appendix D for details).

We can make a more quantitative analysis by directly parameterizing system (2.2) with logistic growth of the prey and prey-dependent or ratio-dependent functional responses (of the form given in 2.1) and demonstrate that there exist parameter values that produce the observed dynamics. This represents some kind of model validation since we check whether the proposed model can show the observed dynamics. We assume the top predator in this chain to increase in abundance during the season. Figure 2.1 shows such an example for both types of the functional response. In this 3-level food chain the ratio-dependent model retains its advantages against the prey-dependent model, notably the correlated prey and predator equilibria along a gradient of richness.

We can also explicitly model the two types of prey, edible (N_e) and inedible (N_i), that are in competition one with each other,

$$\begin{aligned}\frac{dN_e}{dt} &= r_e\left(1 - \frac{N_e}{K_e}\right)N_e - c_eN_eN_i - g(N_e, P)P \\ \frac{dN_i}{dt} &= r_i\left(1 - \frac{N_i}{K_i}\right)N_i - c_iN_iN_e \\ \frac{dP}{dt} &= eg(N_e, P)P - \mu P,\end{aligned}\tag{2.3}$$

the functional response being again of the forms (2.1). A reasonable scenario for this system is that N_e is a superior competitor to N_i (Agrawal, 1998) but does not exclude it due

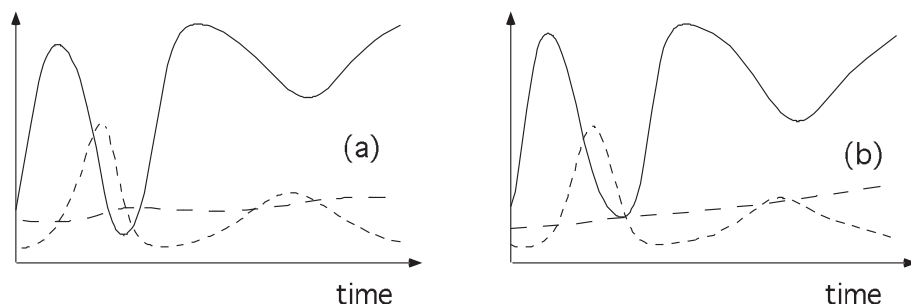


Figure 2.1: Numerical example of a 3-level food chain ‘prey-predator-top predator’ with prey-dependent (a) or ratio-dependent (b) functional response. The characteristic elements of the PEG-model are well preserved. —: prey dynamics; ---: predator dynamics; — — —: top predator dynamics.

to losses by predation. Figure 2.2 shows a numerical realisation of such a system. Again, the dynamics of the PEG-model are clearly reproduced. With this scenario both types of functional response predict a correlation between total prey and predator equilibria along a gradient of richness.

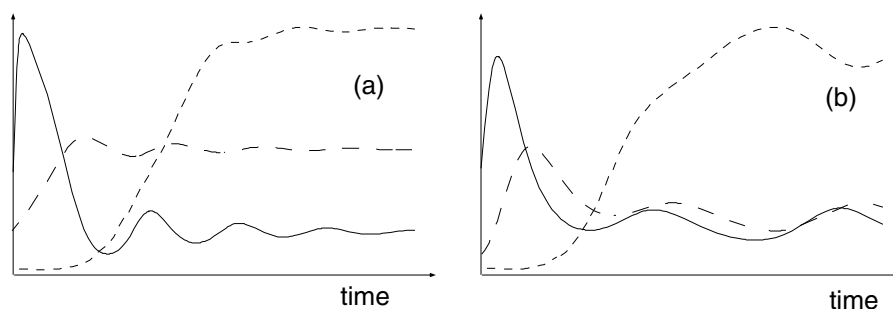


Figure 2.2: Numerical example of the dynamics of a system with edible prey, inedible prey and a predator. Both the prey-dependent (a) and the ratio-dependent (b) model show the characteristics of the PEG-model. —: edible prey dynamics; ---: inedible prey dynamics; — — —: predator dynamics.

2.2.3 Conclusions

In summary, neither the prey-dependent nor the ratio-dependent predator-prey models composed of phytoplankton and zooplankton are able to predict seasonal dynamics of these two levels except if parameters are allowed to change during the season (in which case both models can predict the dynamics). Nevertheless, the ratio-dependent model seems to be more realistic in view of the following properties: 1. both phytoplankton and zooplankton biomasses at equilibrium increase with increasing productivity and 2. there is no effect of productivity on the stability of the system. To obtain the expected pattern, with a clear water phase and a stable equilibrium rapidly reached in the summer, the following modifications of the two-level ratio-dependent model are proposed: 1. parameters of phytoplankton and zooplankton change during the season, 2. introduction of a third

level (carnivorous zooplankton or fish), 3. introduction of phytoplankton mortality other than zooplankton grazing (sedimentation, lysis).

2.3 Boundary dynamics: do they matter?

This section summarises the ideas and results of the analysis developed in chapter 5.

In the previous section we have compared our two predator-prey systems (2.1) to data reaching a stable non-trivial equilibrium. The ratio-dependent model also offers deterministic extinction as a possible outcome (Arditi & Berryman, 1991). However, a ratio-dependent model is not directly defined at the origin since there occurs a division by 0. Nevertheless, if we assume a bounded functional response (as in systems 2.1) then the origin is indeed an equilibrium point, we only cannot apply standard stability analysis to this point, making that the dynamics around the origin have been badly understood for a long time. These badly understood dynamics have been repeatedly used to criticize the ratio-dependent concept (Yodzis, 1994; Abrams, 1997) and wrong or unprecise mathematical results have been published (Getz, 1984; Freedman & Mathsen, 1993).

In collaboration with Ovide Arino I have analysed the analytic behaviour around the origin in detail. The results are best explained graphically. Figure 5.1 shows possible isocline portraits of the ratio-dependent model (2.1). Cases 5.1a and 5.1c offer no mathematical problems, it is the situation in 5.1b that is badly understood. By a transformation of state variables (studying systems $(N/P, P)$ and $(N, P/N)$ instead of system (N, P)) one can show that for certain parameter values the origin indeed behaves like a saddlepoint (Figure 5.2). However, with increasing predator efficiency (visualised by an increasing slope of the predator isocline) the origin becomes attractive for trajectories where ‘ N goes faster to 0 than P ’. This already happens at parameter values where the non-trivial equilibrium is still locally stable (Figure 5.3), thus dividing the phase space into two basins of attraction. The existence of such trajectories is proven for general ratio-dependent models, only using that the functional response is increasing and bounded and the per capita prey growth function is a decreasing function of prey abundance. Further increasing predator efficiency can lead to a destabilization of the non-trivial equilibrium, giving rise to a stable limit cycle (Figure 5.4). However, the existence of this limit cycle is still not analytically proven. The problem is that the origin becomes attractive before the non-trivial equilibrium becomes unstable. Therefore the construction of an invariant set, as required for the application of the Poincaré-Bendixson theorem to prove the existence of a stable limit cycle, would require precise knowledge of the separatrix between the two basins of attraction. Further increasing predator efficiency leads to a homoclinic bifurcation (detected numerically) after which the origin becomes attractive for all initial conditions except the (unstable) non-trivial equilibrium itself (Figure 5.5).

Gragani (1997) raises the point that this deterministic extinction is not a generic behaviour, arguing that if we take an intermediate model of the DeAngelis-Beddington type (1.12) then the origin remains a saddle point for any parameter value but the one that corresponds to the ratio-dependent model. The author does not tell that this argumentation rests completely on the (arbitrary) choice of an intermediate model (by the way, the au-

thor also completely missed the homoclinic bifurcation, i.e., the global attractivity of the origin while there exists a non-trivial equilibrium). If we take the Hassell-Varley-Holling functional response (1.11) as an intermediate model the picture changes somewhat. Callois (1997) studied this model in detail and showed that deterministic extinction occurs for $m \geq 1$, while the origin is a saddle point for $m < 1$. It therefore indeed seems that deterministic extinction is not generic for $m \leq 1$.

2.3.1 Some other models that offer deterministic extinction

The following two sections are not detailed in chapter 5. They contain additional ideas about deterministic extinction and biological control.

Extinction of both prey and predator is usually explained as the result of stochastic events. However, the consistency of extinction occurring in laboratory predator-prey systems (Gause, 1934; Luckinbill, 1973; Veilleux, 1979) suggests that it can also happen as a deterministic outcome. Besides the ratio-dependent model analysed above I only found two other (simple) predator-prey systems that offer this type of extinction. The first one is a model with a strong Allee effect (population rate of change becoming negative below a certain population threshold value ϵ , Allee 1931) in the prey dynamics and Lotka-Volterra functional response, e.g. (from Hastings 1997)

$$\begin{aligned}\frac{dN}{dt} &= r\left(1 - \frac{N}{K}\right)N\left(\frac{N}{\epsilon} - 1\right)\frac{K}{K - \epsilon} - aNP \\ \frac{dP}{dt} &= eaNP - \mu P.\end{aligned}$$

Note that a general Allee effect only means that the per capita population growth rate is maximal not at the origin but at some positive population density (Edelstein-Keshet, 1988). The strong Allee effect I refer to means that this per capita growth rate must even become negative at low densities (see Figure 2.3). Only this strong Allee effect permits extinction of the prey. The second model takes logistic prey growth and a predator-dependent functional response that has been proposed by Hassell & Rogers (1972) or Ashby (1976),

$$\begin{aligned}\frac{dN}{dt} &= r\left(1 - \frac{N}{K}\right)N - \frac{aN}{1 + at_h N} \frac{1}{P} P \\ \frac{dN}{dt} &= e \frac{aN}{1 + at_h N} \frac{1}{P} P - \mu P.\end{aligned}$$

This model is completely donor controlled and can have two non-trivial equilibria (one of them stable), in which case the origin becomes attractive for all initial conditions with sufficiently low prey abundance.

2.3.2 Is there a biological control paradox?

The analysis in chapter 5 revealed another interesting feature of ratio-dependent models: stable coexistence of prey and predator is possible with prey equilibrium values arbitrary

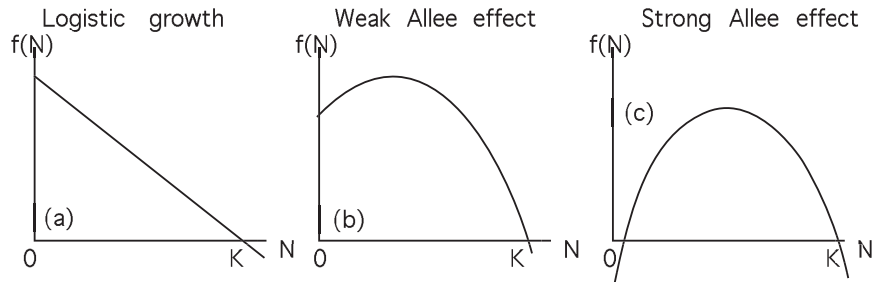


Figure 2.3: Types of prey per capita growth functions $f(N)$ in the model $dN/dt = f(N)N$: (a) the logistic growth, (b) a weak Allee effect, K is the only stable equilibrium and (c) a strong Allee effect, K and 0 are stable equilibria. K is the carrying capacity, N the prey density.

close to 0 . This is in contrast to prey-dependent theory where such low prey equilibrium values either lead to a destabilization of the system or require very high predator abundances (Arditi & Berryman, 1991). In reply to Arditi & Berryman (1991), Åström (1997) pointed out that a nonlinear density dependence in the prey growth function in the form of θ -logistic growth (in ecology introduced by Gilpin & Ayala 1973, but first used by Richards 1959),

$$f(N) = r \left(1 - \left(\frac{N}{K} \right)^\theta \right),$$

could stabilise predator-prey systems with low prey-equilibria. However, few estimates of the parameter θ exist. Åström (1997) cites some tentative studies that indicate this value to be below 1 for insect types of prey and above 1 for mammalian types of prey. Only $\theta < 1$ has the stabilising effect on the prey equilibrium described by Åström. However, a small θ reduces also the population growth rate at low population levels, which is somewhat in contrast to features of a typical pest.

Actually, the biological control problem has been addressed earlier by Beddington et al. (1978). They defined so-called q -values, that are the ratio of the (stable) prey equilibrium coexisting with the predator divided by the prey equilibrium in absence of the predator. Small q -values (< 0.01) thus indicate a successful biological control of the prey by its predator. Beddington et al. (1978) reported q -values ranging in the field from 0.002 to 0.03 and in the laboratory from 0.1 to 0.5 . They explored several possibilities how predator-prey or host-parasitoid models could be adapted to accommodate these observations:

- sigmoidal functional responses had no influence on q ,
- inclusion of mutual interference in a DeAngelis-Beddington way (1.8) gave q -values down to 0.1 ,
- incorporating spatial aggregation of parasitoids with heterogeneous host distributions made q -values below 0.1 possible.

In an earlier paper Free et al. (1977) had shown that spatial aggregation, observed from a global perspective, leads to reduced attack rates a (like predator interference, see equation (1.7)), a phenomenon that they termed ‘pseudo-interference’. Beddington et al. (1978) therefore modelled the last item in the list above with Hassell-Varley’s (1.7) interference model, based on estimates for the interference parameter m ranging from 0.1 to 0.8, and they obtained q -values down to 0.004. Using the Hassell-Varley-Holling (1.11) functional response Arditi & Akçakaya (1990) had shown that the parameter m could even be higher, thus allowing for very low q -values. As already pointed out, the Hassell-Varley-Holling model becomes ratio-dependent for $m = 1$, thus proposing this model as a very rough description of biological control problems.

Let us identify the region in parameter space of a ratio-dependent model that shows such low stable prey equilibrium levels. To simplify this analysis we use the dimensionless form of the ratio-dependent model that was introduced in chapter 4,

$$\begin{aligned}\frac{dN}{dt} &= R\left(1 - \frac{N}{S}\right)N - \frac{SN}{P + SN}P \\ \frac{dP}{dt} &= \frac{SN}{P + SN}P - QP,\end{aligned}$$

with $R = rh/e$, $S = \alpha h/e$ and $Q = h\mu/e$. S is the equilibrium value of the prey in the absence of a predator. We therefore want to identify all parameter combinations that give a low and stable prey equilibrium N^* ,

$$N^* < \epsilon S.$$

Some algebra shows that this is possible for all S that fulfil

$$(1 - \epsilon)\frac{R}{1 - Q} < S < \min\left\{\frac{R}{1 - Q}, \frac{Q - Q^2 + R}{1 - Q^2}\right\}$$

Figure 2.4 illustrates the region in parameter space that fulfils this condition. Approximately, we therefore need that $S \approx \frac{R}{1 - Q}$, which means in the original parameters

$$\alpha \approx \frac{er}{e - h\mu}.$$

This condition can be verified with real data. Bernstein (1985) studied the predator-prey system *Tetranychus urticae* (prey) with *Phytoseiulus persimilis* (predator) and parameterized a predator-prey system with each population structured in three life stages. We can use his estimates to parameterize the ratio-dependent model (in parentheses is the name of the parameter used in the original publication): $r = 5.34d^{-1}$ (r_1), $\mu = 0.0433d^{-1}$ (γ_2), $e = 0.159$ ($\min\{r_m, r_2\}$) (eggs laid per egg eaten) and $h \approx 0.1d^{-1}$ (K_i/j or b_i/α_i). These values give

$$\alpha \approx 5.49\frac{cm^2}{d} = 0.00055\frac{m^2}{d}.$$

This value is close to the $\alpha = 0.0002m^2/d$ reported in (Hassell & Comins, 1978) for this predator-prey system. Of course, this is only a preliminary result, but it is encouraging that the ratio-dependent model may be useful in biological control.

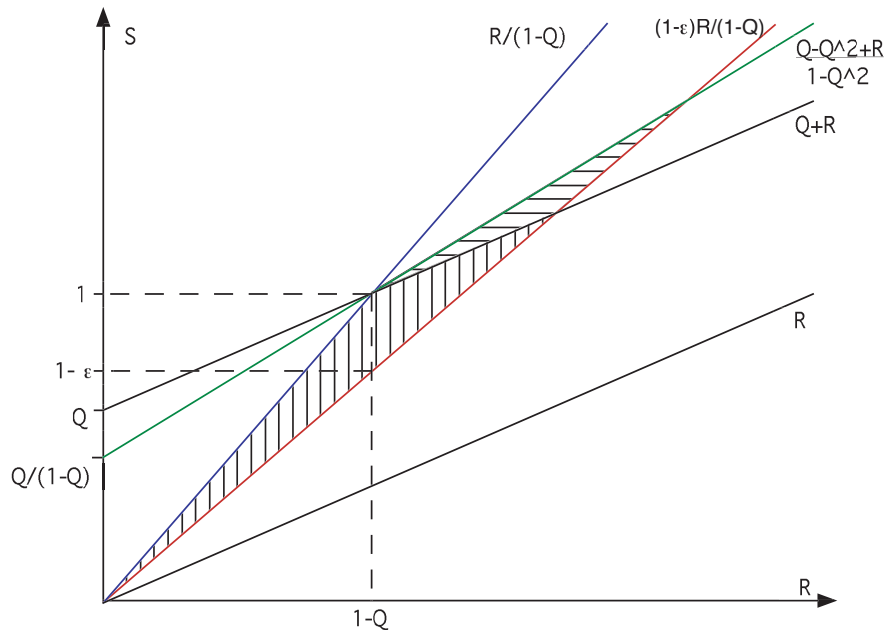


Figure 2.4: The hatched region in the $R - S$ parameter space (for a fixed $Q < 1$) indicates the parameter values for which the predator reduces the prey to a stable equilibrium a fraction ϵ below the levels the prey would attain in the absence of predators. The vertical hatching indicates the area where the origin behaves like a saddle point, while in the area with horizontal hatching the origin is attractive for certain initial conditions.

It might also be that predator-prey systems in biological control do not show a stable equilibrium but some metapopulation dynamics with frequent local extinctions. Luck (1990) reported (based on data from Murdoch et al. (1985)) that “of 9 successful biological control projects, only 1 showed to have a stable N^* , the others could be explained by local extinction”. Again, such local extinctions are possible with a ratio-dependent model describing local dynamics. The condition on parameters is similar to the one found above,

$$S \approx \frac{R}{1-Q} \text{ or } S > \frac{R}{1-Q},$$

and the types of extinction are illustrated in Figures 5.5 and 5.1c.

2.4 Microbiologists did it

This section summarises the ideas and results of the analysis developed in chapter 6.

In fact, while Arditi & Ginzburg (1989) were the first to propose ratio dependence as a general concept (with all its implications to bottom-up and top-down concepts), Getz (1984) published a specific ratio-dependent model several years before them. The very idea that consumption (and with it growth of an organism) is a function of the ratio consumer by resource can be found in the microbiological literature already in Cutler & Crump (1924). Most interestingly, a specific ratio-dependent function of the form (1.10)

has been proposed in microbiology as a growth function (same concept as the functional response) by Contois (1959). This function has since then served as an alternative to the microbiological equivalent of the Holling type II function, Monod's (1942) well known growth function. With the help of Science Citation Index I checked all papers citing Contois' work in the last 40 years to detect results that might be useful in the ecological context.

Most experimental work has been done in the framework of chemostats that are usually described by

$$\begin{aligned}\frac{dN}{dt} &= D(N_0 - N) - Y\mu(N, P)P \\ \frac{dP}{dt} &= \mu(N, P)P - DP\end{aligned}\tag{2.4}$$

with substrate N , inflowing substrate concentration N_0 , consumer P , dilution rate D and yield Y . Comparing this equation with our standard predator-prey system (1.4) shows that there is a subtle difference between the two ways consumption is modelled: microbiologists start with the growth function (called numerical response in population ecology) and consider the substrate uptake function (our functional response) to be proportional to it with yield constant Y , while ecologists start with the functional response and consider the numerical response to be proportional to it with ecological efficiency e . There is therefore a scaling difference between the two concepts,

$$g(N, P) = Y\mu(N, P).$$

However, this difference is of no importance to the results discussed below.

Growth rate $\mu(N, P)$ is usually modelled with the equation proposed by Monod (1942),

$$\mu(N, P) = \mu_{max} \frac{N}{K_s + N}$$

with maximal growth rate μ_{max} and half saturation constant K_s (note that with $a = \mu/K$ and $h = 1/\mu$ we obtain the usual Holling type II functional response (1.6)). With this growth function, system (2.4) predicts that outflowing substrate concentration N^* should only depend on D , μ_{max} and K_s , but not on inflowing substrate concentration N_0 . However, it was soon observed that in many experiments outflowing substrate concentration was proportional to inflowing substrate concentration. Contois (1959) tried to accommodate this observation by hypothesising (and providing experimental support) that the half saturation constant is proportional to inflowing substrate concentration. Combining this observation with mass balance principles (see chapter 6 for details) he derived the form

$$\mu(N, P) = \frac{u_m N}{BP + N}$$

(with constants u_m and B) which is a particular ratio-dependent form.

The papers that tested this function against Monod's or other functions (see Table 6.1 for examples) can be classified into two categories,

- chemostat experiments with varying inflowing substrate concentrations and dilution rates, measuring outflowing substrate concentration,
- direct measurements of growth with varying substrate and organism concentrations, then comparing these measurements quantitatively and qualitatively with different growth functions.

The first category showed that Monod's prediction is correct as long as one works with a unique strain of organisms growing on pure substrate. Any deviation from these conditions (mixed substrate or multiple strains/species of organisms) lead to outflowing substrate concentrations that are proportional to inflowing substrate concentrations. This result can be interpreted that the consumer isocline in chemostats (Figure 6.2) should be slanted. The second category showed that the growth function is a decreasing function of consumer density,

$$\frac{d\mu(N, P)}{dP} < 0,$$

under the same conditions mentioned for the first category (mixed substrate or multiple strains/species of organisms). However, these results are more precise in that they identify predator dependence in the growth function to be the likely cause of the slanted predator isocline, and not some density-dependent consumer mortality as proposed by other researchers. While all these results suggest that we should expect a slanted predator isocline in natural systems, this slanted isocline is also predicted by any consumer-dependent growth function, not only by Contois' equation. As in ecology (section 1.2.5), the comparison between Monod and Contois is not done on equal footing. Fortunately, there were also direct quantitative comparisons between data and models, based on statistical criteria such as goodness-of-fit. These showed that in many cases (wastewater treatment, fermentation processes) Contois' function fitted better than Monod's function, but often the identification was less clear or other functional forms fitted equally well as Contois' equation.

We can learn several things from the work done in microbiology:

- Prey-dependent (or substrate-dependent) functions such as the one proposed by Monod seem to be a good description of consumption processes of single species consumers on a pure substrate.
- Whenever the system becomes more complex (several species involved, heterogeneities in space or time) predator-dependent functions (of any form, not necessarily ratio-dependent) are more adequate.
- If model selection by fitting models to data is already ambiguous with microbiological data, then we cannot expect more conclusive results when working with (noisier) field population dynamics, or we have to develop more sensitive techniques such as proposed in chapters 7 and 8.

2.5 Quantitative comparison of models

This section summarises the ideas and results of the analysis developed in chapters 7 and 8.

In the beginning I have opined that existing comparisons between prey-dependent or ratio-dependent predator-prey models and real data have not been done yet on an equal footing. The analysis in chapter 4 was already closer to this objective by comparing predictions of each model with the dynamics observed in freshwater lakes. Here, I will compare the models (2.1) quantitatively based on their temporal dynamics, by fitting them directly to time-series data of predator-prey systems. The concept of likelihood (Edwards, 1992) provides the statistical framework to ensure that the comparison is done on an equal footing. The idea is to identify the likelihood of the model given the data with the probability of obtaining the data given the model (with model parameters that maximise this probability, maximum likelihood). This identification is intuitive (see Press et al. (1992) for some comments) but very useful for model selection. Estimation by maximum likelihood (ML) has a number of interesting statistical properties: the estimation is consistent and ML is the estimator with the smallest possible variance (Huet et al., 1992). However, the distribution of the error has to be known exactly for these properties to hold. ML estimation is often not very robust against uncertainty concerning this distribution.

If the models that are compared have the same number of parameters (as is the case in our candidate models) then the likelihoods also serve as selection criterion. Therefore, regression of the model to data (with parameter estimates as a byproduct) and model selection are based on the same criterion. Chapter 7 will show that for applications of model selection this is an important point.

The concept of likelihood can also be extended to compare models with a different number of parameters, using so-called information criteria. The best known is Akaike's Information Criterion AIC (Akaike, 1973; Bozdogan, 1987), but others exist, such as Bayesian information criterion BIC, Mallow's C_p (see Hilborn & Mangel (1997) for a discussion and references to all three criteria) or consistent Akaike information criterion CAIC (Jones, 1993). However, since I only worked with models of equal complexity I mention these criteria only for completeness, they are not pertinent for the present analysis.

In contrast to the equilibrium experiments in Arditi & Saïah (1992) we approach the problem of model selection from a dynamic point of view. We investigate whether time-series data of predator-prey systems can reveal if there is predator dependence in the functional response or not. The comparison will be done by fitting our equally complex prey-dependent and ratio-dependent predator-prey models (2.1) to time-series data, and apply goodness-of-fit (likelihood) as a criterion.

The time-series I use in the analyses come either from the literature (protozoan, arthropod and plankton predator-prey systems) or are original phyto- and zooplankton data from lake Geneva. They are characterised, as most ecological data, by small size (10 - 50 data triplets {time, prey, predator}) and by rather large errors with coefficients of variation up to 50%. By such reasons one should be extremely cautious in making any deduction regarding the biological 'correctness' of the used formalism to describe the bi-

ological processes even if some model fits such data very well. The problem has been illustrated convincingly for the case of logistic population growth (introduced by Verhulst (1838)) already very early in the history of mathematical population biology, namely in 1939 by W. Feller. He chose two other mathematical models that are S-shaped and that have the same number of parameters and showed that both forms fit equally well (or even better) to real data that were considered at the time to be some of the best proof that the logistic model has the character of a physical law. Feller continued to show that these models also predict the same response to a constant per capita harvesting rate as the logistic model.

More recently, Simons & Lam (1980) demonstrated that the same caution applies to more complex models such as models describing the dynamics of phosphorous in large lakes. They pointed out that several choices of the parameter values (with or without imposed seasonality) gave equally good fits to one season of data, and thus that the predictive power of such a (fitted) model is very limited.

These two examples amply show that obtaining a good fit of a model to data is far from proving the biological correctness of the chosen mathematical process description. Or, in the words of Cale et al. (1989), ‘multiple process configurations can produce the same pattern’. However, there is a solution, following May’s (1989) advice by ‘generating pseudo-data for imaginary worlds whose rules are known, and then testing conventional methods for their efficiency in revealing these known rules’. In other words, I will generate artificial predator-prey data, apply the model selection criterion to them and then check if the correct model has been identified. Only after detection of the limits in model identification in this simulation analysis will I endeavour to analyse real ecological time-series data. This analysis is summarised in section 2.5.4.

This same approach has been used in Carpenter et al. (1994) for plankton data, but the authors used a discrete model with the time steps being the (arbitrary) intervals between measurements. They also fitted time-series over several years, thus assuming that parameters such as carrying capacity or mortality rates are the same for every year. I will reanalyze their data by fitting our models to data from one season only, in particular to data from the period of spring to autumn where population interactions may be the driving forces behind the dynamics (Sommer et al., 1986), and not physical constraints such as temperature or light. I will also fit the models to protozoan time-series found in the literature, because they show much less variability than whole lake plankton data and there are many similarities between protozoa and plankton (fluid medium, overlapping generations, large numbers etc.). There are also more and more ecological models that include the microbial loop (eg. Fasham et al. 1990, Azam et al. 1983, Stone & Berman 1993) based on a large body of empirical evidence for the important ecological role of the microbial fauna (Berman, 1990; Fenchel, 1988; Sherr & Sherr, 1991). It will be interesting to see how typical ecological models fit the dynamics of these organisms.

Finally, this work will also be different from the approach presented by Harrison (1995). The author used a classical predator-prey time-series from the literature (Luckinbill, 1973) and fitted it to 11 different predator-prey models, trying to determine the key processes necessary to get a qualitatively and quantitatively good fit. Two problems arise in his work: (1) he implicitly assumed that a better fit is due to a better description of the individual processes and (2) without any information about the size of the observation

error no statistical test could be used in the comparison that accounts for the number of parameters in the model, e.g. likelihood ratio tests (Hilborn & Mangel, 1997) or Akaike's information criterion (AIC, Akaike 1973). I will show that already with modest errors in the data assumption (1) may be wrong and detailed simulation studies should be done preliminary to such work. Unsurprisingly, the model with the largest number of parameters gave the best fit in Harrison's (1995) analysis. While this kind of study may yield information about details in processes of specific systems (e.g. importance of lags between consumption of *Paramecium aurelia* and reproduction of *Didinium nasutum* in this case) it does not tell whether addition of these details gives a significantly better fit to the data. I will avoid this kind of fallacy by working only with models that have the same number of parameters.

2.5.1 A remark on model selection criteria

Model selection in this thesis is always based on likelihood (goodness-of-fit), at least when working with real data. Another approach was chosen by Bilardello et al. (1993), who used the joint linearised confidence region as a comparison criterion. This region is minimal if the determinant of $J(\theta)^T \cdot J(\theta)$ is maximal (Hosten, 1974), where $J(\theta)$ is the sensitivity matrix of the state variables with respect to parameter vector θ ($J(\theta)^T \cdot J(\theta)$ is also known as Fishers information matrix, Huet et al. 1992). I did not test this criterion, but it surely would help detecting problems due to overparameterization (which makes this matrix close to singular). I encountered such problems with the highest noise levels in the 'in silico' analysis (2.5.4). Sometimes there was very slow convergence even close to the optimum, at other times several different parameter sets gave equally good fits. Both phenomena indicate that too many parameters were fitted to the data. Another popular criterion for model selection is the standard deviation of the residuals (Carpenter et al., 1994).

All these criteria can pose the problem that model selection is based on a quantity that is not minimised while fitting the model to data. In chapter 7 I analysed some such criteria that were proposed by Carpenter et al. (1994). I often observed that a model was selected that gave visually a worse fit to the data than the rejected model (see section 2.5.4). Using only the likelihood concept for both regression and model selection avoids this problem and is statistically well founded. For this reason I remained in this concept for the analysis of real data.

2.5.2 The errors that govern our modelling world

I have mentioned in the previous section that my model comparison will be based on a likelihood approach. To formulate this likelihood I first have to formulate a stochastic model, i.e., a model that explains how random effects come into the data to which I want to fit my candidate models. These models themselves are deterministic, formulated with ordinary differential equations (ODE) that, for given parameters, give completely predictable results. They form the core of the statistical model to which stochasticities are added.

A first type of stochasticity is pure observation or measurement error: there is some unknown real population abundance and any estimation of it is a realisation of a random number according to some distribution function. If we have data with only this type of error (the dynamics of the population are deterministic) then we fit our model by fitting the whole trajectory (solution of the ODE with given initial conditions that are treated like parameters to be estimated) to the time-series data (note that we assume the time measurements to be exact, without any error). This type of fitting is often called trajectory fitting. See Figure 8.1a for an illustration of this type of fitting.

A second type of stochasticity is process error: the dynamics of a population over time are not completely governed by its deterministic component but also by random influences either from the environment or from inside the population. In the context of an ODE-model process error leads to a stochastic ordinary differential equation (SODE). If our system has this type of error, then the deterministic model trajectory diverges more and more from the actual population abundance, the longer the prediction horizon, the worse the prediction. The population abundance after some fixed time interval with some initial abundance (which is known if we measure the abundance without observation error) is thus a realisation of a random process. To relate in this case the problem of parameter estimation (and of estimating goodness-of-fit) to a regression problem in the classical sense, we have to make the assumption that the distribution of the population abundance after the fixed time interval, given the initial conditions, is known. Usually, the prediction horizon is one time step ahead (defined by the spacing in the available time-series), but it is also possible to predict $s > 1$ time steps ahead. This type of fitting is therefore often called s -step-ahead fitting. See Figure 8.1b for an illustration of this type of fitting.

Solow (1995) distinguishes a third type of error, so-called parameter error. This is a special kind of process error due to the stochastic nature of one (or several) of the model parameters. Solow shows that this type of error can lead to non-stationary error, depending on the probability density function and the algebraic embedding of this parameter. In my fitting I did not see a way to distinguish between parameter error and process error as modelled by a SODE. Furthermore, the algebraic structure of equations (2.1) makes it difficult to deduce how parameter error translates itself into process error, an information necessary to adapt the regression process. I therefore only considered process error in form of a SODE, according to the standard treatment of errors in time-series (Hilborn & Mangel, 1997; Pascual & Kareiva, 1996; Dennis et al., 1995).

Statistical theory has mainly developed methods to fit one single type of error, the problem of considering process and observation error at the same time being much more difficult (discussion in section 3.2.4). If the researcher can design his experimental setup so that one of the errors is eliminated or at least reduced to negligible values (e.g., providing constant environmental conditions in the laboratory and working with population sizes where demographic stochasticity is unimportant, or, developing a sampling method that has no observation error), then the formulation of the stochastic model poses no problem. However, this is difficult to achieve, especially when working in the field. Most time-series data available in the literature or by a researchers own experiment contain both types of errors. Pascual & Kareiva (1996) thus come to the conclusion that the researcher has to decide (as a best guess) which error to model and which error to neglect. Due to its pertinence I will often use their terminology, calling the case of trajectory fitting

‘observation error fit’ and the case of s -step-ahead fitting ‘process error fit’.

The particular choice of one error type or the other can profoundly influence the result of a model selection process. However, the sensitivity of model selection to the particular error type can be tested in a simulation analysis, as proposed by May (1989). This will be the subject of the next section. We discuss and analyse there also two error functions proposed by Clutton-Brock (1967) and applied by Carpenter et al. (1994) that seem to take both types of error into account without increasing the numerical costs too much. However, these error functions do not fit into the likelihood concept, posing the problem of what criterion to use for model selection. The next section will illustrate some consequences of this problem. Another statistical method that takes both errors into account is the errors-in-variables approach that will be discussed briefly in section 3.2.4. I have not used this method because the computing cost is much higher, the method itself is still in its statistical infancy or at best adolescence and the method requires independent knowledge of either process error or observation error. However, the method fits completely into the likelihood concept and looks promising for future research.

Note that I assume for observation error fit and for process error fit stationarity and normality of the error on log scale (constant coefficient of variation CV). With this assumption maximum likelihood becomes equivalent to ordinary least squares (Press et al., 1992), and when I will use the terms goodness-of-fit or likelihood the reader best thinks of them in terms of least squares. However, the size of this error (CV) is for the real ecological time series only approximatively known. Furthermore, as already mentioned, these time-series contain both types of stochasticity and neglecting one of them is only a statistical necessity. This means that the calculated likelihoods will not have an absolute meaning and the information criteria mentioned earlier cannot be used. For this reason, the comparison can only be performed for models of the same complexity.

2.5.3 Implementation of fitting algorithms

Before discussing the actual fitting results I should say some words on the implementation of the fitting algorithms. Most algorithms were first developed in Mathematica© to get an idea if they work satisfyingly. However, numerical calculations in Mathematica are too slow for the analysis of large numbers of time-series. There does not exist much customisable software that allows fitting differential equations to data. Fitting and visualisation are usually separate steps in most software, which further slows down the fitting process. Therefore I implemented all algorithms in C++, using the MacIntosh Toolbox functions to visualise the fitted model in real time. This immediate visual control proved to be an indispensable tool to analyse large numbers of data sets. The numerical algorithms are based on the codes provided with ‘Numerical Recipes in C’ (Press et al., 1992). The software is obtainable on request from the author (it requires a Power Macintosh).

2.5.4 An ‘in silico’ approach to model selection

The objective of the analysis detailed in chapter 7 is to explore numerically how the presence of both observation and process error in time-series data influences model selection

based on goodness-of-fit. For this I created artificial time-series that contain both errors. The deterministic core function is inspired by the dynamics described in the PEG-Model (section 2.2), i.e., dynamics that reach a stable equilibrium after one or two large amplitude oscillations. In a first step I computed parameters and initial conditions for both the prey-dependent and the ratio-dependent candidate model (2.1) in a random procedure. The criteria to accept such a random parameter set are on the one hand the dynamics described above and on the other hand practical requirements such as prey and predator equilibria not differing by more than a factor of 100 and predator dynamics showing at least a five-fold variation. For each model 20 such parameter sets were created. In analogy to replicated experiments in ecology I then simulated 5 replicate time-series with each parameter set, adding process error in the framework of stochastic ordinary differential equations, ‘sampling’ the resulting time-series at 20 equal intervals (also inspired from the PEG-model, 20 is the typical number of plankton samples over one season) and adding an observation error to these. The process error is generated in a standard stochastic process framework (see details in section 7.3.1) with a stochastic component that is proportional to the current population abundance, thus simulating a multiplicative or lognormal error type. Observation error is of a lognormal type with constant coefficient of variation. Time-series with a low observation and process error (comparable to laboratory protozoan systems) and high observation and process error (comparable to aquatic mesocosms, maybe even to whole lakes) were thus created for each model.

Then each candidate model was fitted to each time-series with four methods (or error functions). Method **A** assumes that there is only observation error of a lognormal type, observation error fitting or trajectory fitting. In this setup maximum likelihood corresponds to least-squares fitting on the log-scale. Method **B** assumes that there is only process error of a lognormal type, process error fitting or s -step-ahead fitting. In this setup maximum likelihood corresponds to conditional least squares on the log-scale. The prediction horizon s is chosen such that the autocorrelation drops below 0.5 (Ellner & Turchin, 1995). The reason for this is to fit over a time interval where nonlinearities may be equally (or more important) as linear dependencies. Actually, this criterion for the prediction horizon is adopted from Ellner & Turchin (1995) and justified there mainly as an empirical result from experience. Methods **C** and **D** are both inspired from Clutton-Brock (1967) as presented by Carpenter et al. (1994). **C** corresponds to weighted conditional least squares, where the weights are computed from the sensitivity of the prediction to the initial condition, which is the observation s steps previously and that contains an observation error (see section 7.3.2 for details). The observation error is assumed to be known independently from process error. **D** is based on **C** but is more similar to a negative log likelihood function in that the scaling factor of the normal distribution has been retained (see Carpenter et al. 1994) such that larger weights not only reduce the importance of the residuals but also add a penalising factor to the error function. Note that these so-called loss functions **C** and **D** (Carpenter et al., 1994) do not fit into the likelihood concept. Model selection must therefore be based on a different criterion. I chose the sum of squared residuals (computed on log-scale) as this selection criterion.

Time-series with low observation and process error were reliably identified (with less than 5% wrong identifications) by methods **A**, **B** and **D**. Method **C** had close to 15% wrong identifications and was therefore rejected as a useful method for model selection

(see Figure 7.3).

Time-series with high error levels were best identified by **A** (observation error fit) with less than 5% wrong identifications. **B** and **D** had both $\approx 10\%$ wrong identifications, but **B** was better in the sense that if we require a minimal difference of 5% between the fits then this method identified more than 95% of the time-series correctly (Figure 7.3). No such threshold could be found for **D**.

The problems with **C** and **D** are two-fold. First, the algorithms often rather maximised dependence on initial conditions (larger weights) than minimised the residuals. Second, the model selection criterion often increased while minimising the loss function, and its value at the minimum of the loss function could be arbitrarily far away from its own minimum. Figure 2.5 illustrates these problems for one data set. I therefore concluded that both methods **C** and **D** are unusable for model selection.

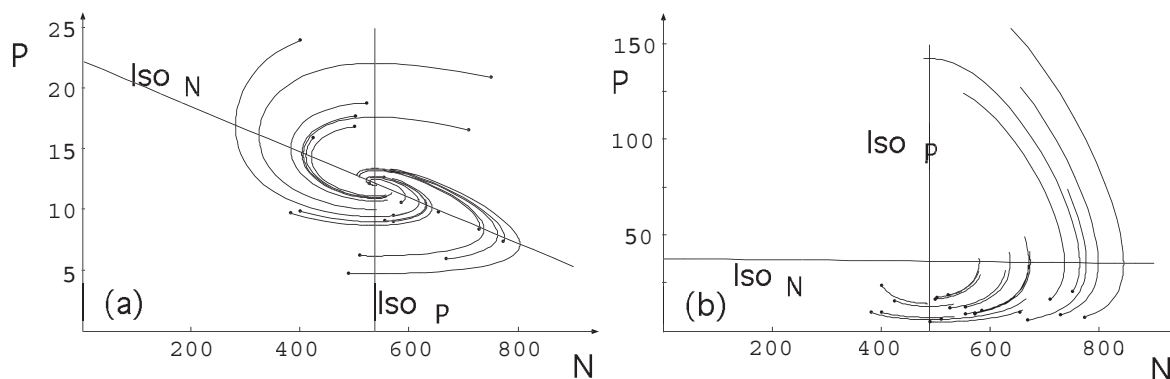


Figure 2.5: Illustration of the problems encountered with regression method **C**. The figures show in phase space (N : prey, P : predator, Iso_N : prey isocline, Iso_P : predator isocline) how the prey-dependent model has been fitted by method **B** (a, process error fit) and by method **C** (b, weighted conditional least squares) to an artificial stochastic time-series (created with a prey-dependent model). Method **C** actually maximised dependence on initial conditions instead of minimising the residuals, resulting in an obviously wrong fit. Similar problems were encountered with method **D**. Note that the predator axes have different scales in (a) and (b).

A more interesting result is that only in 1% of all analysed time-series did methods **A** and **B** both identify the wrong model. The most reliable model identification is therefore to apply several methods based on different assumptions about errors and only accept results where all methods identified the same model.

A side result from this analysis is the quality of parameters estimated by fitting ODE's to time-series data. I computed for each fit of a model to a time-series (that was created by the same model) the ratio of the estimated parameter by the original parameter (that created the time-series). The cumulative distributions of these ratios, after fitting to the time-series with high error levels, are shown in Figure 2.6. If these cumulative distribution curves pass through the point (1.0, 0.5) then the expected median is correct. The steeper these curves, the less the estimates are spread. We see that only parameters r and K are reliably identified in both models, all other parameters are widely spread and the median is often far away from 1 (where it should be). All tested error functions with this error

level performed equally well (or bad).

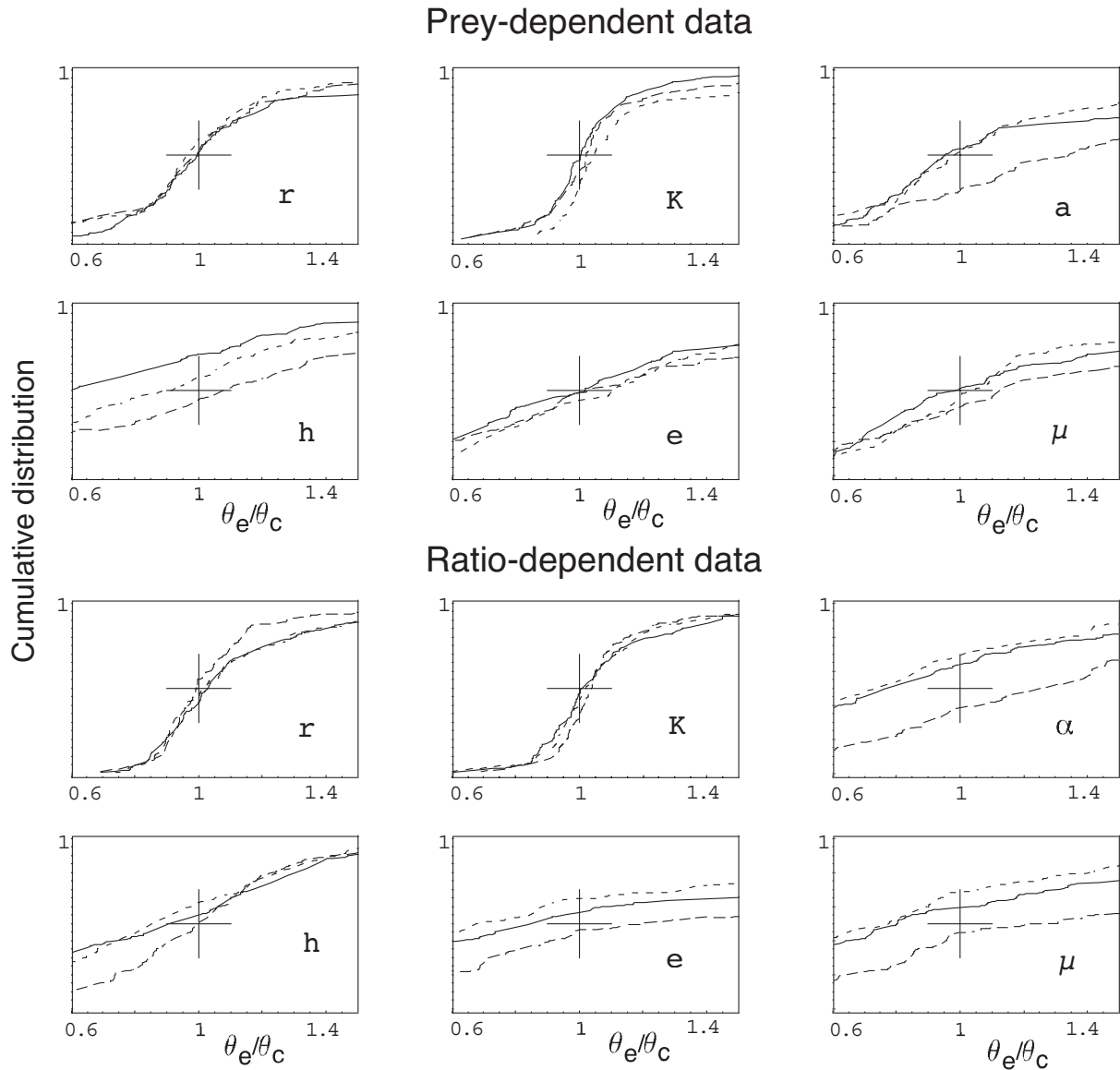


Figure 2.6: Analysis of the quality of each parameter estimate after fitting the time-series with high error levels: cumulative distributions of the ratios θ_e/θ_c (θ_e is the estimated parameter, θ_c the correct parameter that created the data) for all error functions. — — —: observation error fitting **A**; ———: process error fitting **B**; - - - -: weighted process error fitting (method **D**, see text).

The quality of the total parameter set (per model per time-series) can be visualised in a similar way by working with the dominant eigenvalues (local stability) at the non-trivial equilibrium point. These eigenvalues have been computed algebraically to avoid any numerical roundoff errors. Now there emerge strong differences between the error functions. Figure 7.5 shows the cumulative distribution functions of the ratios of the dominant eigenvalues for all estimated parameter sets, error functions and models. The steepness of each curve is approximately the same, therefore each error function shows

the same variation in the estimation of local stability, although there seems to be a slightly smaller variation with ratio-dependent data. With respect to the second criterion, deviation from the expected median, we see that observation error fit **A** performed globally best, followed by weighted process error fitting **D**. Method **B**, process error fitting, always overestimated stability.

Conclusions from the ‘in silico’ approach

The result that should be retained from this analysis is that model identification is in principle possible with both studied error levels and for the time-series analysed (dynamics reaching an equilibrium after one or two oscillations, starting from low initial conditions and sampled at 20 times). Observation error fit is slightly more reliable than process error fit, but the best identification is obtained by fitting with both error functions and only accepting model selections where both types identify the same model. The estimated parameters are generally of poor quality and should be used with much care. The method of fitting ordinary differential equations is therefore better suited for model selection than for parameter estimation.

2.5.5 The ‘in vivo’ data analysis

As found in the previous section, model selection is most reliable when several goodness-of-fit criteria, based on different error models, select the same model. The two best known error functions lead to observation error fit and process error fit. In consequence, I will only analyse real time-series that permit both types of fitting. This is particularly restrictive for observation error fit, because the longer the time-series, the less likely it is to get a reasonable fit of the whole trajectory. Of course, one could split up long time-series into shorter pieces and fit trajectories to all pieces, but there is no standard statistical method how this should be done correctly. To avoid any ambiguity linked to non-standard statistical methods I therefore only used time-series that can be fitted reasonably to whole trajectories. These time-series range from simple protozoan batch cultures (Gause, 1935; Gause et al., 1936; Luckinbill, 1973; Veilleux, 1979; Flynn & Davidson, 1993; Wilhelm, 1993), over spatially more complex laboratory predator-prey systems (Huffaker, 1958; Huffaker et al., 1963) to the very complex plankton systems of freshwater lakes of the temperate zone (Carpenter et al., 1994; CIPEL, 1995). The plankton data from Carpenter et al. (1994) consist of edible phytoplankton and herbivorous zooplankton observed in two North American lakes from 1984 to 1990 (Paul Lake and Tuesday Lake). Edible phytoplankton was defined by the authors to be all phytoplankton with a biovolume less than that of a 30- μm diameter sphere. In the original data from Lake Geneva there were both edible phytoplankton (defined as organisms with length $< 50\mu\text{m}$ and biovolume below $10^4 \mu\text{m}^3$) and total phytoplankton, I therefore fitted two systems: edible phytoplankton - herbivorous zooplankton, and total phytoplankton - herbivorous zooplankton.

What are the differences between these real data and the artificial data analysed in the previous section? The multiplicative nature of observation (and probably also process) error has been confirmed for all systems. However, the normality assumption (for the log-transformed data) might be too strong, outliers (stronger tails, data points farther away

from the mean than expected) are possible in arthropod and in plankton data. I therefore also fitted the data with an error function based on the sum of the absolute values of the residuals in log scale (Laplacian or double exponential distribution). Another difference is the noise levels in the data that might be higher (especially with phytoplankton) than the analysed noise levels. In this case, the 5% difference between the error functions after fitting both candidate systems (2.1) that was computed in the previous section as assuring a 95% confidence in the model selection might not be enough. I therefore also performed a residual bootstrapping (as described by Efron & Tibshirani (1993), see details in section 8.A) to compute a confidence interval for the error with each model and applying a standard t -test to see if one of the models fits significantly better (with $\alpha = 0.05$). The same algorithm also yields an ‘improved estimate of prediction error’ (IEPE, Efron & Tibshirani 1993) of the fitted model that can be tested for significance between both models. A final difference is that with real data we do not know the process that created the data, that is, both candidate model might be completely wrong. To cope with this problem I only considered fits with a likelihood above a threshold level that was estimated from the likelihoods obtained by fitting to the artificial data. In sum, for each type of fitting (process error fit and observation error fit) four selection criteria were applied, and a model selection was only considered significant if all criteria (with sufficiently high likelihoods) with both error functions yielded the same result.

The most significant selection results are obtained with the protozoan data. Most systems are either closer to prey dependence or the samples are too small to detect predator dependence reliably. However, there is one predator-prey system with four datasets (Flynn & Davidson, 1993) that shows significant predator dependence. The predators in this system can show strong cannibalism at low prey-densities (personal communication with the authors). Although such cannibalism was not observed in the analysed data this suggests that the predators are capable of strong interference when they encounter each other. It is also possible that heterogeneities developed in the periods between the stirrings (every 12 h). Both factors might explain the highly significant support for the ratio-dependent model. To our knowledge this is the first example of a protozoan system with monospecific prey and predator that shows this strong predator dependence (compare to chapter 6). This exception illustrates that a modeller has to know the biology of the system to be modelled, and that traits like potential cannibalism can indicate that a model with predator dependence is more appropriate. See section 8.5 for further comments and relations to other experiments.

There also seems to be no predator dependence in Huffaker’s arthropod data. In most cases the prey-dependent model fits better, and in both cases with process error fit where the ratio-dependent model fits better this fit is qualitatively wrong. Two other aspects are important for the fits to these data: 1) quantitatively the models fit rather badly to the data, the experimental systems showing larger variation than can be reproduced by our simple models and 2) trajectory fitting gives qualitatively correct fits with both models. The first point might be explained by Huffaker’s experimental setup, food for prey being dispersed in a 2- or 3-dimensional structure and the prey colonising this food in a fairly heterogeneous manner. Such a laboratory system is structurally more complex than the protozoan batch cultures of the previous paragraph. The second point indicates that the models used can nevertheless be used for qualitative analysis, only quantitative

conclusions should be interpreted with care.

The fits to phyto- and zooplankton data are the most difficult to interpret. The easiest conclusion would be that either the data are too noisy for this kind of model identification or that both models are too simple for lake dynamics. The first point is supported by the qualitative nature of the process error fit regressions (mostly stable or strongly stable systems) that might mean that the best prediction is not obtained by dynamic nonlinear modelling but rather by simply using some mean value of the data as a predictor. The second point is probably true for observation error fit, but not necessarily for process error fit. Despite these drawbacks, many significant model identifications are obtained with observation error fit, showing that there are long term dynamic patterns. These significant fits are of both types, prey- and ratio-dependent, with trends for some lakes and for modelling edible phytoplankton only or total phytoplankton. However, these trends are not sufficiently convincing to give any recommendations when which model might be more appropriate. Brett & Goldman (1997) argued that phytoplankton displays strong bottom-up influence while zooplankton is more sensitive to top-down control. The phytoplankton-zooplankton interaction itself (that is studied in this thesis) is subject to both forces, which might also explain the ambiguity in model identification.

Conclusions from the ‘in vivo’ analysis

Systems with monospecific prey and monospecific predator in a homogeneous environment generally show little predator dependence and are better modelled with the prey-dependent model. However, I found at least one system where the ratio-dependent model fits better than the prey-dependent model for all available time-series. Therefore, before modelling such systems with a prey-dependent model, one should check whether there are any biological traits that indicate strong predator dependence (e.g. potential cannibalism). With lakes no conclusion in favour of one of the models can be drawn. Whenever making predictions with models, such predictions should be cross-checked by using another model. Prey dependence and ratio dependence offer promising frameworks to develop such alternative models and detect ‘robust’ predictions (robust in the sense that they are independent of predator dependence) and direct further research if no clear prediction is possible (e.g., to study how much predator dependence actually occurs in a system or to parameterize an intermediate model).

De Mazancourt et al. (1998) and Zheng et al. (1997) are examples of studies that have chosen this pluralistic modeling approach, both using on the one side a Lotka-Volterra functional response (as an example of top-down control) and on the other side a linear ratio-dependent functional response (to represent donor control). The first study checked the robustness of some theoretical predictions, while the second study contrasted these predictions to guide further research and the interpretation of field results.

Chapter 3

Concluding remarks and perspectives

3.1 General conclusions

The present thesis can be interpreted as a general validation of a ratio-dependent predator-prey model. The mathematical properties of this model are thoroughly analysed, showing that global dynamics are stable coexistence of prey and predator, unstable coexistence (limit cycles), extinction of the predator only or extinction of both prey and predator. For certain parameter values there are two basins of attraction, one for the origin (extinction) and one for stable or unstable coexistence. This naturally explains experimental results where coexistence or extinction were function of the initial population levels. The model is shown to describe qualitatively correctly predator-prey systems in freshwater plankton, protozoan batch and continuous cultures and laboratory arthropod systems.

In a next step the ratio-dependent model is compared to an equally complex prey-dependent model, both qualitatively and quantitatively. The qualitative comparison demonstrates that both models produce very similar dynamic patterns. The major difference lies in the reaction to enrichment, which is destabilizing and increasing only the predator equilibrium in the prey-dependent model, neutral with respect to stability and increasing both prey and predator equilibrium in the ratio-dependent model. The comparison of both models to the PEG-model (that summarises observed plankton dynamics in freshwater lakes of the temperate zone and of different trophic states) shows that they both can explain these dynamics if seasonality is added to one or more parameters. The ratio-dependent model seems to explain the changes that occur in the dynamics with enrichment slightly better than the prey-dependent model.

To compare the models quantitatively to predator-prey time-series I found the likelihood concept to be a firm statistical framework. Protozoan data are generally better described by the prey-dependent model. However, there is also one protozoan system where the ratio-dependent model describes the dynamics more accurately. The analysed arthropod data correspond better to the prey-dependent model. For the phytoplankton-zooplankton interaction both models are valid and none of them better than the other. Consequently, predictions for freshwater plankton systems should be based on both mod-

els to avoid falling victim to mathematical artifacts of one of them (such as the paradox of enrichment).

There exist for both the prey-dependent and the ratio-dependent model equivalent forms in microbiology (Monod's and Contois' model). Microbiologists have also done the kind of quantitative and qualitative comparison that is applied in this thesis. Reviewing their results I found that Monod's model seems correct with monospecific prey and monospecific predators in a homogeneous environment. However, every deviation from these conditions induces predator dependence in the growth function (numerical response), such that often Contois' model describes the observed dynamics better than Monod's model. The main field of application of Contois' model is in plurispecific and heterogeneous systems such as fermentation processes and waste water treatment.

In conclusion, the prey-dependent model seems most appropriate in cases of monospecific prey and monospecific predators in homogeneous environments. In all other cases any degree of predator dependence in the functional response can be observed and the best suited model is a priori unknown. Prey-dependent and ratio-dependent models can be interpreted as two extrema with respect to predator dependence. Using both helps detecting predictions that are sensitive to predator dependence and direct further research if necessary.

3.2 Perspectives for continuation of work

In the following I will list some possible lines of research that could further enhance the work presented in this thesis.

3.2.1 A non-parametric approach

The technique used for model selection in chapters 7 and 8 requires to parameterize the whole predator-prey model, in particular also the prey growth function and the predator mortality function which are of no interest to the detection of predator dependence in the functional response. Even worse, inaccuracies in the chosen formulations (logistic growth and constant predator mortality rate in the case of this thesis) could influence the detection of predator dependence. Another possible problem is the absence of delayed effects in the predator-prey model. A delay in the numerical response with respect to the functional response is theoretically plausible and has improved the goodness-of-fit in Harrison's (1995) reanalysis of Luckinbill's (1973) protozoan data and in the bacteria-bacteriophage system of Bohannan & Lenski (1997).

An elegant solution for both problems has been outlined by Ellner et al. (1997). The authors study the system

$$\frac{dx(t)}{dt} = f(x(t - \tau)) + g(x(t)).$$

Based on a time-series approach they develop a method to estimate the delay parameter τ and to reconstruct f and g non-parametrically. Tested with artificial time-series, adding

both observation and process error with $CV = 0.1$, they find that a correct estimation of τ is possible for time-series as short as 100 data points. The non-parametric reconstruction of f and g looks fairly well and the authors point out that their method can reveal information about the biology of f and g .

This is exactly what could be done to identify the functional response. Estimating the delay in the numerical response (as a byproduct) and reconstructing the functional response non-parametrically with confidence intervals on all involved variables one could now fit the functional response directly to the reconstructed data (also using errors-in-variables techniques) and identify empirically the most parsimonious model to describe it. Protozoan systems such as studied in Veilleux (1979) could provide the data necessary for such an analysis.

3.2.2 Paying more attention to deterministic extinction

The quasi extinction risk of a natural population is usually estimated by parametrising a model of the population (e.g., with a Leslie model, Leslie 1948), doing stochastic simulations and measuring the proportion of simulations during which the population abundance fell below a predefined threshold value. One of the reasons for this approach is that typical population models do not allow for deterministic extinction. Working also with models that include this feature (such as general ratio-dependent food webs or food webs extended from the ideas in the predator-prey models of section 2.3.1) could provide additional information on the risks of endangered populations. Extinction as a deterministic outcome has not been considered at all in the ecological literature.

3.2.3 Modelling plankton data more realistically

I analysed the plankton data from Lake Geneva only in the predator-prey context with constant exogenous factors (in form of model parameters). Actually, there are much more data available: plankton abundances for each species, temperature at several depths of the Lake, nitrogen and phosphorous content in the water. Using these external variables as model input a much better prediction of total phyto- and zooplankton abundances one or two weeks ahead might be possible. However, while adding inputs will always increase goodness-of-fit, this also increases model complexity (with all its inconveniences: more parameters need being estimated, it becomes more difficult to transfer the model to another ecosystem, etc.) and the predictions may not become significantly better by adding these inputs (likelihood ratio tests, information criteria). The identification of the most important driving external variables is an old problem in ecology. The usual statistical approach uses principal component analyses. However, PCA only detects linear dependencies, nonlinearities are only detected as noise. Empirical fitting methods such as neural networks also detect nonlinear patterns (Lek et al., 1996). By splitting the data set in two (in-sample and out-of-sample) one can teach the neural network on the in-sample data and test its predictive power on the out-of-sample data. This procedure can be combined with bootstrap techniques. Such methods could detect the two, three or four most important external variables also with respect to nonlinear dependencies.

These variables could then be used to develop a simple explicit dynamic model to predict the variables of interest, e.g., total phyto- and zooplankton.

3.2.4 How to treat process and observation error together?

The statistical methods I used in this thesis all make the assumption that there is only one type of error in the data, observation error or process error. This is in contrast to the data which always contain both types of stochasticities. Statisticians have developed several strategies how to cope with this problem. In this section I will discuss three possible strategies. All of them are computationally more intensive than the techniques I used, but with the next generation of personal computers the actual computing time might decrease to acceptable values.

Hilborn & Walters (1992) propose to fit the models by assuming that all errors are of one type only (e.g. observation error) and to assess a possible bias by stochastic simulation. In the context of continuous models this means fitting data produced by a stochastic ordinary differential equation (SODE) to a deterministic ordinary differential equation (ODE). This approach may be well suited for parameter estimation if there is no doubt about the model structure. However, we do not know whether the expected trajectory of a SODE maintains the structure of the underlying ODE (which is important for a correct model selection). This is the case for single population exponential growth (Yodzis, 1989) and single population logistic growth (Nisbet & Gurney, 1982; Braumann, 1983), but these results rely on the existence of an analytic solution of the ODE and I am not aware of any such work for more complex systems. Some preliminary studies show that there may be a difference between expectation and the deterministic model: I simulated SODE's by adding white noise with a standard deviation proportional to the actual population size (thus simulating the characteristics of a lognormal process error, see also the artificial data creation in chapter 7), computed a large number of replicates and calculated from them the mean population dynamics (Figure 3.1, dotted curves). Fitting the deterministic model (whole trajectory) to these expectations showed that often the trajectories could not be approximated by the deterministic ODE, and model identification became very difficult. Figure 3.1 shows moderate examples of these deviations from deterministic behaviour, together with the best fit obtainable to the deterministic model that was used as the core of the SODE and the deterministic trajectory with the original parameters. These two examples illustrate that the structure of the expectation of a SODE can be different from the one of its deterministic core function. Further numerical work would be needed to elaborate how stochastic noise can change the actual structure of a SODE.

Errors-in-variables (having uncertainty in both the dependent and the independent variable) offers another approach how time-series could be fitted to models. The idea is to estimate not only the parameters, but also the actual values of the state variables for each measurement (the so-called nuisance parameters). This can be done in a likelihood framework, but requires independent knowledge of one of the errors. In their milestone paper Reilly & Patino-Leal (1981) describe such estimation techniques for models that are linear or nonlinear in the parameters. They propose nested iterations to estimate alternately parameters and state variables. Schnute (1994) and Schnute & Richards

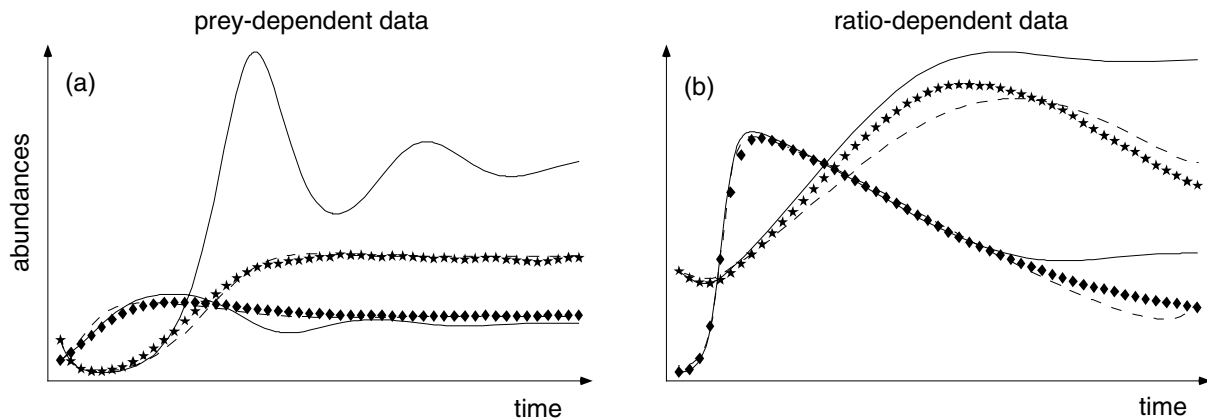


Figure 3.1: Two examples illustrating the problem that expectations of SODE's can have a different structure than the deterministic core function of the SODE. Diamonds and stars are prey and predator data (respectively) of the series of expectations (obtained by Monte Carlo simulation), the continuous line is the deterministic trajectory with the original parameters and the dashed line shows the best fit of the deterministic model to the expected trajectory. (a) is an example for the prey-dependent model where the expectation strongly deviates from the original trajectory while it can still be fitted reasonably to the deterministic core model. (b) shows an example for the ratio-dependent model where the expectation is closer to the original trajectory but it cannot be fitted to the deterministic model.

(1995) discuss the errors-in-variables technique in the context of fisheries management. In other branches of ecology the method does not seem to be used actively.

Yet another set of approaches are simulation-based regression techniques (Ellner & Turchin, 1995; Gouriéroux & Monfort, 1996). The idea is to use the stochastic model to simulate a reference data set which is then used to estimate the discrepancy between the real data and this reference data set (inspired from reconstruction techniques used in chaos theory, see Kantz & Schreiber 1997 for a very readable introduction). The parameters in the stochastic model are chosen such that the discrepancy becomes minimal. As in the errors-in-variables method this technique requires independent knowledge of one of the errors. Little is known about the reliability of parameter estimation and model selection when applying this method to typical ecological time-series.

Part II

Detailed studies (accepted or
submitted articles)

Chapter 4

The clear water phase in lakes: a non-equilibrium application of alternative phytoplankton-zooplankton models

Roger Arditì, Christian Jost, and Vojtĕch Vyhnálek

Abstract

The verbal PEG-model (that describes the plankton dynamics of freshwater lakes of the temperate zone) is interpreted in the context of dynamic predator-prey (phytoplankton-zooplankton) interactions. We then compare two explicit predator-prey models qualitatively with these dynamics. One model represents the ideas of top-down control while the other model includes also ideas of bottom-up control. It is shown that neither model can explain the dynamics of the PEG-model satisfyingly, but that the second model (bottom-up) has more in common with the observed dynamics than the first model (top-down). We then study some extensions of both models (seasonality of parameters or additional interacting trophic levels) and show that both extended models can predict the PEG-model dynamics satisfyingly. We conclude that the PEG-model dynamics have, on the whole, more in common with the model containing bottom-up control, but that we have to add a trophic level to the predator-prey framework (either as a seasonally changing parameter or as an additional state variable) to obtain qualitatively satisfying dynamics.

Nous interprétons le modèle (verbal) “PEG”, qui décrit la dynamique du plancton des lacs d’eau douce de la zone tempérée, dans le cadre d’interactions dynamiques proie-prédateur (phytoplancton-zooplancton). Nous comparons ensuite qualitativement cette dynamique avec deux modèles explicites de systèmes proie-prédateur. L’un d’entre eux est fondé sur une idée de contrôle “descendant” des abondances au sein des niveaux trophiques, tandis que le second inclut également une régulation “ascendante” des effectifs. Nous montrons qu’aucun des deux modèles ne peut rendre compte de façon satisfaisante de la dynamique décrite par le modèle PEG, mais que le second modèle (avec régulation ascendante) présente plus de points communs avec elle que le premier (avec contrôle descendant). Nous étudions ensuite un certain nombre d’extensions des deux modèles (modifications saisonnières des valeurs des paramètres ou niveau trophiques supplémentaires), et nous montrons que les deux modèles ainsi étendus peuvent prédire la dynamique du modèle PEG de façon satisfaisante. Nous concluons que la dynamique décrite par le modèle PEG a, dans l’ensemble, plus de points communs avec le modèle incluant une régulation ascendante, mais qu’il est nécessaire de prendre en compte un niveau trophique supplémentaire par rapport au cadre proie-prédateur (soit sous forme d’un paramètre dont la valeur change de manière saisonnière, soit sous la forme d’une variable d’état supplémentaire) afin d’obtenir une dynamique satisfaisante du point de vue qualitatif.

4.1 Introduction

It is becoming increasingly accepted that ecological processes in lakes are largely determined by trophic interactions (e.g., reviews in Carpenter 1988; Carpenter & Kitchell 1994). Therefore, plankton populations in lakes (or in simpler experimental systems) have become ideal systems for testing the hypotheses and predictions of predator-prey or food web theories (e.g., McCauley & Murdoch (1987), Sarnelle (1992), Mittelbach et al. (1988)). Arditi & Ginzburg (1989) have suggested that the functional response might often be approximated by a function of the prey-to-predator ratio instead of just the prey density (prey dependence) as in classical predator-prey theory (e.g., Rosenzweig & MacArthur (1963)). In the ensuing debate, many arguments have centered on the ability of alternative models to explain observed patterns in the equilibrium abundances (or long-term averages) of the various trophic levels in lakes of different productivities (Arditi et al., 1991a; Gatto, 1993; Sarnelle, 1994; Abrams & Roth, 1994; Mazumder, 1994; Akçakaya et al., 1995; Lundberg & Fryxell, 1995; McCarthy et al., 1995) or in ad-hoc experimental setups (Arditi et al., 1991b; Arditi & Saïah, 1992; Ruxton et al., 1992; Holmgren et al., 1996). Properties of systems out of equilibrium have been much less studied. Particularly noteworthy is the work of Carpenter & Kitchell (1994) and Carpenter et al. (1994). Using artificial data as well as plankton time series from two lakes over seven years, these authors have shown that modest observation errors make it impossible to identify reliably the underlying model. Here, we take a different approach to the study of dynamic properties of alternative predator-prey models. Rather than trying to fit models to noisy data, we will examine the ability of the models to generate, in a qualitative way, a standard non-equilibrium pattern of lakes: the clear water phase that occurs in the spring in lakes of the temperate region. This pattern is commonly thought to be caused by predator-prey interactions.

4.1.1 Seasonality of plankton in lakes

In the last decades, limnologists have come to consider that the sequence of planktonic events in lakes of the temperate zone exhibits a regular pattern that can be predicted to a certain extent. The current knowledge about plankton seasonality is summarized in a set of statements by the Plankton Ecology Group (the so-called PEG-model, Sommer et al. 1986). Three distinct periods can be distinguished during the growing season according to changes in the phytoplankton biomass: (1) the spring peak, (2) the depression of biomass (known as the clear water phase), and (3) the summer peak (see Figure 4.1a). This pattern is more pronounced in meso- and eutrophic lakes than in oligotrophic ones.

The increase of phytoplankton biomass in the spring is caused by a fast growth of algal populations due to a high concentration of nutrients and increasing light (Sommer et al., 1986). The collapse of the phytoplankton bloom in the spring and the induction of the clear water phase is interpreted as being caused by overgrazing of the phytoplankton by the zooplankton (Lampert, 1985; Lampert et al., 1986; Sommer et al., 1986). However, nutrient limitation and subsequent sedimentation of algal cells were found to be the most important factors of the phytoplankton collapse after the spring phytoplankton bloom in several lakes: Lake Geneva, France-Switzerland (Gawler et al., 1988), Lake Constance,

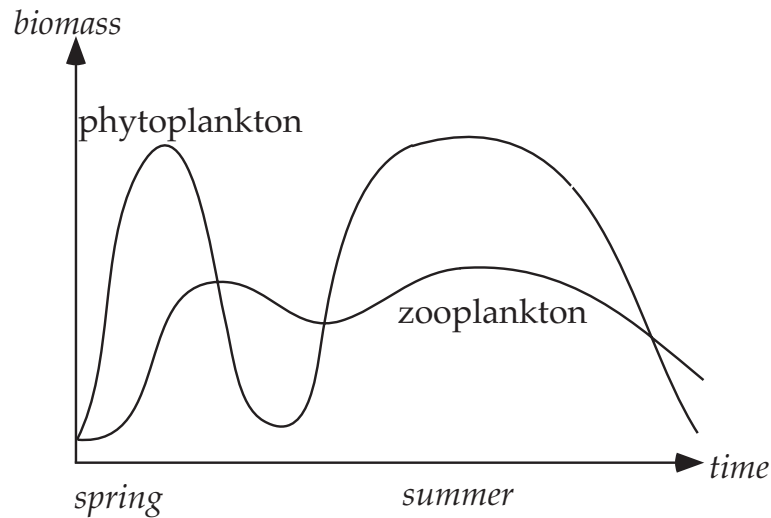


Figure 4.1: (a) Plankton dynamics as proposed by the PEG-model and (b) criteria for the plankton dynamics of a model.

Germany-Switzerland-Austria (Weisse et al., 1990), Lake Søbygård, Denmark (Jeppesen et al., 1990) and the Římov Reservoir, Czech Republic (Vyhnálek et al., 1991). In addition, a lysis of algal cells can play a significant role during this period, according to observations from the Římov Reservoir (Vyhnálek et al., 1993). In those cases in which the clear water phase is induced by nutrient limitation, zooplankton grazing still plays a role in maintaining the biomass of phytoplankton at a low level. Nutrient concentration increases due to the fast turnover through the zooplankton (Fott et al., 1980; Sommer et al., 1986). Food limitation and fish predation cause a decrease of zooplankton. Therefore, conditions become favorable for a second bloom of phytoplankton, followed by an increase of zooplankton in the summer. Finally, reduced light availability results in a decline of phytoplankton followed by a decline of herbivores towards winter.

These quantitative variations are accompanied by a qualitative succession in the nature of species. The spring peak of phytoplankton is formed mostly by small fast-growing algae easily edible by herbivorous zooplankton. This is dominated by large species (especially Cladocera). During the clear water phase, large, colonial, inedible, and toxic phytoplankton species are favored because of their resistance against herbivore grazing (Porter, 1977). These species (especially cyanobacteria) become dominant and form the summer peak of phytoplankton biomass. Large herbivores are replaced by smaller species, less vulnerable to predation, and less affected by perturbation of their feeding apparatus by large algae. Thus, the species composition of both trophic levels changes through the seasons under the influence of predation and resource competition (Sommer et al., 1986).

4.1.2 Simple mathematical models of predator-prey interactions

The general model describing the dynamics of prey-predator populations in continuous time can be written as:

$$\frac{dN}{dt} = f(N)N - g(N, P)P \quad (4.1)$$

$$\frac{dP}{dt} = eg(N, P)P - \mu P \quad (4.2)$$

where N is prey abundance, P is predator abundance, t is the time, $f(N)$ is the per capita net prey production in the absence of predation, $g(N, P)$ is the functional response of predators (the number of prey killed by one predator in a unit of time), e is the conversion efficiency and μ is the per capita death rate of predators. The key role in prey-predator models is played by the functional response g (Solomon, 1949), sometimes called the trophic function (Svirezhev & Logofet, 1983). Traditionally, it is assumed that the functional response g is a function of prey density only [prey-dependent feeding, $g = g(N)$], without any dependence on predator density (Holling, 1959a; Rosenzweig, 1971; May, 1973). The hypothesis $g = g(N)$ is based on an analogy with the law of mass action in chemistry assuming that prey and predator individuals encounter each other randomly in space and time (Royama, 1971). Therefore, the prey-dependent model can be applied to systems which are spatially homogeneous and in which the time scale of prey removal by predators is of the same order of magnitude as that of population reproduction (Arditi & Ginzburg, 1989). These conditions are fulfilled especially in small-scale and well-mixed laboratory systems containing bacteria (Jannasch, 1967; Luckinbill, 1973; Bazin, 1981), algae (Droop, 1966; Goldman, 1977), protozoa (Taub & McKenzie, 1973), and under certain conditions also pelagic rotifers (Droop & Scott, 1978; Boraas, 1980) and cladocera (Arditi et al., 1991b; Arditi & Saïah, 1992).

However, natural ecosystems are usually spatially heterogeneous and the time scales for feeding and reproduction are also often very different. If the spatial heterogeneity can be characterized by a double exponential distribution of the encounter time, Ruxton & Gurney (1994) showed that a purely prey-dependent functional response may still be derived. However, various other mechanisms (e.g., pseudo-interference, etc.) might lead to explicit dependence on predator density [$g = g(N, P)$]. Arditi & Ginzburg (1989) have argued that, in many cases, this predator dependence could be simplified as a ratio-dependent model [$g = g(N/P)$] instead of modeling explicitly all conceivable interference mechanisms (and thus adding parameters to the model). A most striking difference between prey-dependent and ratio-dependent models is the response of the equilibria of trophic levels after an increase in prey production. The prey-dependent model predicts an increase of predator abundance only, with prey abundance remaining unchanged. In systems consisting of more than two trophic levels, the prey dependent model predicts various responses of the several levels to an increase of primary input, depending on the chain length and on the level considered: no response, proportional response, non-linear increasing response and non-linear decreasing response (Oksanen et al., 1981; Persson et al., 1988). On the other hand, the ratio-dependent model predicts proportional responses of all trophic levels to an increase of primary input (Arditi & Ginzburg, 1989).

Recent analysis of data from freshwater ecosystems have shown evidence that aver-

age biomasses of fish, zooplankton and phytoplankton are positively correlated along a gradient of productivity (summarized by Arditi et al. 1991a; Ginzburg & Akçakaya 1992; Mazumder 1994). These positive correlations between trophic levels are in agreement with the predictions of the ratio-dependent model if the equilibria of all trophic levels are approximated by average biomasses over the whole year or over the growing season. On the opposite, the empirical findings from freshwater ecosystems are in contradiction with the prey-dependent model predicting a mixture of positive, negative and zero correlations between trophic levels (Oksanen et al. 1981; Arditi & Ginzburg 1989; Arditi et al. 1991a), and also a density-dependent mortality rate as proposed by Gatto (1991) predicts these positive correlations only for two-level systems, not for food chains (see 4.B).

Further insights into this controversy may be gained by comparing directly the trajectories of the two models with time series from real ecosystems. This may be done by fitting the models to the data and using goodness-of-fit methods as a criterion. Carpenter et al. (1994) found that by this method the two models could be reliably distinguished only if the ecosystems underwent considerable perturbations (e.g. caused by introducing or removing fish populations). Applying this method to such a dataset [zooplankton and edible phytoplankton in Tuesday lake (Carpenter & Kitchell, 1994)] they detected a slightly better fit of the ratio-dependent model.

Another method to compare the trajectories is the mathematical analysis of the dynamics. Despite numerous results on the equilibrium properties of the two alternative models, our knowledge about the non-equilibrium properties is limited. In this paper we present a comparison of the transient behavior of both models before reaching the equilibrium. Then, the trajectories of population densities predicted by the models are compared with the seasonal development of the plankton community in lakes of the temperate zone, which is understood as a process reaching equilibrium (or quasi-equilibrium) during the summer. Furthermore we study the qualitative changes of the system dynamics if the model parameters change (during season or with eutrophication). Suggested seasonal changes are decreasing predator attack rate (due to increased proportions of inedible algae), increasing predator mortality rate (due to predation by higher trophic levels) and increasing prey growth rate (due to higher light intensity and water temperature). The effects of eutrophication are studied by increasing the carrying capacity (see McCauley et al. 1988).

4.2 Problem formulation

4.2.1 The alternative models

Two-level models consisting of phytoplankton as prey (N) and zooplankton as predators (P) will be built with differential equations of type (4.1–4.2). The production of phytoplankton follows the usual logistic growth:

$$f(N) = r\left(1 - \frac{N}{K}\right). \quad (4.3)$$

The functional response of zooplankton is described by a concave monotonic upper-

bounded expression. In the prey-dependent model, it is a function of prey density N (type II, Holling 1959a):

$$g(N, P) = g(N) = \frac{aN}{1 + ahN}, \quad (4.4)$$

where a is the searching efficiency and h is the handling time.

In the ratio-dependent model, g is a function of the ratio N/P :

$$g(N, P) = g\left(\frac{N}{P}\right) = \frac{\alpha N/P}{1 + \alpha h N/P} = \frac{\alpha N}{P + \alpha h N}, \quad (4.5)$$

where α has different units from a .

4.2.2 The required patterns

In order to be satisfied that a simple prey-predator model approximates the complex succession of events of the PEG-model (Sommer et al., 1986), the following conditions are required. These criteria are set mainly for the dynamics of phytoplankton but zooplankton dynamics can be used as a secondary criterion.

1. Starting with a low (winter) biomass, the phytoplankton must present a (spring) maximum followed by a distinct depression (the clear water phase) and then a high biomass (during the summer) (Fig. 4.1).
2. A relatively constant biomass of phytoplankton is expected thereafter.
3. Zooplankton dynamics, starting from a low biomass, must follow the spring phytoplankton increase with some delay and a stabilization of zooplankton biomass is expected in the summer.
4. In lakes with a higher degree of eutrophication, i.e., with a higher prey carrying capacity, the model should show wider amplitudes and a higher algal equilibrium.

Thus, a good qualitative similarity between the simulated dynamics and the PEG-model is required during the spring and the summer. In the autumn, both phytoplankton and zooplankton are expected to remain at steady levels in the simulations because the decline that occurs in nature is assumed to be caused by external physical factors (decreasing light and temperature).

4.3 Model analysis and results

4.3.1 Dimensionless forms

With appropriate changes in variables, the two models built on the functional responses (4.4–4.5) can be simplified to dimensionless forms. This reduces the number of independent parameters and makes the mathematical analysis easier. The prey-dependent model

becomes

$$\frac{dN_p}{dt'} = R\left(1 - \frac{N_p}{C}\right)N_p - \frac{N_p}{1 + N_p}P_p \quad (4.6)$$

$$\frac{dP_p}{dt'} = \frac{N_p}{1 + N_p}P_p - QP_p, \quad (4.7)$$

with $N_p = ahN$, $P_p = ahP/e$, $t' = et/h$, $R = rh/e$, $C = ahK$ and $Q = h\mu/e$.

The dimensionless form of the ratio-dependent model is

$$\frac{dN_r}{dt'} = R\left(1 - \frac{N_r}{D}\right)N_r - D\frac{N_r}{P_r + DN_r}P_r \quad (4.8)$$

$$\frac{dP_r}{dt'} = D\frac{N_r}{P_r + DN_r}P_r - QP_r, \quad (4.9)$$

where $N_r = \alpha hN/(eK)$, $P_r = \alpha hP/(e^2K)$ and $D = \alpha h/e$.

4.3.2 Isoclines

The predator isocline is a straight line, which is vertical in the prey-dependent model and slanted (through the origin) in the ratio-dependent model (Fig. 4.2). The prey isocline is always parabolic in the prey-dependent case. Its ‘‘hump’’ may be in the positive quadrant or not. However, the latter case is considered atypical (Rosenzweig, 1969). In the ratio-dependent model, the prey isocline is usually parabolic-like but it may also have a vertical asymptote [the ‘‘limited predation’’ case in Arditi & Ginzburg (1989)]. In either case, it will always be entirely in the positive quadrant.

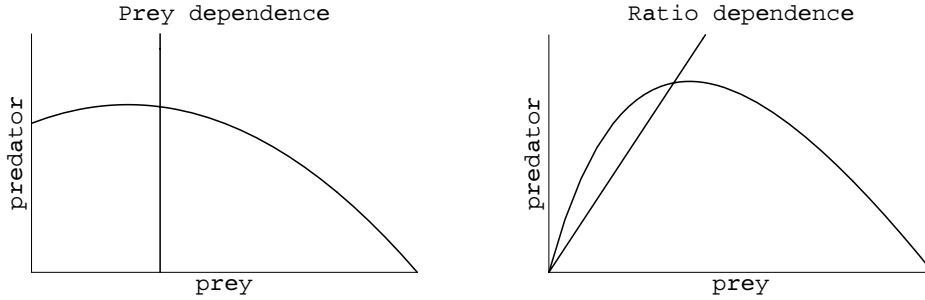


Figure 4.2: Typical isoclines of the prey-dependent model (left) and the ratio-dependent model (right). The humped line is the prey isocline, the straight line is the predator isocline.

4.3.3 Equilibria

Besides the trivial equilibria $(0, 0)$ and $(0, 1)$, both models have one non-trivial equilibrium which is, in the prey-dependent model,

$$N_p^* = \frac{Q}{1 - Q} \quad (4.10)$$

$$P_p^* = \frac{R}{CQ}N_p^*(C - N_p^*) = \frac{R(C - Q - CQ)}{C(1 - Q)^2}. \quad (4.11)$$

and in the ratio-dependent model

$$N_r^* = \frac{D}{R}(DQ + R - D) \quad (4.12)$$

$$P_r^* = \frac{R}{DQ}N_r^*(D - N_r^*) = \frac{D^2}{QR}(2DQ - DQ^2 + R - QR - D). \quad (4.13)$$

Conditions for the positiveness of the equilibrium are thus

$$0 < \frac{Q}{1-Q} < C \quad (4.14)$$

in the prey-dependent model and

$$0 < 1 - Q < \frac{R}{D} \quad (4.15)$$

in the ratio-dependent model.

In the prey-dependent model, when the parameter C approaches the bound $Q/(1-Q)$, the prey equilibrium remains at $Q/(1-Q)$ while the predator equilibrium tends to 0. In the ratio-dependent model both populations go extinct when $1-Q$ approaches the upper bound R/D , while the prey equilibrium tends to D and the predator equilibrium to 0 for Q approaching 1.

4.3.4 Stability of the non-trivial equilibrium

In both models, the non-trivial equilibrium point can be locally stable or unstable. With (m_{ij}) being the community matrix (the Jacobian at the equilibrium point, see 4.A for further details), the characteristic equation for the eigenvalues reduces to a quadratic equation in the case of a two-level model:

$$\lambda^2 - (m_{11} + m_{22})\lambda + m_{11}m_{22} - m_{12}m_{21} = 0. \quad (4.16)$$

The Routh-Hurwitz criterion (e.g., Amann 1990) says that the equilibrium point is stable whenever the two conditions

$$m_{11}m_{22} - m_{12}m_{21} > 0 \quad (4.17)$$

$$m_{11} + m_{22} < 0 \quad (4.18)$$

hold simultaneously (see 4.A for further details).

In the case of the prey-dependent model, the stability conditions are

$$\frac{Q}{1-Q} < C < \frac{1+Q}{1-Q} \quad (4.19)$$

where the lower bound coincides with the condition for existence of the positive equilibrium. In the ratio-dependent model, we have a stable positive equilibrium point whenever the conditions

$$D < \frac{Q - Q^2 + R}{1 - Q^2} \quad \text{and} \quad 1 - Q < \frac{R}{D} \quad (4.20)$$

are fulfilled.

The stable equilibrium may be reached with or without oscillations in both models. Oscillations occur if the discriminant of equation (4.16) is negative, i.e., if

$$(m_{11} - m_{22})^2 + 4m_{12}m_{21} < 0. \quad (4.21)$$

This criterion gives rather complicated upper and lower bounds for C (respectively D) which the interested reader may find in 4.A. More important than the formulas is the visualization in parameter portraits (Fig. 4.3, see next subsection).

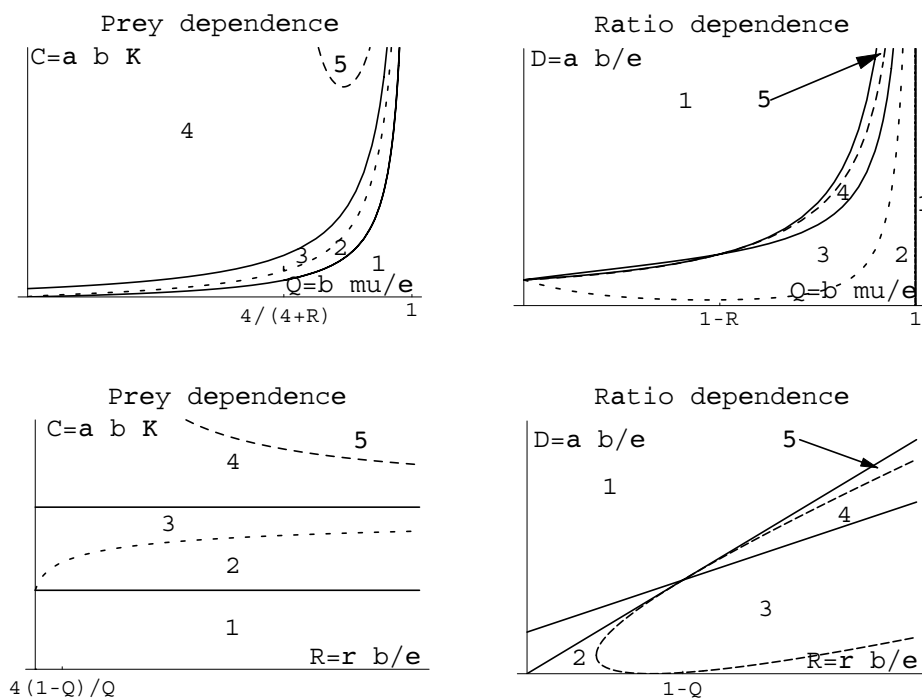


Figure 4.3: Parametric portraits of C versus Q for fixed R (upper left) and of C versus R for fixed Q (lower left) for the prey-dependent model and of D versus Q for fixed R (upper right) and of D versus R for fixed Q (lower right) for the ratio-dependent model. In regions 1 populations go extinct, in regions 2 the stable equilibrium point is reached without oscillations, in regions 3 the equilibrium point is a spiral node, in regions 4 the positive equilibrium point is a spiral repeller and in regions 5 the positive equilibrium is an ordinary repeller.

4.3.5 Comparison of dynamic properties in the two models

The criteria for positive equilibrium point, stability (attractor or repeller) and oscillations (spiral or non-spiral) can be expressed in a graphic form as parametric portraits of the parameters C (resp. D) and Q after fixing R as a constant. In order to identify the effect of changing the growth rate r , another parametric portrait has been created where C (resp. D) is plotted versus R while keeping Q constant (see Fig. 4.3).

Several interesting properties of the models can be pointed out:

- The existence of positive equilibria requires in both models that $Q < 1$ holds or, in the original parameters, that $\mu h < e$.
- There is a fundamental difference regarding the size of the searching efficiency a (resp. α): while in the case of prey-dependence, it has a lower bound ($a > \mu/[K(e - \mu h)]$ because $C > Q/(1 - Q)$), in the case of ratio-dependence it has an upper bound ($\alpha < re/(e - \mu h)$ because $D < R/(1 - Q)$).
- For $C \leq 1$ (resp. $D \leq 1$), in both models the positive equilibrium is stable. However, for $C > 1$ (resp. $D > 1$), the equilibrium can be either stable or unstable. In the initial parameters, this means that an unstable positive equilibrium can exist in the prey-dependent model for $ahK > 1$ and in the ratio-dependent model for $\alpha h > e$.
- In the ratio-dependent model, unstable equilibrium points are possible only for $D > R$, while for $D \leq R$ only stable equilibrium points exist. The reason is that if $\alpha \leq r$ ($\Leftrightarrow D \leq R$), the prey isocline has a vertical asymptote and the equilibrium point is always stable (Arditi & Ginzburg, 1989). On the other hand, if $\alpha > r$ ($\Leftrightarrow D > R$), the prey isocline is “humped” and either stable or unstable equilibrium points can be found. Note that equilibria can be stable even if they lie on the ascending part of the hump in contrast to an erroneous assertion in Arditi & Ginzburg (1989) (see Jost et al. (1999) for an analytical proof). No similar condition is present in the prey-dependent model, which has only humped isoclines, and equilibria lying on the ascending part of the prey isocline are always unstable.
- In the prey-dependent model, since $C = ahK$, increasing the carrying capacity K in Eq. (4.3) acts as a destabilizing factor (see Fig. 4.3: increasing K increases C , thus leaving the area of stable positive equilibrium). This fact is well known as the “paradox of enrichment” (Rosenzweig, 1971) (see Fig. 4.4a). No such destabilizing effect of K exists in the ratio-dependent model: K is used (in the dimensionless form) as a scaling factor only for N_r and P_r , but not for any of the parameters D , Q , or R . Therefore, the only influence of increasing K is to increase both populations N and P in the same proportion (see Fig. 4.4b).
- The prey growth rate r does not influence stability in the prey-dependent model, since changing r moves the parameter pair (C, R) along a horizontal line (lower graphs in Fig. 4.3) which does not intersect any of the stability bounds (it may only influence the oscillatory behavior). In the ratio-dependent model, on the contrary, for any $Q < 1$ and any D , increasing r will stabilize the equilibrium, while decreasing r will make the system leave the area of positive equilibrium points (extinction of both populations).

4.3.6 Model trajectories and plankton seasonality

According to the criteria 1–2 stated above (Fig. 4.1), plankton dynamics must reach a stable equilibrium after one oscillation. Therefore, the trajectories obtained in the areas of stable equilibrium points reached after oscillations (regions 3 in Fig. 4.3) must be

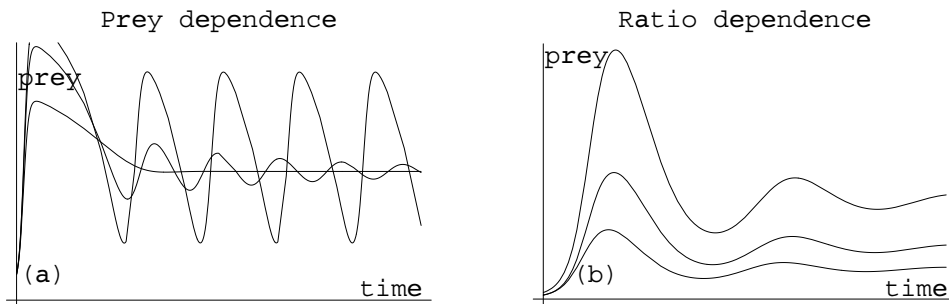


Figure 4.4: Influence of K on the stability, shown here for the prey dynamics (higher amplitudes with higher K), for the prey-dependent model (a) and for the ratio-dependent model (b).

examined. Typical prey (phytoplankton) trajectories in this region are presented in Fig. 4.5 for both models. A distinct maximum is formed if the starting biomass is low. Then, a deep minimum can follow. However, in such case, a low equilibrium point is reached after many oscillations, gradually decreasing in amplitude. If it is attempted to reach a high steady state after few oscillations, this can only be the case with a very mild depression of the prey biomass after the first maximum (see Fig. 4.5). That there can only be a gradual decrease of amplitudes and not a first strong oscillation followed by small oscillations around a high equilibrium is intuitively apparent for both models already when looking at the isocline portraits (Fig. 4.2).

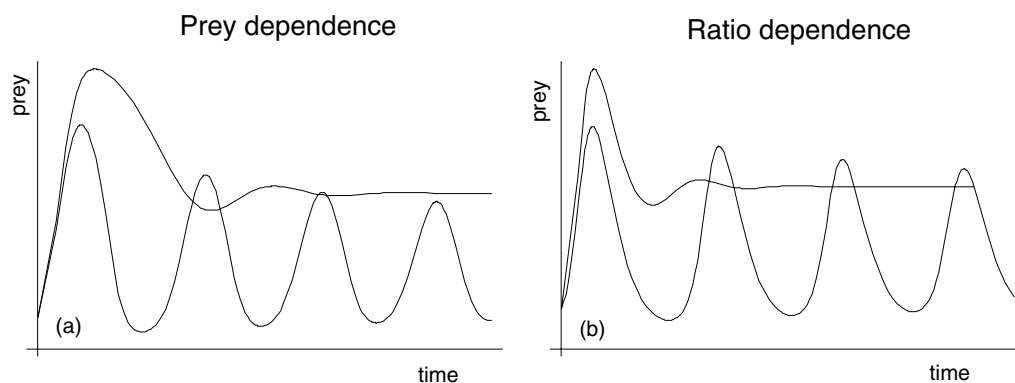


Figure 4.5: Trajectories of prey in the area of stable equilibrium points reached with oscillations (prey-dependent model (a) and ratio-dependent model (b)). The highly oscillating trajectory was produced with parameters near the criterion of stability, the other with parameters near the criterion of oscillations.

The predator (zooplankton) exhibit similar trajectories, lagging behind the prey trajectory. In this respect criterion 3 can be considered satisfied by both models.

With respect to criteria 1-2, it is clear that neither the prey-dependent nor the ratio-dependent model are able to generate satisfactory trajectories. Both are unable to generate the spring clear water phase, along with a stable equilibrium in the summer, of a magnitude similar to the first peak and reached after few oscillations.

However, increasing eutrophication (increasing K) behaves differently in both models

(Fig. 4.4). Increasing K has a destabilizing effect (higher amplitudes, increasing frequency, finally sustained oscillations) with an unchanged prey equilibrium in the prey-dependent model. In the ratio-dependent model, there are no effects on stability properties; only a quantitative, proportional increase in the amplitudes and in the level of the prey equilibrium. With respect to criterion 4, the ratio-dependent model behaves therefore much better than the prey-dependent model.

4.3.7 Seasonal changes of parameter values

The above analysis assumed autonomous equations, i.e., time-independent parameters. However, it can be argued that one or several parameters must change along the seasons. First, it is most reasonable to assume that the phytoplankton intrinsic growth rate r increases as temperature increases from spring to summer. Second, zooplankton parameters may also change: the attack rate a (resp. α) can decrease as a result of an increased proportion of inedible algae and the mortality rate μ can increase because of increased fish predation. Using the expressions for the non-trivial equilibria (4.10–4.13), and inspecting Fig. 4.3, it can be seen that variations of the parameters as just suggested have the effects summarized in Table 4.1. Variations in a (resp. α) or in μ have in both models more or less the same effect, i.e., an increase of the prey equilibrium and a stabilization, which is in agreement with our required criteria. Increasing the prey growth rate r has practically no qualitative effect in the prey-dependent model, while it has a desirable effect in the ratio-dependent model (i.e., an increase of the prey equilibrium and a stabilization). Given these properties, it is not difficult to find scenarios with varying parameters that will generate the desired trajectories with either model. Examples are given in Fig. 4.6.

Table 4.1: Summary of the possible trends of parameters during the season or with eutrophication and their effects on system stability and equilibria.

Parameter varied	Cause	Time scale	effects in			
			prey-dependence		ratio-	
			equ.	stab.	equ.	stab.
$K \nearrow$	Eutrophication	Decades	-	\searrow^{1+}	\nearrow	$^{2+}$
$r \nearrow$	Temp. increase	Seasonal	-	-	\nearrow	\nearrow
$a \searrow$ ($\alpha \searrow$)	increase of inedible algae	Seasonal	\nearrow	\nearrow^*	\nearrow	\nearrow
$\mu \nearrow$	higher predation	Seasonal	\nearrow	\nearrow^*	\nearrow	\nearrow^*

$^{1+}$: increasing frequency and amplitude

$^{2+}$: same frequency, increasing amplitude

*: with further change the parameters leave the area of positive equilibria

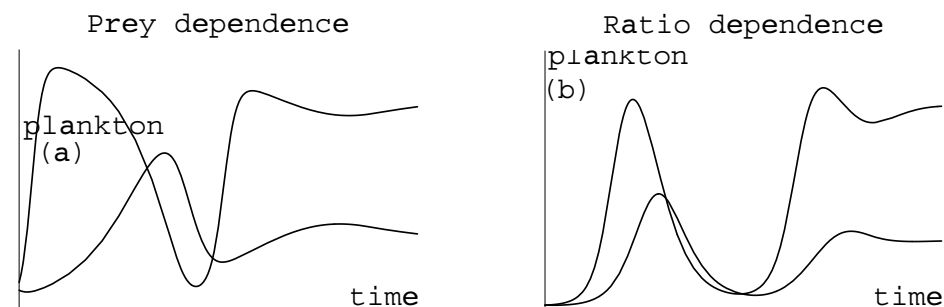


Figure 4.6: Resulting trajectories if the predator death rate μ is increasing during the season. Both the prey-dependent (a) and the ratio-dependent (b) model may thus show the desired trajectories.

4.4 Discussion

The most important difference between the prey-dependent and ratio-dependent two-level models is the fact that an increase of prey carrying capacity K causes an increase of both prey and predator equilibrium densities in the ratio-dependent model, whereas only predator equilibrium density increases in the prey-dependent model (Arditi & Ginzburg, 1989). This property at steady-state conditions has to be considered also when studying nonsteady-state characteristics of both models. Moreover, general plankton dynamics seem to be relatively independent of trophic input, because similar seasonality of plankton was found in lakes of different levels of eutrophication. This enabled the formulation of the PEG-model (Sommer et al., 1986). This property is only found in the ratio-dependent model, where changes of K , the main parameter changing with the trophic input, have no influence on the qualitative behavior, only on the amplitudes (see figure 4.4). On the other hand, the stability of the prey-dependent model depends on K and the trajectories can be qualitatively different for different values of K .

However, despite the mentioned slight advantages of the ratio-dependent model, both models give qualitatively similar trajectories which cannot fulfill our criteria for plankton seasonality. Their basic property is a gradual decrease of the amplitude of oscillations after the first maximum, which is affected by the starting conditions. It is impossible to obtain a distinct clear water phase period followed by a sudden decrease of amplitude and fast reaching of stable equilibrium. The desirable trajectories in two-level models can only be obtained if some parameter (or parameters) change during the season, shifting the system from the area of unstable to the area of stable equilibrium. An analogous approach was used in (McCauley et al., 1988) to explain the proportional growth of phytoplankton and zooplankton with increasing productivity on the basis of prey-dependent models. They assume the following trends with increasing nutrient status of lakes: 1. the realized per capita growth rate of phytoplankton (both edible and inedible) increases, 2. *Daphnia's* attack rate decreases in response to increasing concentration of inedible algae, 3. *Daphnia's* death rate increases in response to greater predation pressure.

Similar trends can be expected also during a growing season. A seasonal shift from edible to inedible algae has been documented in many lakes (Sommer et al., 1986). Colonial cyanobacteria often dominate in lakes exceeding a certain level of eutrophication during

a summer period (Sas, 1989). Therefore, a decrease of the attack rate of *Daphnia* can be expected in the summer. An increase of the maximum growth rate of phytoplankton (r) is probable due to a rise of temperature and light. The death rate of herbivorous zooplankton is probably extremely variable and changing in the spring, while in the summer it seems more uniform (Seda, 1989). Lampert (1978) found in Lake Constance, that the *Daphnia* population is not controlled by food in the spring but by adult individuals of carnivorous *Cyclops vicinus*. The spring maximum of *Daphnia* can develop only when *Cyclops* dies out. Feeding activity of planktivorous fish increases during the season along with increasing temperature. In addition, some species do not feed during reproduction in the spring (...). Therefore, a general increase of grazing pressure on herbivores during the season (thus an increasing predator mortality rate μ in our models) can be expected, probably with dramatic short-term changes in the spring.

Gatto (1991) proposes to introduce a density dependent mortality of predator $\mu(P)$. After this modification, the prey-dependent two-level model predicts a proportional increase of both equilibrium densities, but the trajectories still exhibit qualitatively similar properties as in the standard prey-dependent models, especially a gradual decrease of the amplitude of oscillations after the first maximum. Moreover, when applying this to three levels the positive correlations in general only hold for the top two levels, not for the lower two levels under consideration (see 4.B).

One might suggest that the clear water phase is the result of cycling populations rather than populations reaching equilibrium. Several arguments speak against this interpretation. Sommer et al. (1986) analyzed 24 different lakes and interpreted the high summer abundances as being in steady state. Furthermore, there are no reported limit cycles of plankton in tropic lakes, which are permanently in the summer state of lakes in temperate zones.

A further explanation for the insufficiency of a two-level model for application in plankton dynamics can be that some processes not included in the model play an important role. It can be true especially in the spring, generally understood as a disequilibrium period (McCauley et al., 1988). Physical and chemical parameters change suddenly and these changes can influence the development of organisms in water. Vyhnálek et al. (1994) found that the spring bloom of phytoplankton grown in the canyon-shaped Římov Reservoir is formed by phytoplankton grown in the head of the reservoir and then drifted downstream to the main lake. This process accelerates spring dynamics of phytoplankton. The collapse of phytoplankton and the induction of the clear water phase appears to be the key problem of plankton dynamics. In the PEG-model, it is interpreted as a consequence of prey-predator interactions (Sommer et al., 1986). However, several authors found that the sudden crash of phytoplankton is a consequence of nutrient limitation and subsequent sedimentation of phytoplankton (Gawler et al., 1988; Jeppesen et al., 1990; Weisse et al., 1990) or even of lysis of algal cells (van Boekel et al., 1992; Vyhnálek et al., 1993). In these cases grazing of herbivores is a parameter of second rate importance and the depression of phytoplankton biomass (the clear water phase) is not caused by prey-predator relationships.

In summary, neither the prey-dependent nor the ratio-dependent prey-predator models composed of phytoplankton and zooplankton are able to predict seasonal dynamics of these two levels. Nevertheless, the ratio-dependent model seems to be more realistic in

view of the following properties: 1. both phytoplankton and zooplankton biomasses at equilibrium increase with increasing productivity and 2. there is no effect of productivity on the stability of the system. To obtain the expected prediction, with a clear water phase and a stable equilibrium rapidly reached in the summer, the following modifications of the two-level ratio-dependent model are proposed: 1. parameters of phytoplankton and zooplankton change during the season, 2. introduction of a third level (carnivorous zooplankton or fish), 3. introduction of phytoplankton mortality other than zooplankton grazing (sedimentation, lysis).

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Appendix

4.A Detailed matrix analysis

In this chapter we will develop the detailed Jacobian matrices for both (dimensionless) models. Since we will analyze one model after the other we will omit the subscripts p for prey-dependent and r for ratio-dependent for easier notation.

4.A.1 Prey-dependent model

The differential equations are given by

$$\frac{dN}{dt} = R\left(1 - \frac{N}{C}\right)N - \frac{N}{1+N}P \quad (4.22)$$

$$\frac{dP}{dt} = \frac{N}{1+N}P - QP. \quad (4.23)$$

This system has the two trivial equilibria $(0, 0)$ and $(C, 0)$ and the non-trivial equilibrium

$$\left(\frac{Q}{1-Q}, \frac{(C-Q-CQ)R}{C(1-Q)^2} \right). \quad (4.24)$$

The Jacobian is

$$\begin{bmatrix} R - \frac{2NR}{C} - \frac{P}{(1+N)} + \frac{NP}{(1+N)^2} & -\frac{N}{1+N} \\ \frac{P}{(1+N)^2} & \frac{N}{1+N} - Q \end{bmatrix}. \quad (4.25)$$

At the equilibrium $(0, 0)$ this matrix evaluates at $\begin{bmatrix} R & 0 \\ 0 & -Q \end{bmatrix}$, thus $(0, 0)$ is a saddle point. At $(C, 0)$ we get $\begin{bmatrix} -R & -\frac{C}{1+C} \\ 0 & \frac{C}{1+C} - Q \end{bmatrix}$, thus $(C, 0)$ is stable whenever $\frac{C}{1+C} < Q$. At the non-trivial equilibrium point the Jacobian is

$$\begin{bmatrix} \frac{Q(1-C+Q+CQ)R}{C(Q-1)} & -Q \\ R - QR - \frac{QR}{C} & 0 \end{bmatrix} = \begin{bmatrix} m_{11} & m_{12} \\ m_{21} & m_{22} \end{bmatrix} \quad (4.26)$$

and its stability analysis is done in the text, while the oscillation criterion,

$$(m_{11} - m_{22})^2 + 4m_{12}m_{21} < 0, \quad (4.27)$$

resolves to

$$\frac{-2Q + 4Q^2 - 2Q^3 + QR - Q^3R - 2\sqrt{(1-Q)^3Q(Q - Q^2 + R + QR)}}{(1-Q)^2(4(Q-1) + QR)} < C < \quad (4.28)$$

$$\frac{-2Q + 4Q^2 - 2Q^3 + QR - Q^3R - 2\sqrt{(1-Q)^3Q(Q - Q^2 + R + QR)}}{(1-Q)^2(4(Q-1) + QR)}. \quad (4.29)$$

The first expression tends to a finite value for $Q \rightarrow \frac{4}{4+R}$, while the second expression is not defined at this value. Therefore the first inequality holds over the whole range of Q ($0 < Q < 1$), while the second inequality only applies for Q between $\frac{4}{4+R}$ and 1.

4.A.2 Ratio-dependent model

The differential equations are given by

$$\frac{dN}{dt} = R\left(1 - \frac{N}{D}\right)N - D\frac{N}{P + DN}P \quad (4.30)$$

$$\frac{dP}{dt} = D\frac{N}{P + DN}P - QP. \quad (4.31)$$

This system has the two trivial equilibria $(0, 0)$ and $(D, 0)$ and the non-trivial equilibrium

$$\left(\frac{D(DQ + R - D)}{R}, \frac{D^2(1-Q)(DQ + R - D)}{QR} \right). \quad (4.32)$$

The Jacobian is

$$\begin{bmatrix} R - \frac{2NR}{D} - \frac{DP}{DN+P} + \frac{D^2NP}{(DN+P)^2} & -\frac{D^2N^2}{(DN+P)^2} \\ \frac{DP^2}{(DN+P)^2} & \frac{D^2N^2}{(DN+P)^2} - Q \end{bmatrix}. \quad (4.33)$$

At the equilibrium $(D, 0)$ this matrix evaluates at $\begin{bmatrix} -R & -1 \\ 0 & 1 - Q \end{bmatrix}$, thus $(D, 0)$ is stable whenever $1 < Q$ (i.e. when the predator isocline has a negative slope and there is no non-trivial positive equilibrium for prey and predator).

At the non-trivial equilibrium point the Jacobian is

$$\begin{bmatrix} D - DQ^2 - R & -Q^2 \\ D(1 - Q)^2 & Q(Q - 1) \end{bmatrix} \quad (4.34)$$

and its stability analysis is done in the text, while the oscillation criterion,

$$(m_{11} - m_{22})^2 + 4m_{12}m_{21} < 0, \quad (4.35)$$

resolves to

$$\frac{-Q + 3Q^2 - 3Q^3 + Q^4 + R - Q^2R - 2\sqrt{(Q-1)^3Q^2(Q-Q^2-R-QR)}}{(1-Q^2)^2} < D < (4.36)$$

$$\frac{-Q + 3Q^2 - 3Q^3 + Q^4 + R - Q^2R + 2\sqrt{(Q-1)^3Q^2(Q-Q^2-R-QR)}}{(1-Q^2)^2}. \quad (4.37)$$

The equilibrium $(0, 0)$ is less easy to analyze since neither the differential equations nor the Jacobian are defined at this point. Since the local behavior depends on how the flow looks like close to $(0, 0)$ we reformulate our equations for the variables P and $L := \frac{N}{P}$:

$$\frac{dL}{dt} = L(R + Q - \frac{R}{D}LP) - D\frac{L(1+L)}{1+DL} \quad (4.38)$$

$$\frac{dP}{dt} = D\frac{LP}{1+DL} - QP. \quad (4.39)$$

This new system has three equilibria, a non-trivial one that shows the same behavior as the non-trivial equilibrium in the original system, and two equilibria on the L axis, $(0, 0)$ and $(0, \frac{D-Q-R}{D(Q+R-1)})$. The former is stable whenever $D > Q + R$ and the latter is a saddle point whenever the non-trivial equilibrium is positive in both variables, as may be seen on the isocline graph. Applied to the original system this means that for $D < Q + R$ and if there exists a positive non-trivial equilibrium $(0, 0)$ is a saddle point, else it is attractive for all trajectories where N/P approaches 0.

4.B Some effects of a density dependent mortality rate

Gatto (1991) and Gleeson (1994) pointed out that in food chains with Lotka-Volterra functional responses and a top predator with a mortality rate that is proportional to its density the equilibrium densities of all trophic levels are correlated with primary productivity. We will study the equilibrium behavior in a more general food chain with three trophic levels, prey-dependent functional responses and a general density-dependent mortality rate of the top predator,

$$\frac{dP}{dt} = f(P)P - g_1(P)H \quad (4.40)$$

$$\frac{dH}{dt} = e_1g_1(P)H - g_2(H)C \quad (4.41)$$

$$\frac{dC}{dt} = e_2g_2(H)C - \mu(C)C, \quad (4.42)$$

where P are plants, H are herbivores and C are carnivores. $f(P)$, $g_1(P)$ and $g_2(H)$ are increasing, bounded functions of their respective arguments. We assume that plant and herbivore natural mortality is negligible compared to the mortality due to predation and that the carnivore abundance is never close to 0.

In most models, the carnivore mortality rate is assumed to be a constant, $\mu(C) = \mu$. Here we assume that $\mu(C)$ is some increasing, bounded function (due to passive or active direct inhibition of competitors or if this trophic level is itself subject to predation by some higher predator with Holling type III functional response Holling (1959a)).

Setting (4.42) to 0 and solving for C we get

$$C = \mu^{-1}(e_2 g_2(H)), \quad (4.43)$$

thus at equilibrium C is positively correlated with P . Solving (4.41) for P we get

$$P = g_1^{-1}\left(\frac{g_2(H)\mu^{-1}(e_2 g_2(H))}{e_1 H}\right). \quad (4.44)$$

For small H g_2 may be approximated by some linear function, $g_2(H) \approx cH$. In this case we get

$$P = g_1^{-1}\left(\frac{c\mu^{-1}(e_2 cH)}{e_1}\right), \quad (4.45)$$

therefore P and H are positively correlated for small H . For large H g_2 may be approximated by some constant, $g_2(H) \approx c$. This gives

$$P = g_1^{-1}\left(\frac{c\mu^{-1}(e_2 c)}{e_1 H}\right), \quad (4.46)$$

therefore P is negatively correlated with H . We may conclude that a density dependent mortality rate of the top predator only leads to positive correlations between equilibrium abundances of the top two levels, nothing specific can be said about correlations with the lowest level.

Figure 4.7: Dynamics of total phytoplankton, herbivorous zooplankton and temperature in 1989. The development is representative for all years.

Chapter 5

About deterministic extinction in ratio-dependent predator-prey models

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Abstract

Ratio-dependent predator-prey models set up a challenging issue regarding their dynamics near the origin. This is due to the fact that such models are undefined at $(0, 0)$. We study the analytical behavior at $(0, 0)$ for a common ratio-dependent model and demonstrate that this equilibrium can be either a saddle point or an attractor for certain trajectories. This fact has important implications concerning the global behavior of the model, for example regarding the existence of stable limit cycles. Then, we prove formally, for a general class of ratio-dependent models, that $(0, 0)$ has its own basin of attraction in phase space, even when there exists a non-trivial stable or unstable equilibrium. Therefore, these models have no pathological dynamics on the axes and at the origin, contrary to what has been stated by some authors. Finally, we relate these findings to some published empirical results.

Les modèles proie-prédateur du type ratio-dépendant posent un défi concernant leurs dynamiques proches de l'origine. Ceci est due au fait que ces modèles ne sont pas définis à $(0, 0)$. Nous étudions le comportement analytique autour $(0, 0)$ pour un modèle ratio-dépendant simple et démontrons que cet équilibre peut être un point de sel ou un attracteur pour certains trajectoires. Ce fait à des implications importantes concernant le comportement globale du modèle, par exemple concernant l'existence de cycles limites stables. Ensuite, nous prouvons formellement pour une classe générale de modèles du type ratio-dépendant que $(0, 0)$ tient son propre bassin d'attraction, même s'il y a un équilibre non-trivial stable ou instable. Donc, ces modèles n'ont pas de comportements dynamiques pathologiques sur les axes et à l'origine, contrairement aux énoncés de certains auteurs. Finalement, nous comparons ces résultats avec quelques résultats empiriques trouvés dans la littérature.

5.1 Introduction

Continuous predator-prey models have been studied mathematically since publication of the Lotka-Volterra equations. The principles of this model, conservation of mass and decomposition of the rates of change into birth and death processes, have remained valid until today and many theoretical ecologists adhere to these principles. Modifications were limited to replacing the Malthusian growth function, the predator per capita consumption of prey or the predator mortality by more complex functions such as the logistic growth, Holling type I, II and III functional responses or density-dependent mortality rates.

The mentioned functional responses all depend on prey-abundance N only, but soon it became clear that predator abundance P can influence this function (Curds & Cockburn, 1968; Hassell & Varley, 1969; Salt, 1974) by direct interference while searching or by pseudo-interference (in the sense of Free et al. (1977)) and models were developed incorporating this effect (Hassell & Varley, 1969; DeAngelis et al., 1975; Beddington, 1975). However, these models usually require more parameters and their analysis is complex. Therefore, they are, on one side, rarely used in applied ecology and, on the other side, have received little attention in the mathematical literature. A simple way of incorporating predator dependence into the functional response was proposed by Arditi & Ginzburg (1989) who considered this response as a function of the ratio N/P . Interesting properties of this approach have emerged that are in contrast with predictions of models where the functional response only depends on prey abundance (e.g. Arditi et al. (1991a), Ginzburg & Akçakaya (1992), Arditi & Michalski (1995)). Two principal predictions for ratio-dependent predator-prey systems are: (1) equilibrium abundances are positively correlated along a gradient of enrichment (Arditi & Ginzburg, 1989) and (2) the ‘paradox of enrichment’ (Rosenzweig, 1971) either completely disappears or enrichment is linked to stability in a more complex way. However, we will not discuss here the general ecological significance of this class of models but rather study a particular mathematical feature of this model: the behavior around the point $(0, 0)$ (where the models are not directly defined) and its implications on global behavior. Interesting dynamic behaviors such as deterministic extinction and multiple attractors can occur.

There are only few mathematical publications that study ratio-dependent models. Many of them use logistic-type models where density dependence in the growth equation is proportional to the ratio consumer/resource (e.g., the popular Holling-Tanner model (Tanner, 1975)). However, these models do not abide by the conservation of mass rule (reproduction rate of predators is a function of the consumption rate, Ginzburg (1998)). We are rather interested in ratio-dependent models that respect this conservation of mass (or energy) as an important aspect of ecological modelling. This further reduces the available literature on this class of models. Cosner (1996) developed floor- and ceiling functions to understand the behavior of complex systems that include temporal variability, and ratio-dependent formulations proved to be more adapted to this kind of study. Beretta & Kuang (1998) studied the influence of delays on the stability behavior of the non-trivial equilibrium.

Freedman & Mathsen (1993) studied conditions for persistence of a specific ratio-dependent predator-prey model. They restricted their analysis to parameter values that ensure that the equilibrium $(0, 0)$ behaves like a saddle point. They based this restriction

on the assertion that attractivity of this trivial equilibrium is possible only with parameter values for which the predator abundance $P(t)$ increases without bound as a function of time. In this paper, we will show that this assertion is erroneous and we will reanalyze the general stability behavior of a typical ratio-dependent model around the equilibrium $(0, 0)$. Furthermore, we will give a formal proof (for a general ratio-dependent model) that this point can become attractive for all initial conditions sufficiently close to the predator axis, while the non-trivial equilibrium remains either locally stable or becomes unstable. This gives rise to global behaviors that range from global attractivity of the non-trivial equilibrium, coexistence of two different attractors (each with its own basin of attraction) to global attractivity of the equilibrium $(0, 0)$.

Extinction is a frequent outcome in simple laboratory predator-prey systems (Gause, 1935; Luckinbill, 1973) and biologists had to modify conditions in order to obtain (cyclic) coexistence [e.g., spatial heterogeneities (Huffaker, 1958) or viscous medium to slow down the predators (Veilleux, 1979)]. Since traditional predator-prey models predict cyclic dynamics, extinction has been explained as the result of stochasticity occurring when the trajectories come close to the axes. In this paper we show that, for some region in the parameter space of a ratio-dependent model, multiple attractors can appear, one of them being the origin. Therefore, extinction can be explained as a simple deterministic process.

5.2 The model and its equilibria

A predator-prey system that incorporates conservation of mass and division of population rates of change into birth and death processes has the following canonical form:

$$\frac{dN}{dt} = f(N)N - g(N, P)P \quad (5.1)$$

$$\frac{dP}{dt} = eg(N, P)P - \mu P \quad (5.2)$$

with prey abundance $N(t)$ and predator abundance $P(t)$, conversion efficiency e and predator death rate μ . We will use the traditional logistic form for the growth function f with maximal growth rate r and carrying capacity K :

$$f(N) = r\left(1 - \frac{N}{K}\right).$$

The functional response g (prey eaten per predator per unit of time), that in general depends on both prey and predator density, will be considered as a (bounded) function of the ratio prey per predator,

$$g := g\left(\frac{N}{P}\right) = \frac{\alpha N/P}{1 + \alpha h N/P} = \frac{\alpha N}{P + \alpha h N} \quad \forall (N, P) \in [0, +\infty)^2 \setminus (0, 0) \quad (5.3)$$

with total attack-rate α and handling time h . Note that the second equality is strictly correct only for $P > 0$. In the case of $P = 0$ and $N > 0$ we can define $g(N, 0) := 1/h$ (the limit of $g(x)$ for $x \rightarrow \infty$).

In a first step we simplify this model by non-dimensionalisation. Let $\hat{N} = \frac{\alpha h N}{e K}$, $\hat{P} = \frac{\alpha h P}{e^2 K}$, $R = \frac{r h}{e}$, $Q = \frac{h \mu}{e}$, $S = \frac{\alpha h}{e}$ and $\hat{t} = \frac{e t}{h}$. In these new variables the system becomes:

$$\frac{d\hat{N}}{d\hat{t}} = R \left(1 - \frac{\hat{N}}{S}\right) \hat{N} - \frac{S \hat{N}}{\hat{P} + S \hat{N}} \hat{P} \quad (5.4)$$

$$\frac{d\hat{P}}{d\hat{t}} = \frac{S \hat{N}}{\hat{P} + S \hat{N}} \hat{P} - Q \hat{P} \quad (5.5)$$

with initial conditions $\hat{N}(0) = n_0$, $\hat{P}(0) = p_0$. For simplicity we will not write the hat $\hat{}$ in the rest of this paper.

This system has at most three equilibria in the positive quadrant: $(0, 0)$, $(S, 0)$ and a non-trivial equilibrium (n^*, p^*) with

$$n^* = \frac{S(R + (Q - 1)S)}{R}$$

$$p^* = \frac{S(1 - Q)}{Q} n^*.$$

A simple calculation shows that n^* is positive for all $S < R/(1 - Q)$, which implies $Q < 1$ and therefore ensures the positivity of p^* .

To see why $(0, 0)$ is indeed an equilibrium (despite the fact that g is undefined in that case) note that for any g that is a non-negative bounded function in its domain (such as (5.3)) the right sides of system (5.1-5.2) become 0 at this point, which is the definition of an equilibrium (boundedness of g is a sufficient condition, but not a necessary one).

Figure 5.1 shows the possible isoclines of the system. For $S > R$, the prey isocline is a humped curve through the origin and the point $(S, 0)$. For $S < R$, the denominator of the prey isocline can become 0 for some $N \in (0, S)$. The part of the isocline that remains in the positive quadrant becomes in this case a strictly monotonically descending curve through the point $(S, 0)$. The predator isocline is always a straight line through the origin. See Arditi & Ginzburg (1989) for more details. While the cases of Figures 5.1a and 5.1c do not raise mathematical difficulties, the case of Figure 5.1b presents interesting and unexpected mathematical properties that will be studied below.

5.3 Stability of the equilibria

The community matrix (Jacobian at the equilibrium) at the point $(S, 0)$ is

$$\begin{bmatrix} -R & -1 \\ 0 & 1 - Q \end{bmatrix}$$

and therefore, if the non-trivial equilibrium exists ($\implies Q < 1$), this point is always a saddle point.

The community matrix at (n^*, p^*) has the form

$$\begin{bmatrix} -R + S - Q^2 S & -Q^2 \\ (Q - 1)^2 S & (Q - 1)Q \end{bmatrix}.$$

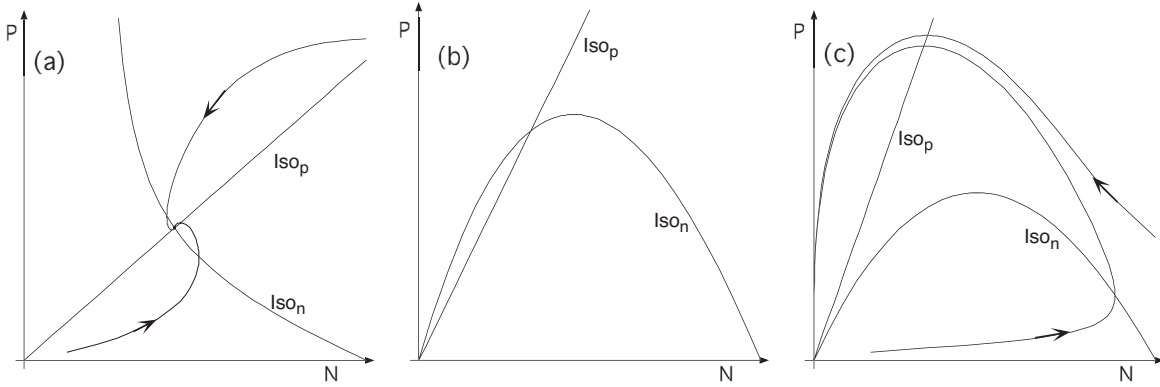


Figure 5.1: The three general types of isoclines that can occur. (a): the non-trivial equilibrium is stable and $(0,0)$ behaves like a saddle point ($R = 0.5$, $Q = 0.3$, $S = 0.4$). (b): both equilibria can be attractive or repelling, creating dynamics that are illustrated in Figures 5.2 - 5.5. (c): the equilibrium $(0,0)$ is globally attractive ($R = 0.5$, $Q = 0.79$, $S = 3.0$). The lines with arrows are examples of trajectories, Iso_n is the prey isocline and Iso_p the predator isocline.

Applying the Routh-Hurwitz criterion shows that this equilibrium is stable whenever

$$S < \min \left\{ \frac{R}{1-Q}, \frac{Q-Q^2+R}{1-Q^2} \right\}. \quad (5.6)$$

Note that, if $\frac{R}{1-Q} < \frac{Q-Q^2+R}{1-Q^2}$ ($\Leftrightarrow R+Q < 1$), then the non-trivial equilibrium is always stable (if it exists). This is possible with two types of isoclines, Figures 5.1a and 5.1b. The case of Figure 5.1b together with this condition (allowing arbitrarily low stable equilibrium densities of both prey and predator) is particularly interesting in the context of biological control where the interest is in non-trivial stable equilibria with $n^* \ll S$. The non-trivial equilibrium in Figure 5.1a is also always stable (independently of the above criterion), because its existence ensures that $Q < 1$, therefore, if $S < R$, then S also fulfills criterion (5.6). However, this case is less interesting because it requires high predator densities to keep the prey density low.

At the equilibrium $(0,0)$ the community matrix cannot be calculated directly because the ratio N/P is not defined at this point. To understand the stability behavior of this point we must expand it on a whole axis by studying the transformed systems $(N/P, P)$ and $(N, P/N)$. Setting $L := N/P$, then we have the system

$$\begin{aligned} \frac{dL}{dt} &= L(R+Q - \frac{R}{S}LP) - S \frac{L(1+L)}{1+SL} \\ \frac{dP}{dt} &= (\frac{SL}{1+SL} - Q)P. \end{aligned}$$

There are two equilibria on the L -axis, $(0,0)$ and $(\frac{S-Q-R}{S(Q+R-1)}, 0)$. $(0,0)$ is a saddle point for $S < Q+R$ (eigenvalues of the community matrix are $-Q$ and $Q+R-S$), otherwise it is attractive. The latter equilibrium has the eigenvalues

$$\lambda_1 = \frac{S(1-Q)-R}{S-1}, \quad \lambda_2 = \frac{SQ+R-S+Q+SR-(R+Q)^2}{S-1}$$

and it is unstable whenever a non-trivial equilibrium exists.

Proof. Let $S < 1$. If the non-trivial equilibrium exists ($S < R/(1 - Q)$) then $\lambda_1 > 0$, therefore the equilibrium is unstable.

Now let $S > 1$. The existence of the non-trivial equilibrium ensures in this case that $R + Q > 1$. Furthermore, $\frac{S-Q-R}{S(Q+R-1)}$ must be positive to be of interest, therefore

$$S > Q + R \quad (5.7)$$

and

$$\begin{aligned} \lambda_2 &= \frac{1}{S-1}(S(Q-1) + (Q+R) - (R+Q)^2 + SR) \\ &\stackrel{(5.7)}{>} \frac{1}{S-1}((Q+R)(Q-1+1-R-Q) + SR) \\ &= \frac{1}{S-1}(R(S - (Q+R))) \stackrel{(5.7)}{>} 0. \end{aligned}$$

This equilibrium is therefore unstable. \square

Finally, we need the stability behavior of $(0, 0)$ for the system (N, M) with $M := P/N$,

$$\begin{aligned} \frac{dN}{dt} &= N \left(R - \frac{NR}{S} - \frac{KS}{K+S} \right) \\ \frac{dM}{dt} &= \frac{M(S(NR - (Q+R-1)S) + M(NR + S(S-Q-R)))}{S(M+S)}. \end{aligned}$$

The community matrix at $(0, 0)$ has the eigenvalues $\lambda_1 = 1 - R - Q$, $\lambda_2 = R$ and the point $(0, 0)$ is therefore always unstable.

Summarizing we can conclude for the original system (N, P) that for $S < Q + R$ the equilibrium $(0, 0)$ behaves like a saddle point. For $S > Q + R$ we have seen that the system $(N/P, P)$ has an attractive equilibrium at its origin $(0, 0)$. Interpreted in the original state variables N and P this point can only be attained by a trajectory for which ‘ N goes faster to 0 than P ’. Below, we will discuss the existence of such trajectories.

Freedman & Mathsen (1993), who studied in their paper the same model (5.4) and (5.5), excluded the latter case ($S > Q + R$) from their persistence analysis of ratio-dependent models by stating (p. 823) that “this implies that there are solutions $(N(t), P(t)) \rightarrow (0, +\infty)$ as $t \rightarrow \infty$ ”. The following proposition proves that this statement is erroneous.

Proposition 5.3.1. *The system of equations (5.4-5.5) is ultimately bounded with some bound independent of the initial values.*

Proof. Let $b, c > 0$ such that $\frac{(R+b)^2S}{4R} < c$ (for any b , such a c can be found).

$$\begin{aligned} &\frac{(R+b)^2S}{4R} < c \\ \Leftrightarrow &(R+b)^2 - 4\frac{R}{S}c < 0 \\ \Leftrightarrow &0 < \frac{R}{S}N^2 - N(R+b) + c \quad \forall N \end{aligned} \quad (5.8)$$

Therefore we have

$$\begin{aligned} \frac{d}{dt}(N + P) &= RN - \frac{R}{S}N^2 - QP \\ &\stackrel{(5.8)}{<} -bN - QP + c \\ &< -d(N + P) + c \end{aligned}$$

with $d := \min(b, Q)$. So we can conclude that $\limsup_{t \rightarrow \infty} (N(t) + P(t)) \leq \frac{c}{d}$. Note that we have $N(t) + P(t) \leq \max(N(0) + P(0), \frac{c}{d}), \forall t \geq 0$. \square

Freedman & Mathsen (1993) also point out that a general ratio-dependent model can pose definition problems on the predator axis. However, if the functional response is restricted to being positive and bounded (two properties not contested in ecology and implicit in the model studied here), then (5.1) and (5.2) are perfectly well defined on the whole positive quadrant $[0, +\infty)^2 \setminus (0, 0)$, and the analysis in this paper shows that the behavior at $(0, 0)$ has nothing abnormal that would justify its exclusion.

If the non-trivial equilibrium were unstable and the point $(0, 0)$ a saddle point, then we could construct easily a positive invariant set that contains these two equilibria and apply the Poincaré-Bendixson theorem to prove the existence of a limit cycle. However, the following proposition holds:

Proposition 5.3.2. *For $S < Q + R$ the non-trivial equilibrium (if it exists) is locally stable.*

This means that, if the non-trivial equilibrium is unstable, then $S > Q + R$, implying, as shown earlier, that $(0, 0)$ is not a saddle point. This complicates considerably the construction of the positive invariant set required to apply the Poincaré-Bendixson theorem. We have not found such a set but do not exclude that it can exist.

Proof of proposition. a) For $R + Q < 1$ we have already seen above that all existing non-trivial equilibria are stable.

b) For $R + Q > 1$, we have

$$\begin{aligned} R &= R(1 - Q^2 + Q^2) \stackrel{R > 1 - Q}{>} R(1 - Q^2) + (1 - Q)Q^2 \\ \implies R &> (1 - Q)(R + Q^2 + RQ) \\ \implies \frac{R}{1 - Q} &> (Q + R)(1 + Q) - Q \\ \implies \frac{R + Q(1 - Q)}{(1 - Q)(1 + Q)} &> Q + R > S \end{aligned}$$

and, according to criterion (5.6), the non-trivial equilibrium is stable. \square

Getz (1984) gave a proof of existence of a stable limit cycle for a ratio-dependent model that only differed from the model used here by its prey growth function $[ar/(bN + r) - c$ instead of $r(1 - N/K)]$. He did not study rigorously the behavior at $(0, 0)$, simply

stating that the isocline graph ‘demonstrates’ that it is a saddle point (as required by the Poincaré-Bendixson theorem, since the origin is part of the positive invariant set that he constructed). However, the general analysis in the next section applies also to his system and it shows that $(0, 0)$ can become attractive. His graphical interpretation is therefore incorrect. It can be seen numerically that there are cases for which $(0, 0)$ becomes globally attractive instead of having a stable limit cycle around the non-trivial equilibrium (as in Figure 5.5).

5.4 $(0, 0)$ as an attractor

So far we have only shown that the equilibrium $(0, 0)$ can be attractive for trajectories where ‘ N goes faster to 0 than P ’, but we do not know yet if this type of trajectory really exists. In this section we will give a formal proof for this. This proof will be given for any growth function f and any functional response g in the general form of system (5.4-5.5),

$$\begin{aligned}\frac{dN}{dt} &= f(N)N - g(N/P)P \\ \frac{dP}{dt} &= g(N/P)P - QP,\end{aligned}$$

with f and g having the following properties:

- f and g are continuous in R^+ and both functions are bounded
- $f(N) < f(0) \quad \forall N > 0$
- $g(0) = 0$, $g'(v)$ exists and is positive for any $v \geq 0$.

Proposition 5.4.1. *Assume $f(0) < g'(0) - Q$ (i.e. $Q + R < S$, in our system (5.4-5.5)). Then, any trajectory for which n_0 is sufficiently small compared to p_0 converges to the point $(0, 0)$.*

Note that this proposition is a generalisation of a recent result by Kuang & Beretta (1998).

Proof. Consider the system (N, L) with $L := \frac{N}{P}$,

$$\begin{aligned}\frac{dN}{dt} &= f(N)N - g(L)\frac{N}{L} \\ \frac{dL}{dt} &= f(N)L - (1 + L)g(L) + QL.\end{aligned}$$

For $L > 0$ we have

$$\frac{d}{dt}L < f(0)L - (1 + L)g(L) + QL \stackrel{Lg(L) > 0}{<} L(f(0) - \frac{g(L)}{L} + Q).$$

Because of our assumption $f(0) < g'(0) - Q$ we have for any $\epsilon \in (0, g'(0) - Q - f(0))$ the stronger inequality

$$f(0) < g'(0) - Q - \epsilon. \tag{5.9}$$

Since $\lim_{L \rightarrow 0} \frac{g(L)}{L} = g'(0)$ there exists some $\eta > 0$ such that

$$\left| \frac{g(L)}{L} - g'(0) \right| < \epsilon \quad \forall 0 < L < \eta. \quad (5.10)$$

We can now conclude that

$$\begin{aligned} f(0) - \frac{g(L)}{L} + Q &\stackrel{(5.9)}{<} g'(0) - \frac{g(L)}{L} - \epsilon \stackrel{(5.10)}{<} 0 \quad \forall 0 < L < \eta \\ &\implies \frac{d}{dt}L < 0 \quad \forall 0 < L < \eta. \end{aligned} \quad (5.11)$$

Therefore, if there is some t_0 with $L(t_0) \leq \eta$, then $L(t) \leq \eta \quad \forall t \geq t_0$ and $\frac{d}{dt}L < 0$

$$\implies \lim_{t \rightarrow \infty} L(t) = 0.$$

On this basis, we can further conclude that

$$\frac{d}{dt}N \leq N \left(f(0) - \frac{g(L)}{L} \right) \stackrel{(5.11)}{<} 0 \quad \forall t \geq t_0.$$

Therefore $\lim_{t \rightarrow \infty} N(t) = 0$. Finally, consider the equation $\frac{d}{dt}P = P(g(L) - Q)$, since $L(t) \rightarrow 0$ and $g(0) = 0$ there is some t_ω such that

$$\frac{d}{dt}P < 0 \quad \forall t > t_\omega$$

$$\implies \lim_{t \rightarrow \infty} P(t) = 0.$$

This proves the proposition. □

The condition $Q + R < S$ is possible with isoclines as shown in Figures 5.1b and 5.1c. Examples of trajectories converging to the origin are shown in Figures 5.3–5.5. The numerical simulations of the trajectories in these figures were done using Mathematica with the built-in high order adaptive step size procedure (the accuracy goal had to be set higher than the default value to avoid numerical problems close to the origin).

5.5 Discussion

We saw that the equilibrium $(0, 0)$ can behave in several ways depending on parameter values. The following sequence of figures illustrates these behaviors by steadily increasing parameter S while keeping parameters R and Q at fixed values. Figure 5.2 illustrates the case for which it is a saddle point. All trajectories converge to the non-trivial stable equilibrium independently of the initial conditions (this equilibrium is therefore a global attractor). Freedman & Mathsen (1993) derived for this case conditions that ensure persistence of the predator-prey system. Figure 5.3 shows the case of having two attractive equilibria, each with its own basin of attraction. The two basins were determined numerically by overlaying the phase space with a small scale grid, taking each grid point as

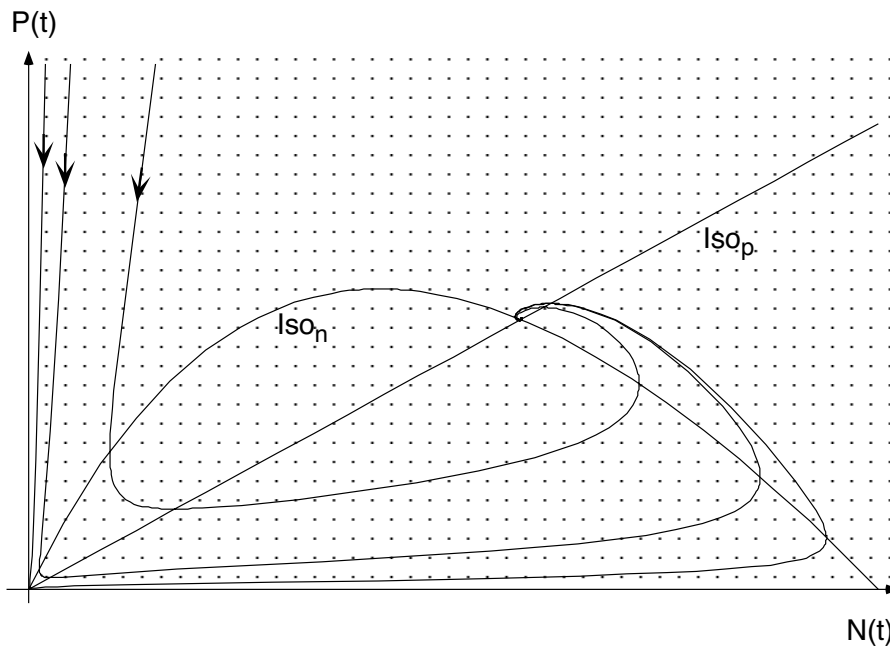


Figure 5.2: The non-trivial equilibrium is a global attractor and $(0, 0)$ behaves like a saddle point, $S < Q + R$. Parameter values are $R = 0.5$, $Q = 0.79$, $S = 1.0$.

initial value and determining whether the simulation ends in $(0, 0)$ or in the non-trivial equilibrium. There must be a separatrix between these two basins. Figure 5.4 shows again a case with two basins of attraction, but the non-trivial equilibrium is now unstable and we have a stable limit cycle. As was shown in the previous section we cannot use the Poincaré-Bendixson theorem to prove the existence of this stable limit cycle because the construction of a positive invariant set would require knowledge of the analytic form of the separatrix. This figure also shows that the limit cycles will be very sensitive to stochastic influences: random perturbations to the populations occurring while the cycle is not far from the separatrix can bring the trajectory into the basin of attraction of $(0, 0)$, thereby causing extinction. Figure 5.5 shows the case when $(0, 0)$ becomes attractive for all positive initial conditions except the non-trivial equilibrium itself. There is no formal proof of this global attractivity, and several trials with Dulac's criterion failed. Further increase of parameter S will make the non-trivial equilibrium disappear and $(0, 0)$ becomes (trivially) globally attractive (Figure 5.1c). The present mathematical analysis establishes that a general class of ratio-dependent models have well defined dynamics on the axes and at the origin.

Extinction of one or both populations in predator-prey systems have occupied ecologists since the classic experiments of Gause (1935), who tried to reproduce in the laboratory the cycles predicted by the Lotka-Volterra predator-prey equations. However, instead of the desired coexistence, the most frequent result was that the populations (*Paramecium* sp. preyed upon by *Didinium nasutum*) went extinct either immediately or after a couple of oscillations. Other researchers encountered the same problem (e.g. Huffaker (1958), Luckinbill (1973)). By thickening the medium to reduce mobility of the predator, Luckinbill (1973) obtained repeatedly several predator-prey oscillations before extinction and Veilleux (1979) refined this technique to have finally sustained cycles without extinction.

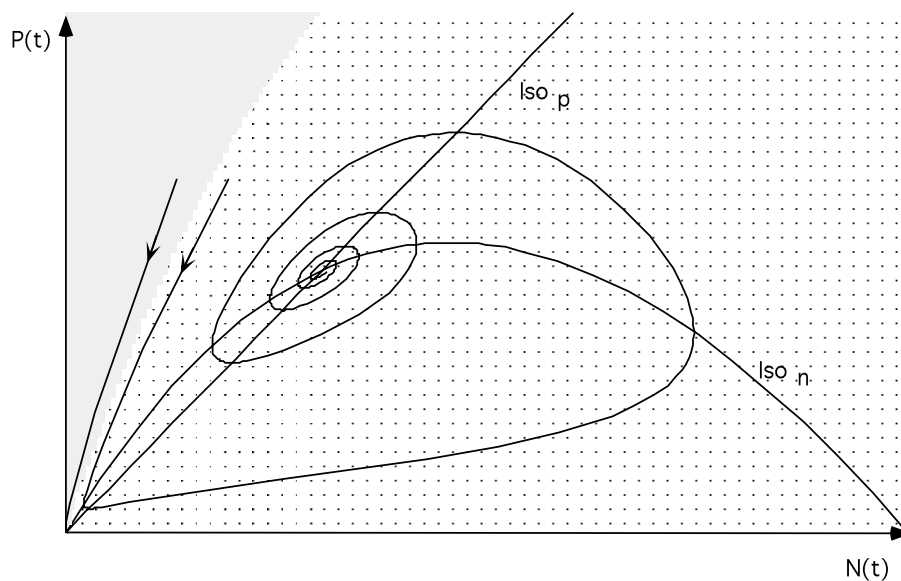


Figure 5.3: The non-trivial equilibrium is locally stable, but $(0,0)$ becomes also attractive, $S > Q + R$. The light gray area is the basin of attraction of the non-trivial equilibrium, the dark gray area is the one of equilibrium $(0,0)$. Parameter values are $R = 0.5$, $Q = 0.79$, $S = 1.66$.

He also did extensive experiments for various initial conditions and detected two basins of attraction (his Figure 11) that are similar to those in our Figure 5.3. Since the classical predator-prey systems like Lotka-Volterra or more complex ones with logistic growth and Holling type II functional responses cannot show deterministic extinction, these results have usually been explained by demographic stochasticity: limit cycles bring the popula-

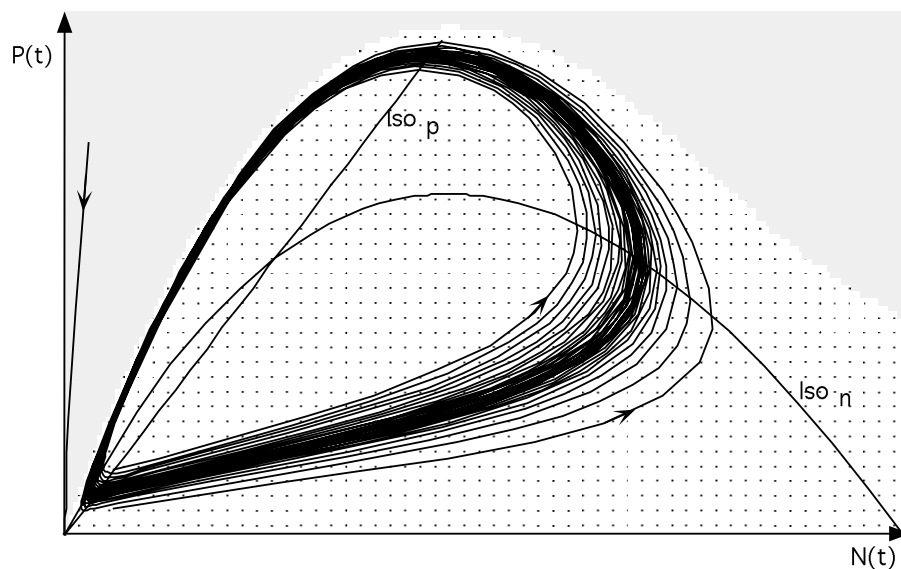


Figure 5.4: The non-trivial equilibrium is unstable and $(0,0)$ becomes attractive, $S > Q + R$. There are two attractors, a stable limit cycle and $(0,0)$. Parameter values are $R = 0.5$, $Q = 0.79$, $S = 1.78$.

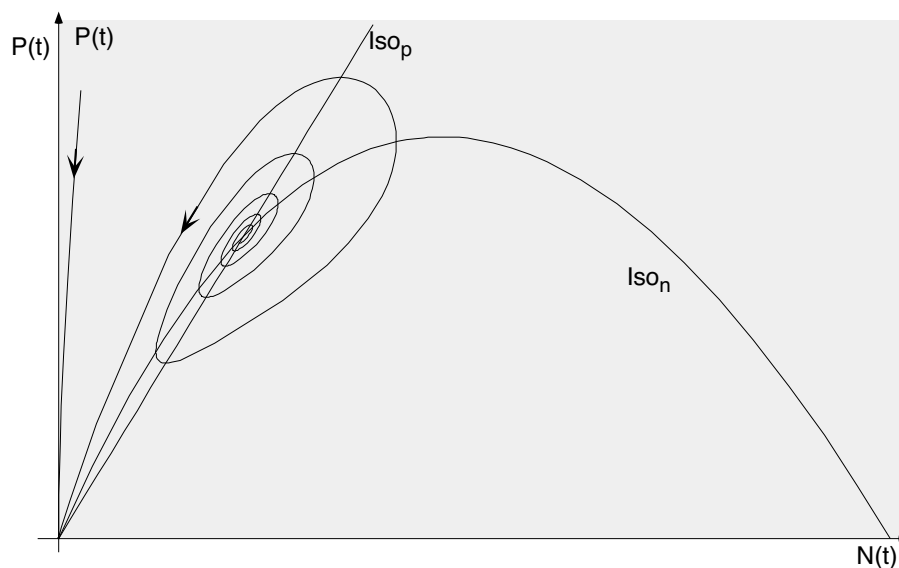


Figure 5.5: The equilibrium $(0,0)$ is a global attractor, $S > Q + R$. Parameter values are $R = 0.5$, $Q = 0.79$, $S = 1.85$. There is no formal proof for the global attractivity.

tions very close to 0 during the cycle and small stochasticities suffice to cause extinction. The model studied here can explain the extinction as a deterministic result, with no need for stochasticity. The simultaneous existence of an unstable non-trivial equilibrium and an attractive trivial equilibrium $(0,0)$ extends the behaviors of this model from extinction after one simple oscillation, as briefly described by Arditi & Berryman (1991), to extinction after a number of oscillations. Furthermore, the technique of thickening the medium to stabilize the predator-prey interaction (Luckinbill, 1973; Veilleux, 1979) can be interpreted as reducing the attack rate α (Harrison, 1995) which, in the present ratio-dependent model, has a stabilizing effect. By varying this parameter, the whole spectrum of observed behaviors (stable coexistence, sustained oscillations, extinction after several cycles, immediate extinction) can be predicted, as illustrated by Figures 5.2-5.5.

Acknowledgements

We thank Lev Ginzburg for emphasizing repeatedly the ecological interest of understanding extinction in predator-prey systems. This research was supported by the Swiss National Science Foundation and by the French CNRS.

Chapter 6

Predator-prey theory: why ecologists should talk more with microbiologists

Christian Jost

(Oikos (in press, with modifications))



Figure 6.1: David Ely Contois (1928–1988)
(Photo courtesy to the Department of Microbiology, University of Hawaii)

Abstract

Consumption of a resource by an organism is a key process in both microbiology and population ecology. Recently, there has been a debate in population ecology about the importance of organism density in functions describing this process. Actually, microbiologists have had this debate over the last 40 years. Reviewing their principal results I show that even for the most simple systems there is no unique correct function to describe consumption. Organism density influences consumption to various degrees. I conclude that, for predictions based on model simulation, one should use a pluralistic approach, working with different models to identify robust predictions (that is, common to all studied models) and guide further research to understand model-specific predictions.

La consommation de ressources par des organismes est un processus-clé à la fois en microbiologie et en écologie des populations. Un débat récent s'est ouvert en écologie quant à l'importance de la densité des organismes dans les fonctions décrivant la consommation. En fait, cette question a également été débattue par les microbiologistes durant les quarante dernières années. Par une revue de leurs principaux résultats, je montre que, même

pour les systèmes extrêmement simples, il n'existe pas une fonction universelle permettant de décrire correctement la consommation. La densité des organismes influence leur consommation à différents degrés. Je conclus que, lorsqu'on fait des prédictions fondées sur des simulations, il est nécessaire d'avoir une approche pluraliste en travaillant avec plusieurs modèles, de manière à identifier les prédictions robustes (c'est à dire celles qui sont communes à tous les systèmes étudiés), et à diriger des études spécifiques vers les points sur lesquels différents modèles font des prédictions divergentes.

6.1 Introduction

Describing the consumption process in predator-prey interactions is a research topic in population ecology since the early theoretical works of Lotka and Volterra. The quantitative description of this process has faced several questions: does the instantaneous consumption depend only on food (prey) availability, or also on the consumers (predators)? What function should be used in mathematical models? How should parameters for these functions be estimated? In this note I want to draw attention to the work of microbiologists and its relevance to current debates in population ecology. Microbiologists have often faced similar problems in describing the growth of bacteria or protozoa on some substrate. Although hidden behind different names and notations, several mathematical forms of consumption used in ecology have an equivalent microbiological growth function (Table 6.1). Most interestingly, there is also a twin (Contois, 1959) to a model that has aroused a heated debate in ecology: the ratio-dependent model introduced by Arditi & Ginzburg (1989). I will review in this note the results in microbiology with respect to this twin model and discuss how they can help to find a consensus in the ecological debate.

The functional response (prey eaten per predator per unit of time, Solomon 1949) is traditionally considered to be a function of prey abundance only (prey-dependent, Holling 1959b). However, predator density can also influence individual consumption rate, an effect that I will call predator dependence. Such predator dependence (usually a decreasing functional response with increasing consumer density) has been observed in many vertebrate and invertebrate species (reviews in Hassell 1978 and Sutherland 1996). A particularly simple way to include predator dependence has been proposed in the ratio-dependent model where the functional response depends on the ratio prey density per predator density. This approach naturally predicts the experimentally observed decreasing feeding rates with increasing predator densities and the positive correlations between population abundances of producers and consumers observed along gradients of productivity (see Arditi & Ginzburg 1989 and the review in Pimm 1991, p. 290). Despite this empirical evidence supporting it, there is an on-going debate about the validity of the ratio-dependent approach (Abrams, 1994; Gleeson, 1994; Akçakaya et al., 1995; Abrams, 1997). The particular ratio-dependent growth function introduced in microbiology much earlier by Contois (1959) has served there as an alternative to the well known (prey-dependent) growth function of Monod (1942), a twin to the popular Holling type II functional response (Table 6.1). Microbiologists have worked during the last 40 years with Contois' function, compared it to others or elaborated it further. I have followed citations of Contois' paper during this period of time and I will highlight the results that are relevant for the on-going ecological debate. Brackets will indicate in this review parallels and similar concepts in predator-prey theory.

6.2 A short historical perspective

The introduction of Monod's growth function in 1942,

$$g(s) = \mu_{max} \frac{s}{K_s + s}, \quad (6.1)$$

(parameters are explained in Table 6.1) together with its mathematical handyness and strong experimental and theoretical/methodological support, was a major breakthrough in the mathematical description of bacterial growth. Microbiologists have applied Monod's model to the description of monospecific organisms growing on a homogeneous substrate in batch and chemostat cultures (reviews in Jannasch & Egli (1993) and Fredrickson (1977)). These chemostats can be described by:

$$\begin{aligned}\frac{ds}{dt} &= D(s_0 - s) - Yg(s)x \\ \frac{dx}{dt} &= g(s)x - D(x - x_0)\end{aligned}\tag{6.2}$$

with yield Y , dilution rate D , inflowing substrate concentration s_0 , and inflowing organism concentration x_0 (usually equal to 0). The last three parameters can be controlled entirely by the researcher. [These equations correspond to predator-prey equations with constant prey immigration. However, there is a subtle difference between microbiological and ecological modeling: while microbiologists start with the growth function (ecologists call it numerical response) and consider the substrate uptake function to be proportional to it (yield Y), ecologists often start with the functional response and consider the numerical response to be proportional to the functional response (with conversion efficiency $e = 1/Y$, see equations 6.2 and 6.4 below). This difference is nevertheless of little importance for the qualitative results that will be discussed below.]

Table 6.1: References to the same model in ecology and microbiology. s is prey density or substrate concentration, x is predator density or density of organism that grows on s , a is predator attack rate, h is handling time, μ_{max} is the maximum growth rate, K_s the Michaelis-Menten or half saturation constant, α total searching efficiency and c, m are empirical positive constants.

functional response or growth rate	reference in ecology	reference in microbiology
$\begin{cases} as & s \leq s_b \\ as_m & s \geq s_b \end{cases}$	Holling (1959) I with upper limit	Blackman (1905)
$\frac{as}{1+ahs} = \mu_{max} \frac{s}{K_s+s}$	Holling (1959) II	Monod (1942)
$a(1 - e^{-cs})$	Ivlev (1961)	Teissier (1936)
$\frac{as^m}{1+ahs^m}$	Real (1977)	Moser (1958)
$\frac{\alpha s/x}{1+\alpha hs/x} = \frac{\alpha s}{x+\alpha hs}$	Arditi & Ginzburg (1989)	Contois (1959)
$\mu_{max} \frac{s}{K_s+s} \frac{1}{x}$	Hassell & Varley (1972) (special case)	Ashby (1976)

Despite its initial success, there were experimental results that could not be explained with Monod's function. At first, these were attributed to apparatus effects such as incomplete mixing or growth on chemostat walls (e.g., Herbert et al. 1956). Contois (1959) was the first to suggest and to present experimental results that the half saturation 'constant' K_s is in fact not a constant (estimates of this 'constant' varied up to three orders of magnitude, see Jannasch & Egli 1993) but that it is proportional to inflowing substrate

concentration, $K_s = ks_0$. Together with the occurrence of mass balance ($\frac{ds}{dt} + Y\frac{dx}{dt} = 0$ in system (6.2), which suggests the relation $(x - x_0) = x = Y(s_0 - s)$) model (6.1) changes to

$$g(s, x) = \frac{\mu_{max}s}{k(x/Y + s) + s} = \frac{\mu_{max}s}{(k/Y)x + (k+1)s} = \frac{\mu_{max}s/x}{(k/Y) + (k+1)s/x} \quad (6.3)$$

which is a particular case of a growth function that depends on the ratio substrate per organism s/x .

Curds & Cockburn (1968) gathered experimental evidence that the growth rate of protozoa feeding on bacteria is a decreasing function of the protozoan concentration. [The same phenomenon in ecology is what I termed predator dependence]. This is in contrast to Monod's function which predicts that the growth rate should be independent of organism concentration. This negative dependence of the growth rate on organism concentration was also confirmed by Aiba et al. (1968), Fayyaz et al. (1971) and Wilhelm (1993), and was usually explained as the result of accumulation of metabolic byproducts that inhibit growth.

Monod's function (6.2) also predicts that effluent substrate concentration in chemostats should only depend on dilution rate D and be independent of influent substrate concentration s_0 . [This is equivalent to the vertical predator isocline in Lotka-Volterra or Rosenzweig-MacArthur predator-prey systems; Figure 6.2]. This prediction was tested by varying dilution rates and influent substrate concentration, letting the chemostat reach steady state and measuring then effluent substrate concentration s . Monod's prediction was confirmed for pure cultures growing on glucose (Grady Jr. et al., 1972), but the results consistently diverged from this prediction when working with mixed cultures (e.g., in wastewater treatment or fermentation processes) (Grady Jr. et al., 1972; Grady Jr. & Williams, 1975; Elmaleh & Ben Aim, 1976; Daigger & Grady Jr., 1977). In the latter, the outflowing substrate concentration was proportional to inflowing concentration, as predicted from the chemostat equations (6.2) with Contois' function (6.3). [It corresponds in ecology to the prediction that the prey equilibrium in a ratio-dependent predator-prey system is proportional to prey carrying capacity].

The first approach to reconcile theory and experiment was to introduce intermediate models that contain both Monod's and Contois' functions as special cases, e.g., Roques et al. (1982) and Borja et al. (1995),

$$g(s, x) = \frac{\mu s}{K_s + s + cx}.$$

[This form was introduced independently in ecology by DeAngelis et al. (1975) and by Beddington (1975).] Kargi & Shuler (1979) proposed another intermediate function that attempted to unify Monod's, Contois', Teissier's and Moser's growth functions in the context of chemostats. However, experimentalists rarely use these intermediate functions because of the effort required to estimate the additional parameter, while theoreticians do not like them because of the considerably more complicated analytical expressions. [The DeAngelis-Beddington function encounters the same fate in ecology.]

The second approach was to confront data directly with different functional forms of the growth rate, by fitting either the dynamic model (6.2) to time series data of substrate

and organism abundances, or by fitting direct measurements of the growth rate as a function of organism and substrate. Model selection was then based on the goodness-of-fit criterion. Table 6.2 lists these studies together with the tested models (the best fitting model in capitals). Often Contois' function fitted best, but the differences in goodness-of-fit were usually small. In an interesting application of catastrophe theory to the analysis of a protozoan system Bazin & Saunders (1978) found that, if the ratio prey per predator is taken as the critical variable, then "a comparatively simple mechanism can account for the observed behaviour".

In summary, the experimental results illustrate that Contois' model was successfully used in the context of mixed cultures on multicomponent substrates such as wastewater treatment, fermentation processes or biogas production from manure. While most of its support is empirical, Contois' equation has also been derived by mechanistic reasoning (Fujimoto, 1963; Characklis, 1978) based on enzyme kinetics or saturation kinetics applied to mass transfer limited growth. The empirical evidence suggests a mixed result: Contois' model has only been contradicted by experimental results for monospecific cultures growing on pure medium. In all other cases (mixed medium or several species/strains present) it was rather Monod's model that should have been rejected. [Similarly in ecology, where the particular predictions of prey-dependent food chains could only be found in protozoan laboratory systems with pure strains for prey and predator species (Kaunzinger & Morin, 1998)]. Monod's function remained nevertheless the predominant one in the microbiological literature (e.g., Barford & Hall 1978; Jannasch & Egli 1993). Why so? I think this is due mainly to historical reasons (Monod published before Contois and he is by far a more influential biologist), but the current teaching of microbial modeling also bears its share for generally presenting Monod's model as the basic model, without mentioning alternatives. [In the same way, introductory ecology books only mention the prey-dependent Holling type I, II and III models, rarely do they present any alternative functions]. Modeling efforts often start with Monod's model and stop upon obtaining a reasonable fit, without testing whether an alternative model can explain the results as well or better (the papers cited in Table 6.2 show that most consumption functions fit qualitatively correctly to the experimental data). Like a vicious circle, Monod's model confirms itself without giving another model the chance to be tested as well.

6.3 Lessons for ecology

Microbiological experiments are usually done in well controlled laboratory situations, following the observed processes with precise measurement techniques. In contrast, field ecology has to cope with various stochastic influences and unprecise census techniques. Therefore, empirical validation of a model from data is higher valued in microbiology than in ecology where model rejection by reason of data incompatibility is rare. However, Table 6.2 also lists results where several growth functions fitted equally well to the same (microbiological) data. Therefore, as a first lesson, if model selection based on goodness-of-fit is ambiguous even with microbiological data, then model selection based on ecological field data cannot be expected to be any better. I would speculate that this is one of the reasons why many ecologists consider mechanistic underpinning an essential part for the

Table 6.2: Collection of studies that compared Contois' function quantitatively with other functions (1-4, the tested models are noted in the third column with the best fitting model, if there was one, in capitals) or studies that did a simple model validation with Contois' function (5-12). References are: (1) Chiu et al. (1972), (2) Morrison et al. (1987), (3) Dercová et al. (1989), (4) Wilhelm (1993), (5) Fujimoto (1963), (6) Goma & Ribot (1978), (7) Kristiansen & Sinclair (1979), (8) Pareilleux & Chaubet (1980), (9) Lequerica et al. (1984), (10) Tijero et al. (1989), (11) Bala & Satter (1990), (12) Ghaly & Echiegu (1993), (13) Benitez et al. (1997).

ref.	studied system	tested functions
(1)	microbial sewage	Moser, Monod, Contois
(2)	nutrient limited phytoplankton growth	Monod, CONTOIS, LOGISTIC
(3)	growth and glucose consumption of yeast	CONTOIS, Monod
(4)	protozoan feeding rate on bacteria	Contois, Monod and 9 others *
(5)	bacterial growth on yeast	
(6)	hydrocarbon fermentation (with Contois' function at low substrate concentrations, a modified one at higher concentrations)	
(7)	production of citric acid in single stage continuous culture	
(8)	aerobic cultures of apple fruit cells	
(9)	anaerobic fermentation of rice straw	
(10)	anaerobic digestion of glucose and sucrose	
(11)	substrate degradation and biogas production from cattle waste	
(12)	continuous flow no-mix anerobic reactor of daily manure	
(13)	aerobic degradation of olive mill wastewaters	

*best fits were obtained with functions that are sigmoid with respect to substrate concentration, either Contois or Monod type

validity of a model, even though the models, by their very simplicity, cannot be much more than a phenomenological account of the observed biological processes. Furthermore, "one scientists' mechanism is another scientists' phenomenon" (Pimm, 1991). This quote best summarizes that the very definition of mechanistic is controversial and 'mechanisms' are rather a methodological support than a true representation of what is happening in a population. Ratio dependence was also introduced as an empirical way to include predator dependence, only recently have mechanistic derivations been developed (Poggiale et al., 1998; Cosner et al., 1999).

Let us now interpret the ecological meaning of the cited results in microbiology. The most often tested prediction of Monod's approach has been that the effluent substrate

concentration in chemostats should be independent of influent substrate concentration. This prediction is equivalent to the one that in predator-prey systems with prey-dependent functional response $G(s)$,

$$\begin{aligned}\frac{ds}{dt} &= r\left(1 - \frac{s}{K}\right)s - G(s)x \\ \frac{dx}{dt} &= eG(s)x - \mu x,\end{aligned}\tag{6.4}$$

the equilibrium prey-density is independent of carrying capacity K (that takes the role of inflowing substrate concentration) and that the predator isocline is vertical (as in Lotka-Volterra or Rosenzweig-MacArthur predator-prey systems). See Figure 6.2a and b for examples in chemostats or predator-prey systems. This prediction from Monod's function has been confirmed only in the case of growth of a single organism type on a single substrate within the constant environment of chemostat or batch cultures. Every deviation from these conditions leads to effluent substrate concentration being proportional to inflowing concentration. This result can only be explained with a slanted predator isocline (see Figure 6.2c to f), and it is also an essential prediction of the ratio-dependent model. The second series of results in batch and continuous cultures shows that the growth function is a decreasing function of predator density whenever heterogeneities occur either in consumer species composition or in the substrate, again suggesting that the predator isocline should be slanted. Such a slanted predator isocline seems to be the rule rather than the exception and ratio-dependence with its isocline through the origin (Figure 6.2e and f) can be considered a parsimonious way to model it.

The consideration of a vertical predator isocline lies also at the base of two so-called paradoxes: the paradox of enrichment (Rosenzweig, 1971) that predicts that richer systems (high K) should be less stable, and the paradox of biological control (Arditi & Berryman, 1991) that predicts that biologically controlled pests should have unstable dynamics. These paradoxes are often resolved by creating more complex models with additional state variables or additional parameters (e.g., McCauley et al. (1988), Scheffer & de Boer (1995)). These additions rapidly lead to analytically intractable models and discourage any further investigation. Instead of fixing the theory in an ad hoc manner to accommodate to particular cases, we might alternatively ask whether the 'basic model' itself might have flaws and start in a modeling framework that inherently has a slanted predator isocline. After all, "modeling philosophies . . . should be treated in the same way as models – retained only as long as they assist progress" (Nisbet & Gurney, 1982).

To continue this line of thought, consider the ecological equivalent to the cited finding that the growth function decreases with increasing consumer density (i.e., the question of predator dependence). There is ample empirical evidence that interference between foraging predators (a likely cause for predator dependence) is a frequent phenomenon in invertebrates (review in Hassell 1978) and in vertebrates (review in Sutherland 1996). However, this reported interference usually just triggers the remark that a functional response of the Hassell-Varley type (Hassell, 1978) would be most appropriate to model the system. However, due to a lack of experimental data to parameterize this model and because of analytical reasons, one is compelled to return to simple prey-dependent types that do not take this predator dependence into account. Ratio dependence offers a simple theoretical framework that inherently contains predator dependence either for food

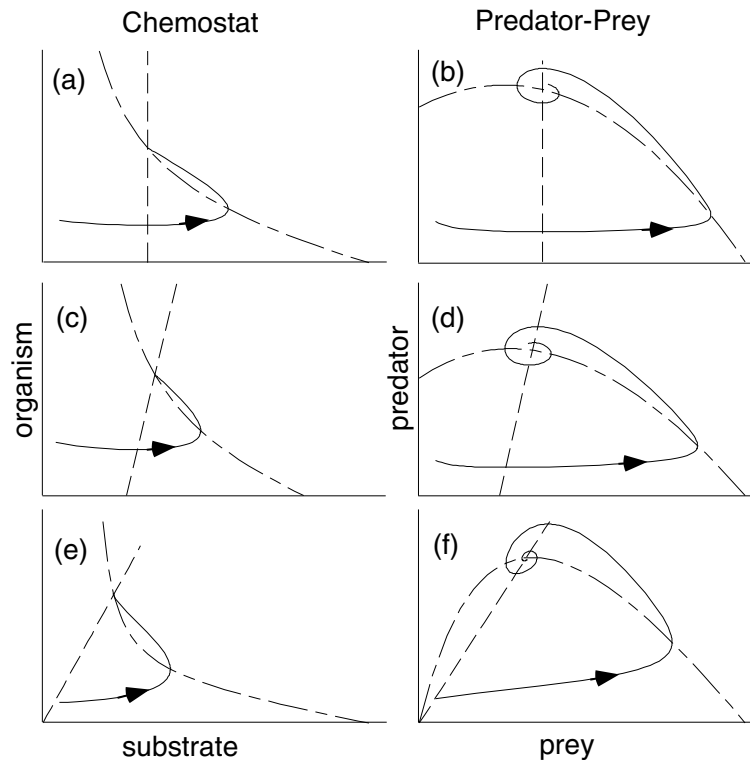


Figure 6.2: Typical isoclines in chemostats (left) and predator-prey systems (right) with prey-dependent Holling II growth functions (a,b), DeAngelis-Beddington type growth functions (c,d) and ratio-dependent growth functions (e,f). Prey isoclines are long-short dashed, predator isoclines are short dashed. Straight lines represent typical trajectories.

chains (Arditi & Ginzburg, 1989) or for whole food webs (Arditi & Michalski, 1995), while keeping models as simple and as tractable as those coming from the modeling frameworks based on Holling type functional responses.

Some authors continue arguing that the ‘recent focus on ratio dependence is unfortunate’ (Abrams, 1997; Murdoch et al., 1998), deflecting attention from more general forms of predator dependence. I think that, on the contrary, ratio-dependent theory has enhanced the status of predator dependence. It provides a simple mathematical framework to test whether strong predator dependence changes predictions that were originally derived from prey-dependent concepts, and to guide further research when these predictions are not ‘robust’ against predator dependence such as the two paradoxes mentioned above. While modeling frameworks based on prey-dependent interactions can be linked to top-down mechanisms (Arditi & Ginzburg, 1989) and account for cycling systems (Rosenzweig, 1971), the ratio-dependent approach includes elements of top-down and bottom-up regulation (Arditi & Ginzburg, 1989) and offers the possibility of deterministic extinction (Jost et al., 1999).

Ecology can profit from all these modeling frameworks. The reviewed results show that natural systems contain in general predator dependence, but they do not tell which of the modeling frameworks is a better approximation. Using both and comparing their predictions can serve to guide further research in case of different predictions, while similar

predictions give confidence having found ‘robust’ features of the studied systems.

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Chapter 7

Identifying predator-prey processes from time-series

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(Theoretical Population Biology (in press, with modifications))

Abstract

The functional response is a key element in predator-prey models as well as in food chains and food webs. Classical models consider it as a function of prey abundance only. However, many mechanisms can lead to predator dependence, and there is increasing evidence for the importance of this dependence. Identification of the mathematical form of the functional response from real data is therefore a challenging task. In this paper we apply model-fitting to test if typical ecological predator-prey time-series data, that contain both observation error and process error, can give some information about the form of the functional response. Working with artificial data (for which the functional response is known) we will show that with moderate noise levels, identification of the model that generated the data is possible. However, the noise levels prevailing in real ecological time-series can give rise to wrong identifications. We will also discuss the quality of parameter estimation by fitting differential equations to this kind of time-series.

La réponse fonctionnelle est un élément clé dans les modèles proie-prédateur, ainsi que dans les modèles de chaînes et de réseaux trophiques. Dans les modèles les plus classiques, la réponse fonctionnelle dépend uniquement de l'abondance des proies. Toutefois, divers mécanismes peuvent également faire intervenir l'abondance des prédateurs. Des données empiriques de plus en plus nombreuses suggèrent que celle-ci joue un rôle primordial. Il est donc important d'identifier la forme mathématique de la réponse fonctionnelle. Dans le présent article, nous utilisons les techniques d'ajustement de modèle pour déterminer si cette identification est possible sur des données écologiques réelles, comportant un "bruit" dû aux erreurs de mesure et aux stochasticités environnementales et démographiques. Sur des données artificielles, créées avec une réponse fonctionnelle connue, nous montrons qu'avec un "bruit" modéré l'identification du modèle ayant généré les données est possible. Toutefois, les niveaux de "bruit" typiques que l'on rencontre dans les séries temporelles en écologie peuvent mener à des identifications erronées. Nous discutons également de la qualité des estimations de paramètres obtenus par ajustement d'équations différentielles à de telles séries temporelles.

7.1 Introduction

Finding the functional relationship between observed data is one of the major tasks in ecology. Often several functional forms, that are based on different assumptions about the dominant mechanisms at work, are available. Fitting these functions to the data and applying goodness-of-fit as a criterion to select the best model is then used to detect the dominant mechanism for the particular system from which the data were obtained.

One particular application of this concept is to test dynamic predator-prey models against predator-prey time-series data. Harrison (1995), for example, reanalysed Luckinbill's (1973) classical protozoan data and fitted them to 11 different (continuous) predator-prey models. He assumed that the data contain only noise due to observation error (measurement error), which leads to fitting the whole trajectory of the predator-prey system to the time-series (termed observation error fit by Pascual & Kareiva 1996). Unfortunately, his statistical analysis did not take into account the number of parameters. It is therefore not too surprising that a rather complicated model with 11 parameters fitted the data best. Carpenter et al. (1994) fitted (discrete) predator-prey models to phyto- and zooplankton time-series from North American freshwater lakes to test whether the predation process depends significantly on predator density. Their analysis was designed to treat data that contain noise due to observation error and noise due to process error (environmental or demographic stochasticity), fitting such that the prediction one time step ahead is minimized (termed process error fit by Pascual & Kareiva 1996). To avoid any assumptions about the presence or absence of higher predation on the predators they fitted only the prey equation, using the predator data as input. While they took the number of parameters into account, they did not justify the use of discrete models (with the time step being the time between measurements) to describe a system showing the characteristics of a continuous system.

However, does a better fit of one model compared to another one always imply that its functional form represents the actual processes at work more accurately? There exist, for example, simple algebraic differential equations that can fit perfectly to any finite time-series (Rubel, 1981). It can also happen that very different models fit equally well to the same data (Feller, 1939). A slightly better fit of one of these models could be an artifact of the time-series being one particular realisation of an ecological process with all its random influences. Another realisation (replicate) might give a very different result. Therefore, the reliability of goodness-of-fit to determine the functional form of a process from time-series data should be tested in advance, e.g., with artificial data for which the functional form is known.

Carpenter et al. (1994) were aware of this problem and they tested their method with artificial data that they created with parameters characteristic for their limnological system. In this article we will perform a similar analysis for a larger range of ecological systems. We will test whether predator-prey time-series that represent the (continuous) dynamics of a stable focus contain sufficient information to detect if predator density influences the predation process strongly enough to influence the dynamics of the system. Such time-series typically contain noise due to observation error and noise due to process error. The fitting techniques will include observation error fit (Harrison, 1995) and a modified process error fit (Carpenter et al., 1994) that predicts s -steps ahead instead of

simply one-step ahead. The idea is to predict over a time range where non-linear effects become detectable. The determination of s will be based on the arguments developed and justified in Ellner & Turchin (1995).

We will work with very simple predator-prey models whose purpose is not to describe the data perfectly well but rather to describe them in a qualitatively correct manner. Simplicity in the description of the key processes (growth, death) is essential in models of more complex food chains or whole food webs, where the number of parameters becomes a limiting factor for analysis and parametrization. Although such complex models are not the subject of this article, it is with this purpose in mind that we deliberately consider simple predator-prey models.

Based on the principles of mass conservation and decomposition of the dynamics of a population into birth and death processes, the canonical form of such a predator-prey model is

$$\begin{aligned}\frac{dN}{dt} &= f(N)N - g(N, P)P =: F_N(N, P) \\ \frac{dP}{dt} &= eg(N, P)P - \mu P =: F_P(N, P)\end{aligned}\tag{7.1}$$

where N and P are the abundances of prey and predator respectively, e the conversion efficiency and μ the death rate of the predator in the absence of prey. The key processes are the prey growth function f and the link between prey and predator, the functional response g (prey eaten per predator per unit of time, Solomon 1949). The latter represents the predation process. We will test if model fitting can reveal whether g is approximately a function of prey abundance only ($g = g(N)$, as it is the case in traditional functional response models, e.g., Lotka 1924 or Holling 1959b) or if g also depends significantly on predator abundance. Such predator dependence influences the stability of predator-prey systems (DeAngelis et al., 1975; Murdoch & Oaten, 1975) and the response of the prey equilibrium to an enrichment of the system (Arditi & Ginzburg, 1989). Its detection from natural predator-prey time series is therefore a challenging task.

Introducing explicit predator dependence, $g = g(N, P)$, as was done by DeAngelis et al. (1975), normally increases the complexity of the function g , making it difficult to compare with the simpler prey-dependent form $g = g(N)$. A special case of a simple predator-dependent function was suggested by Arditi & Ginzburg (1989), assuming that $g = g(N/P)$. Models of this type are equally simple as prey-dependent models and can therefore be directly compared with them. However, ratio dependence represents only one particular case of predator dependence, and the only reason to favour it against other predator-dependent functions is its simplicity. This ratio-dependent functional response, like other predator-dependent functional responses, but in contrast to prey-dependent functional responses, leads to the observed correlated equilibria of prey and predators along a gradient of richness (Arditi & Ginzburg, 1989; Mazumder, 1994; McCarthy et al., 1995). The issue of ratio-dependence is currently subject to some debate (Abrams, 1994; Sarnelle, 1994; Akçakaya et al., 1995; Abrams, 1997; Bohannan & Lenski, 1997; Hansson et al., 1998).

In this article, we do not address the question of the ecological significance of one or the other model. We will merely attempt to answer the question of whether typical predator-prey time-series can help evaluating the importance of predator dependence. In particular,

we want to analyse the dynamics of predator-prey systems with low initial conditions and whose trajectory reaches a stable, non-trivial equilibrium (both populations coexisting) after one or two large amplitude oscillations. Such dynamics are considered characteristic for seasonal dynamics of phyto- and zooplankton in freshwater lakes of the temperate zone (Sommer et al., 1986) or for chemostat and batch culture experiments with protozoa (another source of published time-series data, e.g., Gause et al. 1936, Luckinbill 1973). Typically, such time-series are short (about 20 data points per season in lakes, 10-50 data points with protozoa), and may have considerable observation and process error. Differential equations seem the adequate tool to describe these systems since there are overlapping generations and large numbers of individuals. Using a simulation approach, we will generate artificial time-series (termed pseudo-data by May 1989) with a prey-dependent and a ratio-dependent functional response of the same simplicity to which we will add process and observation error. Regression techniques will then be applied and we will test whether the best-fitting model is indeed the one that created the data. A by-product of this kind of identification is the computation of the actual model parameters. We will analyze the quality of these estimates (value, standard deviation) to test the power of the regression method for parameter estimation.

7.2 The alternative models

Building on the canonical form (7.1) we use a standard logistic growth for the reproduction function f ,

$$f(N) = r\left(1 - \frac{N}{K}\right),$$

with maximum growth rate r and carrying capacity K . Two models are chosen for the functional response, a prey-dependent one and a predator-dependent one, that have both the same number of parameters. We chose the classical Holling type II model on the one side and a ratio-dependent model (Arditi & Michalski, 1995) on the other side,

$$\frac{aN}{1 + ahN} \longleftarrow g(N, P) \longrightarrow \frac{\alpha N/P}{1 + \alpha hN/P},$$

where a is the searching efficiency, h the handling time and α some kind of ‘total’ predator searching efficiency. We selected the Holling type II form rather than equally plausible alternatives such as the Ivlev functional response (Ivlev, 1961) simply because it is more widely used in ecology as well as in microbiology (Monod, 1942). The particular form of the predator-dependent functional response closely resembles the Holling type II function, thus making direct comparison between the two models possible. This form also tends to be regarded as the standard form of a ratio-dependent functional response in mathematical studies (Freedman & Mathsen, 1993; Cosner, 1996; Kuang & Beretta, 1998) and it is known in the microbiological literature as Contois’ model (Contois, 1959).

Despite their structural difference, the two models can produce very similar temporal dynamics. This is illustrated in Figure 7.1: time-series were created with both models (with parameters corresponding to a stable focus), adding stochastic noise and observation

error, and then fitting both models crosswise to these time-series (see the next section for the details of these methods). It can be seen that both models fit very well to the data created by the other model. A good fit alone is therefore a poor indicator whether the used model correctly describes the processes that generated the data.

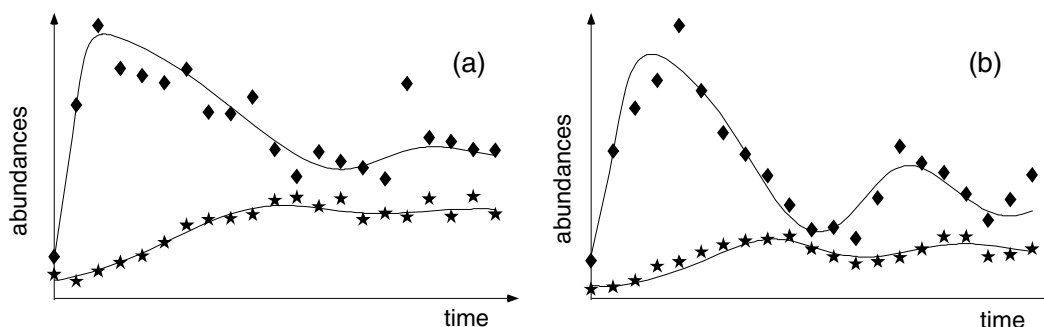


Figure 7.1: Examples illustrating that each model (the prey-dependent and the ratio-dependent one) can approximate satisfactorily time series data that were created by the other model. (a) Ratio-dependent model fitted to prey-dependent data. (b) Prey-dependent model fitted to ratio-dependent data. Diamonds represent the prey time-series and stars the predator time-series. See the text for further details.

7.3 Materials and methods

7.3.1 Artificial time-series

For this analysis to be valid for many different predator-prey systems, the pseudo-data must be generated with widely differing parameter values. Possible parameter values must abide to ecological and dynamical constraints. Such a constraint applies to the conversion efficiency e that should be within the interval $(0, 1)$ if abundances of both prey and predator are measured in biomass (the usual case in freshwater studies). Parameters K and h can be chosen arbitrarily since they depend entirely on the time and weight scales that are used. Given these three parameters, we can find intervals for the remaining parameters by the requirement defined above: existence of a non-trivial stable equilibrium reached with oscillations. Within these intervals, the parameters are chosen randomly. Initial values of prey and predator abundances are then chosen two to ten times below their equilibrium abundances. Such a randomly created parameter set (with initial values) is retained only if the following properties are respected: (1) prey and predator equilibria do not differ by more than a factor of 100, and (2) the deterministic trajectories of prey and predator show at least two distinct oscillations before reaching the equilibrium. The simulation time T is set in order to have these two oscillations. These final criteria assure an at least twofold variation in predator abundance (that is essential for model identification) and keep prey and predator abundances on comparable scales (see Figure 7.1 for two examples).

For each functional response, 20 such parameter sets were created. In analogy with the replicates of a typical ecological experiment, we created with each parameter set 5

replicate time-series by numerical integration of the stochastic version of the differential equations (7.1),

$$\begin{aligned} N_{t+\Delta t} &= N_t + F_N(N_t, P_t)\Delta t + \sigma_p N_t \epsilon_{N,t} \Delta t \\ P_{t+\Delta t} &= P_t + F_P(N_t, P_t)\Delta t + \sigma_p P_t \epsilon_{P,t} \Delta t, \end{aligned} \quad (7.2)$$

with $\epsilon_{N,t}$ and $\epsilon_{P,t}$ being random normal variates with mean zero and variance one, $\Delta t := T/500$ and σ_p the process error level. This stochastic process was sampled at 20 equal time steps and a lognormally distributed observation error (with coefficient of variation CV) was incorporated by multiplication with the exponential of a normal variate with mean zero and variance $\log(1 + CV^2)$. With this formulation, both process error and observation error are of a multiplicative type as suggested to be typical for natural populations (Hilborn & Mangel, 1997; Carpenter et al., 1994). Time-series with two noise levels were created, with CV and σ_p both set to 0.05 and to 0.1. The first case is comparable to protozoan laboratory data and the latter to data from freshwater plankton experiments (Carpenter et al., 1994). This makes a total of 400 data sets (2 models * 20 parameter sets * 5 replicates * 2 noise levels).

7.3.2 Error functions

The key part in fitting a model to data is the formulation of the function to be minimized. Depending on the stochastic elements in the data (process and/or observation error), the error function must be chosen accordingly. Ecological data have usually both types of error. However, statistical methods that take both into account are rare and little is known in the case of nonlinear regression. The usual practical solution is therefore to neglect one of the errors and to develop the error function for the other (Pascual & Kareiva, 1996). We will follow this approach, but also test two error functions that claim to be able to take both errors into account.

For ease of notation, consider a simple autonomous differential equation $\dot{y} = f(y)$ with time-series data $(t_i, Y_i)_{1 \leq i \leq m}$, where t_i is the time at which the population y is observed to have density Y_i , and m is the number of data points. [For predator-prey models y has to be replaced by the pair (N, P) and adaptations for this case that are not obvious in the development below will be noted in brackets]. Let $y(t_i)$ be the deterministic solution of the differential equation at time t_i and \hat{y}_i the (unknown) real population density at time t_i . If the data have only observation error, then there is only one initial condition, $y(t_0) = \hat{y}_0$, that is treated as a free parameter. If there is only process error, then the initial conditions are different for each consecutive data point and are defined as the data value s steps previously, $y(t_{i-s}) = Y_{i-s}$ (see Figure 7.2). s is chosen as the smallest value for which the autocorrelation in the time-series is below 0.5. Ellner & Turchin (1995) had developed this method to choose s on empirical grounds and argued that nonlinear patterns can be detected more reliably with this s -step ahead prediction than by the traditional one-step ahead prediction. In our artificial data, s always took the value 2.

With these notations, the process can be written as

observation error only $\hat{y}_i = y(t_i, \theta)$ $Y_i = \hat{y}_i \omega$ $y(t_0) = \hat{y}_0$	process error only $\hat{y}_i = y(t_i, \theta) \nu(\Delta t_i, f, \theta)$ $Y_i = \hat{y}_i$ $y(t_{i-s}) = Y_{i-s}$
--	--

where θ is the vector of model parameters. We will suppose that the observation error ω in the densities is of a multiplicative type (lognormal), as used in Carpenter et al. (1994) and Hilborn & Mangel (1997), with a constant coefficient of variation CV_ω . The (accumulated) process error ν_i depends in general on the time interval $\Delta t_i = t_i - t_{i-1}$ and on the dynamics f over this interval. However, for many ecological time-series the interval Δt_i is constant and we further simplify by ignoring the effect of the dynamics of f . Thus, process error $\nu \equiv \nu_i$ will be considered to be a lognormal variate with constant CV_ν (Carpenter et al., 1994). These two lognormal errors are considered to be exponentials of two normal variates with expectation 0 and variance $\sigma_k^2 = \log(CV_k^2 + 1)$, $k = \omega, \nu$.

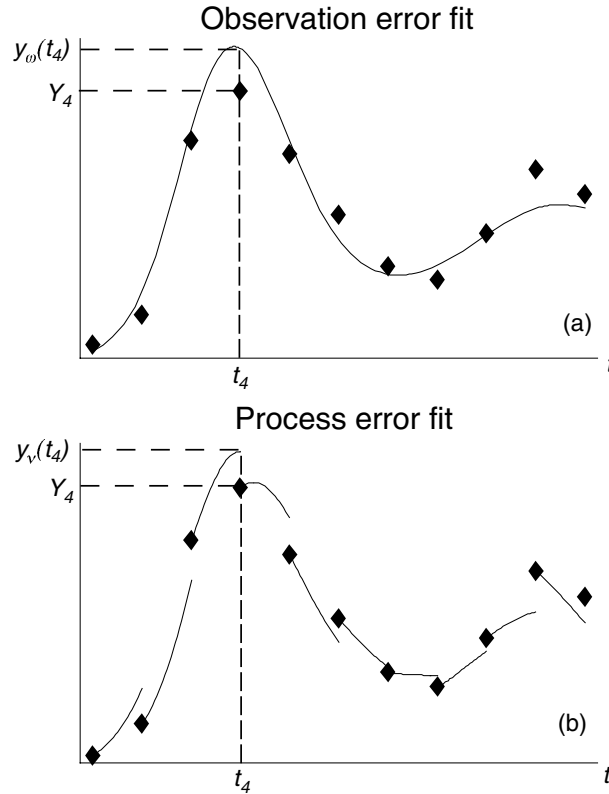


Figure 7.2: The fitting procedure changes with different types of error in the data. (a) Observation error only. The whole trajectory is fitted to the data, treating initial conditions as parameters. (b) Process error only. The best approximation is to fit from one point to the next (one-step ahead prediction).

The log-transformed data Y_i are therefore Gaussian with expectation $\log(\hat{y}_i)$ and standard deviation σ_k . We define the residuals

$$d_{i,k} = \log(Y_i) - \log(y_k(t_i)), \quad k = \omega, \nu. \quad (7.3)$$

The index k refers to the values $y_k(t_i)$ which are computed with different initial conditions according to the type of error. [Note that the residual $d_{i,k}$ is a vector for vector-valued $y_k(t_i)$]. Assuming now only one type of error, the error function to be minimized becomes:

$$X_k^2 = \sum_{i=1}^m \frac{d_{i,k}^2}{\sigma_k^2}, \quad k = \omega, \nu. \quad (7.4)$$

Figure 7.2 shows the difference between the error functions assuming observation error ω or process error ν only. It is visible on this figure that in the case of process error, the first summand ($i = 1$) is 0. Minimizing equation (7.4) is equivalent to a maximum likelihood approach (Press et al., 1992) and since σ_k is a constant it is also equivalent to the traditional least-squares regression.

Notice that the expectations of ν and ω are not 1 but $\exp(\sigma_k^2/2) = \sqrt{CV_k^2 + 1}$, $k = \omega, \nu$. This may seem strange on first view, but in fact allows the simple formulation of the residuals as the difference of the log's. Had we $E(\nu) = E(\omega) = 1$, then we would have to add $\sigma_k^2/2$ to the residual (7.3) for it to have expectation 0 (Hilborn & Mangel 1997, personal communication with Ray Hilborn). The problem is purely technical: one may prefer the lognormal variate to have expectation 1 or its log-transform to have expectation 0. With real data one does not know which assumption is more reasonable. Furthermore, since the σ_k 's are often not known very precisely, there is a risk of doing more harm than good by adding the term $\sigma_k^2/2$ to the residuals $d_{i,k}$. Therefore, one usually finds in the statistical literature the difference of the log's only (Ratkowsky, 1983; Hilborn & Mangel, 1997), and we will follow this safer approach.

If both types of errors are present simultaneously, $y(t_i)$ also depends on the observation error in the data point s steps previously, Y_{i-s} . The statistical literature proposes several solutions on how to treat this problem of 'errors-in-variables'. Clutton-Brock (1967) suggested to use weighted loss functions with the weights taking account of the uncertainty in Y_{i-s} :

$$CB_1 = \sum_{i=1+s}^m \frac{(y(t_i) - Y_i)^2}{w_i}$$

with

$$w_i = \eta_{\omega,i}^2 + \eta_{\omega,i-1}^2 \left(\frac{dy(t_i)}{dY_{i-s}} \right)^2, \quad (7.5)$$

The last term in this equation, $dy(t_i)/dY_{i-s}$, is the derivative of the predicted abundance $y(t_i)$ with respect to the initial condition $y(t_{i-s}) = Y_{i-s}$. [Note that for $y(t_i) = (N_i, P_i)$, the weight for state variable $y_j(t_i)$ is calculated by

$$\omega_{j,i} = \eta_{\omega,j,i}^2 + (\partial_{N_{i-s}} y_j(t_i), \partial_{P_{i-s}} y_j(t_i)) \begin{bmatrix} \eta_{\omega,1,i-s}^2 & 0 \\ 0 & \eta_{\omega,2,i-s}^2 \end{bmatrix} \begin{pmatrix} \partial_{N_{i-s}} y_j(t_i) \\ \partial_{P_{i-s}} y_j(t_i) \end{pmatrix}$$

and adapted similarly for higher dimensional state variables]. The standard deviation of the observation error, $\eta_{\omega,i}$, must be known in advance (by multiple samples) and independently of the process error. Here, we assume that the observation error has a constant CV_ω

known from replicate measurements. The standard deviation can thus be approximated by $\eta_{\omega,i} = CV_{\omega} Y_i$.

Another loss function, similar to the negative log-likelihood, was also introduced by Clutton-Brock (1967),

$$CB_2 = \sum_{i=i+s}^m 0.5 \left(\frac{(y(t_i) - Y_i)^2}{w_i} + \log(2\pi w_i) \right)$$

with w_i defined as in equation (7.5).

Note that in error functions CB_1 and CB_2 the residual is no longer the difference of the log's as suggested with the lognormal error type. However, the property of the lognormal error, that the standard deviation is proportional to population size, is preserved. We have also tested the lognormal versions of these equations, as proposed by Clutton-Brock (1967) and by Carpenter et al. (1994), but these functions converged very often to strange solutions, maximizing the dependence on the initial condition ($dy(t_i)/dY_{i-s}$) rather than minimizing the residuals. They also converged much slower. Using functions CB_1 and CB_2 thus simplifies the regression task without losing much generality with respect to the error type.

In sum, if the source of error in the data is assumed to be observation error only, the function X_{ω}^2 must be used as a regression criterion. If it is thought that process error only is present, the criterion X_{ν}^2 must be used. And if both errors are present simultaneously, CB_1 or CB_2 can be used. In our study of identifiability with artificial data, we will consider all situations and we will assess empirically the discriminative performance of all four error functions.

7.3.3 Model selection

The quality of adjustment of models to data is assessed with the familiar sum of squares X^2 (7.4). This selection criterion is identical to the regression criterion when regression has been done using X_{ω}^2 or X_{ν}^2 . The error functions CB_1 and CB_2 cannot be used directly for model selection because the estimators use weightings that differ among models (Carpenter et al., 1994). We based therefore model selection for all error functions on the sum of squared residuals of log-transformed values (7.4).

To quantify the identifiability of the models, we calculate the ratio X_c^2/X_f^2 for each time-series with X_c^2 being the sum of squares after fitting the correct model and X_f^2 the sum of squares after fitting the false model (i.e., a ratio smaller than one indicates that the correct model has been identified). Plotting the cumulative distributions of these ratios gives a visual representation of the selection performance of the different types of error functions.

If the model is linear in the parameters, then the probability distribution of X^2 near the optimal parameter values is the chi-square distribution with $DF = 2m - p$ degrees of freedom (p being the number of parameters). A convenient way to calculate this

probability is to use the incomplete Gamma function Γ (Press et al., 1992):

$$\ell = \Gamma\left(\frac{X^2}{2}, \frac{DF}{2}\right). \quad (7.6)$$

ℓ is a measure of the improbability that this fit was obtained by chance. Although this equation gives the correct improbability only for models that are linear in the parameters, it is quite common to use it also with nonlinear models (Press et al., 1992). However, in this case, ℓ is only a measure of this improbability. The actual values of ℓ obtained after fitting our models to the artificial data sets will give an indication of the threshold value below which fits to real data should be rejected because the improbability that the fit was obtained by chance becomes too low.

7.3.4 Parameter estimation

Before trying to fit our six-parameter models, it should be verified that the models are well defined, in the sense that parameters are uniquely identifiable (Walter, 1987). Based on a Taylor-series expansion approach, this problem can be reduced to the algebraic problem of solving six equations for six unknowns. It can be shown (C.2) that, in both models, the six parameters are indeed uniquely identifiable if the state variables are known with arbitrary precision and arbitrary resolution in time.

Since system stability is of much interest in ecosystems (return time after perturbations, persistence in stochastic environments), the local stability of the non-trivial equilibrium will be used as an overall measure of the correct estimation of the entire parameter set. Stability is measured by $-Re(\lambda)$, with λ being the dominant eigenvalue of the community matrix (the Jacobian at the equilibrium point). This value has been calculated analytically (to reduce numerical roundoff errors). We will plot the cumulative distribution of the ratios, $|Re(\lambda_e)/Re(\lambda_c)|$, with λ_e the dominant eigenvalue for the estimated parameters, and λ_c the dominant eigenvalue for the correct parameters. The steepness of this curve indicates the variation in the estimation of stability and, if the curve passes through the point (1.0, 0.5), then there is no deviation from the expected median.

The quality of the individual parameter estimates will be assessed by computing their coefficients of variation from the fits to each set of five replicated time-series. Averaging these CV 's over all parameter sets will give a general idea of the quality to be expected with this type of fitting and data.

7.3.5 Algorithmic details

There does not exist much customizable software that allows fitting differential equations to data. Fitting and visualization are usually separate steps in most software, which further slows down the fitting process. Therefore we programmed the whole procedure directly in C++ to create an application that allows immediate visual control of the fitted model. This proved to be an indispensable tool to analyze large numbers of data sets. (The software can be obtained from the first author upon request, and it requires a Power Macintosh.)

In a first step, the time-series data were used to determine upper and lower bounds of the parameters. These bounds were found by first computing a rough estimate of each parameter. For r , a (α), μ and h , this was done by an analogy with exponential growth:

$$\dot{y} = ry \Leftrightarrow r = \frac{\log(y(t_{i+1})) - \log(y(t_i))}{t_{i+1} - t_i}.$$

For example, a rough estimate of the maximal prey growth rate r was obtained by calculating

$$\max_{1 \leq i \leq m-1} \left\{ \frac{\log(N_{i+1}) - \log(N_i)}{t_{i+1} - t_i} \right\}.$$

The parameter K was roughly estimated as the maximal prey abundance. These estimates were then multiplied by some constants to get upper and lower bounds. The constants were calibrated with the artificial data sets in such way that the intervals contained the real parameters that had generated all these data sets. e was restricted to the ecologically reasonable interval $(0, 1)$.

In a second step, a genetic algorithm (GAlib 1.4.2 from <http://lancet.mit.edu/ga/>) was used to search within these bounds, with population size 50, mutation rate 0.01, crossover rate 0.1 and 400–600 generations. In this and the following step the solutions of the ordinary differential equations needed to calculate X_k^2 were simulated with the adaptive stepsize fifth-order Runge-Kutta method `odeint` from Press et al. (1992).

In a third and final step, starting from the parameter values found by the genetic algorithm, the fitting was completed by using repeatedly a Levenberg-Marquardt method and the downhill simplex method of Nelder and Mead combined with simulated annealing (routines `mrqmin` and `amotsa` from Press et al. 1992) until the fit could not be improved any further. The Levenberg-Marquardt method requires at each step the simulation of a system of 20 (or more) coupled ordinary differential equations (see Appendix 7.A). The parameters were forced to remain within the calculated intervals during the optimization (by blocking the parameter in the Levenberg-Marquardt method or by penalizing the error function in the simplex algorithm, with a penalty that grows exponentially with increasing distance from the bound).

The stopping criterion for both algorithms was determined dynamically from the data set: let E_n be the error at step n (expressions X_k^2 , CB_1 or CB_2), θ_n^j the estimate of parameter j at step n ($1 \leq j \leq p$), and $c = \max_{1 \leq i \leq m} \{Y_i\} \cdot CV \cdot m \cdot C$ (C being a constant, set to 10^{-8}). Then the algorithm was stopped if either

$$0 \leq \frac{E_n - E_{n+1}}{E_n} \leq c$$

or

$$0 \leq \max_{1 \leq i \leq p} \left| \frac{\theta_n^j - \theta_{n+1}^j}{\theta_n^j} \right| \leq c$$

(Seber & Wild, 1989). With simulated annealing, the error E_n might actually increase at the beginning of the optimization process. Therefore, this algorithm was not stopped if the first expression became negative.

In sum, both models were fitted with each of the four error functions to each of the 400 time-series with the following procedure: (1) Calculate upper and lower bounds for the parameters, (2) run a genetic algorithm, (3) use alternately and repeatedly the Levenberg-Marquardt method and the simulated annealing simplex algorithm with the stopping criteria above until the error did not diminish any further.

7.4 Analysis and results

After fitting the correct models to all data sets with low and high noise, we computed the mean $\bar{\ell}$ over all realizations of ℓ (equation 7.6). When assuming observation error only (X_ω^2 , calculated with a total $CV = 0.2$) this gave an approximate value $\bar{\ell} \approx 0.5 - 0.9$ for the time-series with high noise. If we assume having process error in the data (X_ν^2 , calculated with a total $CV = 0.2$), then we obtain $\bar{\ell} \approx 0.03 - 0.5$ for the time-series with high noise. These values suggest that fits to real data with ℓ -values considerably smaller than these should be rejected. Interestingly, the values of ℓ for the ratio-dependent data were always much higher than those for the prey-dependent data. It seems that process error of the same level (σ_p in equations 7.2) adds on average less accumulated process error in the ratio-dependent model than in the prey-dependent model.

Regarding the numerical efficiency of the algorithms, the Levenberg-Marquardt search worked fast and efficiently close to the optimum (compared to the simplex algorithm), but it often failed when the starting values obtained with the genetic algorithm were far from the optimum. In these cases, the simplex algorithm usually found the basin of attraction much faster. The combination of both algorithms ensured almost always the convergence to the optimum.

7.4.1 Model identification

Figure 7.3 shows the cumulative distributions of the ratios X_c^2/X_f^2 for all error functions and noise levels. At low noise levels ($CV = 0.05$, $\sigma_p = 0.05$) we see that error functions X_ω^2 , X_ν^2 and CB_2 led to less than 5% wrong identifications, while CB_1 had about 15% erroneous identifications. Therefore, we did not use the error function CB_1 at the higher noise levels ($CV = 0.1$, $\sigma_p = 0.1$). At this higher noise, the error function X_ω^2 still had less than 5% wrong identifications, while the error function X_ν^2 had up to 10% and function CB_2 performed even worse. Therefore, we concluded that error functions CB_1 and CB_2 are not useful for model selection, probably because the function that is minimized and the model selection criterion are not the same. If we want 95% confidence in the identification with error function X_ν^2 , then there can be at most 5% wrong identifications. Estimating this from Figure 7.3(c) (by drawing a line at the 95% level and projecting the intersection point with the distribution curve onto the x -axis (point β), then taking the inverse of this value, $1/\beta$), we obtain the criterion that the ratio of better fit by worse fit should be smaller than 0.95.

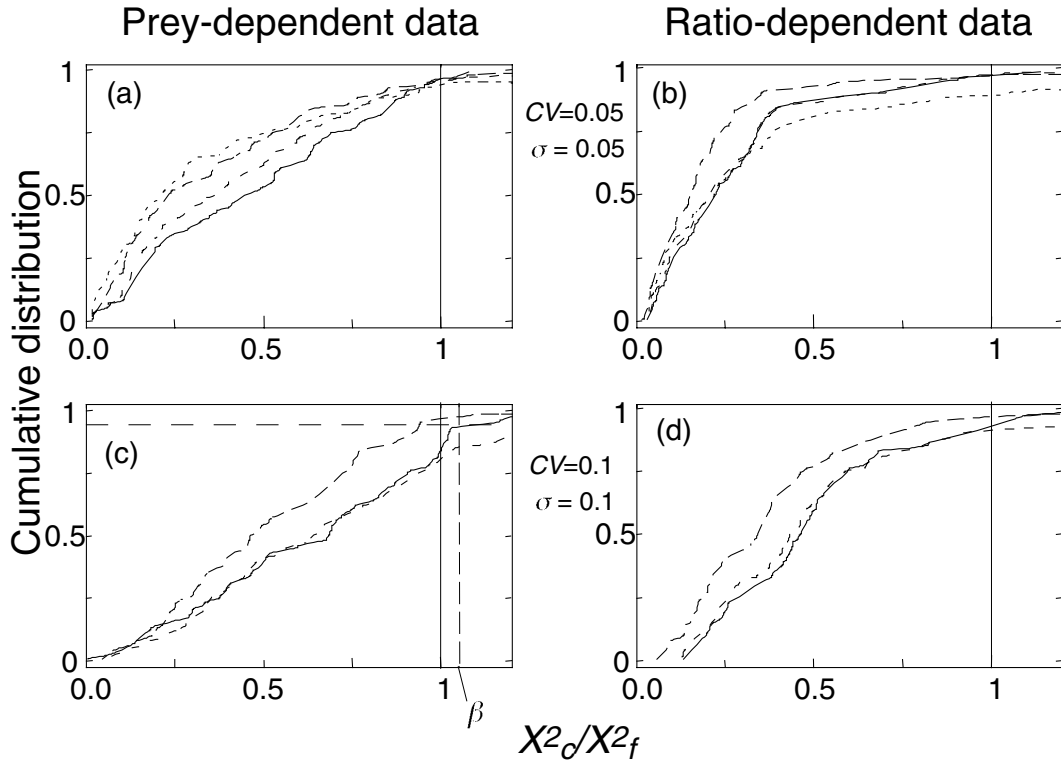


Figure 7.3: Quantile plots of fitting the models to the artificial data. — — —: error function X_ω^2 ; ———: error function X_ν^2 ; - - - - -: error function CB_1 ; - - - - -: error function CB_2 . X_c^2 is the error after fitting the correct model and X_f^2 is the error after fitting the wrong model. CV is the coefficient of variation of the observation error and σ is the standard deviation of the process error. The dashed straight lines in (c) show how the confidence level of 95% for model selection with error function X_ν^2 is calculated. See the text for more details.

7.4.2 Parameter estimation

Figure 7.4 shows the sensitivity of all four error functions to variations of one parameter at a time (fixing the others at the values with which the time-series was created) for a ratio-dependent data set with high noise ($CV = 0.1$, $\sigma = 0.1$). We see that they are all quite unbiased with mostly symmetric error functions. Observation error X_ω^2 gave always the most narrow function, often asymmetric and the error increasing very fast with the distance from the true parameter value [the steepest increase occurs if a too efficient predator (high α and e or low h , μ and r) drives the system to extinction]. This illustrates why we needed a genetic algorithm to find initial parameter estimates within the basin of attraction of the optimal parameter values. But once this basin is found, convergence with the simplex algorithm or the Levenberg-Marquardt method is very fast. CB_1 and CB_2 show the flattest error functions, indicating slower convergence rates of the optimization process. This same picture emerged with other data sets and models.

Comparing directly the dominant eigenvalues of the non-trivial equilibrium with the estimated and the correct parameters, strong differences between the error functions emerge. Figure 7.5 shows the cumulative distribution functions of the ratios of the dominant eigen-

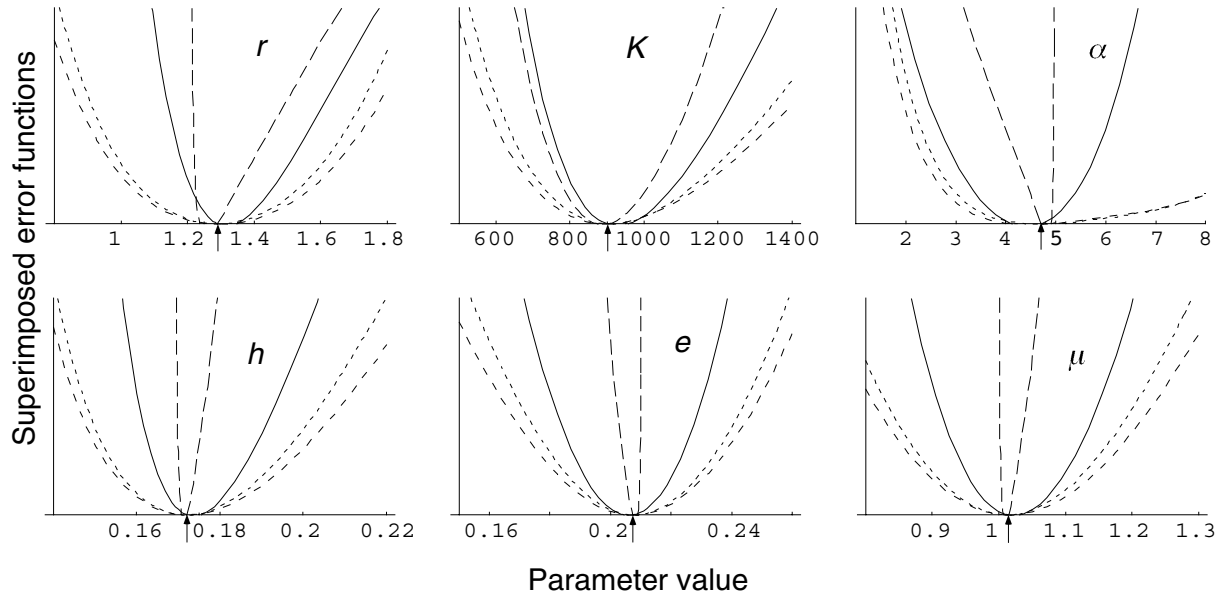


Figure 7.4: Four error functions vs. parameter values for a ratio-dependent time-series with large noise. The curves were shifted vertically to put their minimum all at the same height. Patterns are the same as in Figure 7.3. Actual parameters are: $r = 1.29$, $K = 900$, $\alpha = 4.7$, $h = 0.172$, $e = 0.207$, $\mu = 1.01$. They are indicated by an arrow.

values for all estimated parameter sets, error functions and models. The steepness of each curve is approximately the same, meaning that each error function shows the same variation in the estimation of local stability, although there seems to be a slightly smaller variation with ratio-dependent data. With respect to deviation from the expected median, we see that error function X_ω^2 (fitting the whole trajectory) performed overall best, followed by CB_2 . Error function X_ν^2 always overestimated stability.

The coefficients of variation CV_θ for each parameter, each model and each error function (computed from the fits to data with high noise only) are shown in Table 7.4.2. The important point is that these values are generally high (15-90%), indicating that even with 5 replicates, there remains much uncertainty in the estimated parameters. The estimation of K and r were the most reliable, and all other parameters had CV 's above 40%.

7.5 Discussion

We addressed in this article the problem of model selection by fitting dynamic models to predator-prey time-series that contain both observation and process error. Fitting assuming observation error only (error function X_ω^2) allowed for the most reliable model identification with both noise levels. Figure 7.3 suggests that identification should remain possible even with noise levels slightly higher than $CV = 0.1$ and $\sigma_p = 0.1$ or with some outliers in the data.

Fitting assuming process error (function X_ν^2) leads to much less reliable identification. Identification worked well with the low noise level. But for the higher noise level, the

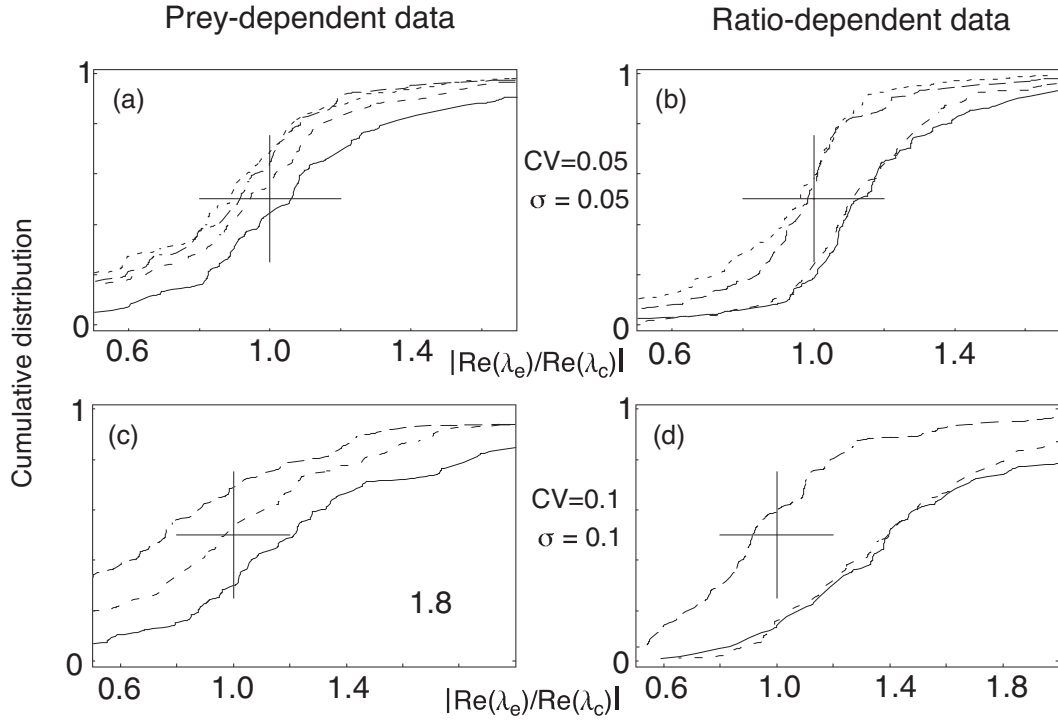


Figure 7.5: Quality of the estimated local stability: cumulative distributions of the ratios of the real part of the estimated dominant eigenvalue $Re(\lambda_e)$ by the real part of the correct dominant eigenvalue $Re(\lambda_c)$. Line patterns are the same as in Figure 7.3.

ratio of the lower error by the larger error should be below 0.95 to have 95% confidence in the result. Higher noise levels or outliers in the data will further aggravate the reliability of model selection. The error functions CB_1 and CB_2 that were supposed to take both observation and process error into account gave unreliable identification results, probably because the function that is minimized is not identical to the selection criterion, as this

Table 7.1: The mean coefficients of variation for the fitted parameters and the mean standard deviations of the estimated dominant eigenvalues, η_λ . All values are calculated from the results of fitting the data with high observation and process error ($CV = 0.1, \sigma_p = 0.1$) to the correct model. The first column indicates the error function that was minimized.

prey-dep. data	CV_r	CV_K	CV_a	CV_h	CV_e	CV_μ	η_λ
X_ω^2	0.16	0.14	0.43	0.33	0.6	0.52	0.04
X_ν^2	0.25	0.22	0.56	0.54	0.78	0.69	0.047
CB_2	0.2	0.17	0.57	0.44	0.7	0.62	0.045
ratio-dep. data	CV_r	CF_K	CV_α	CV_h	CV_e	CV_μ	η_λ
X_ω^2	0.31	0.28	0.7	0.63	0.54	0.59	0.036
X_ν^2	0.35	0.14	0.61	0.93	0.54	0.5	0.027
CB_2	0.38	0.24	0.61	0.82	0.51	0.44	0.031

is the case with with error functions X_k^2 . Preference must be given to functions X_k^2 (or more general maximum likelihood approaches) that use for regression and selection the same function.

Comparing our results with the work of Carpenter et al. (1994), we can notice that model selection is more reliable for the continuous models studied here than for the discrete models studied by these authors. However, Carpenter et al. fitted the prey equation only (using predator data as input into this prey equation). Therefore, they only selected for agreement with the prey dynamics, while we selected for agreement with both prey and predator dynamics. These authors also state that manipulation of the biological system is necessary to identify models. Our analyses show that it is needed to have initial conditions far from the equilibrium state, in order to generate strong dynamics of the system on its way back to the equilibrium. This can be accomplished in natural lakes by stocking or in laboratory cultures (batch or chemostat) by using low initial populations.

There is an interesting difference between the two models: the ratio-dependent time-series were always identified more reliably, in the sense that the difference between the sum of squares X^2 after fitting both models was on average larger with ratio-dependent data than with prey-dependent data ('pushing' the cumulative distribution functions to the left in Figure 7.3). It seems that the ratio-dependent model is more flexible, adjusting itself more easily and with smaller residuals to given data. Carpenter et al. (1994) had found the same difference (their Figures 3 B and E). This raises the problem that prey-dependent time-series are more often (wrongly) identified as being ratio-dependent than the other way round.

A most interesting observation is that the error functions X_ω^2 and X_ν^2 made simultaneous wrong selections in only 2 of the 400 time-series. We can therefore conclude that the most reliable model identification can be obtained by fitting both error functions and by accepting a selected model only if both functions give the same result. Unfortunately, observation error fit can become unreasonable in long time series because of the accumulated process error that increasingly diverts the system from the deterministic description.

Regarding the performance of the error functions with respect to individual parameter identification, all error functions give parameter estimates close to the actual values (Figure 7.4). However, Table 7.4.2 (calculated *CV*'s from the replicated time-series) shows that only parameters r and K are estimated with high precision, all others having large *CV*'s. Assessing the quality of parameter estimates with the method of the dominant eigenvalue (Figure 7.5) shows that, at the low noise level, this estimation is quite reliable for all error functions but with the higher noise level, there is a large variation with a considerable deviation from the expected median (Figure 7.5). The error functions X_ν^2 and CB_1 overestimate local stability (the estimated dominant eigenvalue λ is too negative).

There exist alternatives to the way we addressed the problem of model selection in this article. In particular, one could take a versatile model that is either prey-dependent or ratio-dependent, depending on a specific parameter value (e.g., using the models of Hassell & Varley (1969) or DeAngelis et al. (1975)), and then directly estimate this parameter. However, estimating it by fitting the whole model (as done in this paper) will also result in a large uncertainty of the estimate, thus reducing the selective power of this approach. Using Bayesian approaches to estimate posterior distribution functions of this

parameter are another possibility (Stow et al., 1995), but they require sophisticated multidimensional integration techniques. The direct comparison performed in this paper is more parsimonious and has the additional advantage of choosing between models that can be incorporated into complex food webs (Arditi & Michalski, 1995; Michalski & Arditi, 1995a).

In fact, there is no general statistical solution to the problem of fitting nonlinear models to data that have both observation and process error. As stated by Pascual & Kareiva (1996), the practical solution is often to fit as if there were only one type of error in the data. If neither of the error types should be neglected we suggest to use both types of fitting and base model selection on the joint result. This conclusion will probably remain valid for systems that do not fit into the framework of this study (e.g., systems that have only one state variable, unstable dynamics or more available data points), but in these cases identifiability should again be verified by a simulation analysis similar to the one presented in this paper.

Our general conclusion is that, to address the question of identification of dynamic models, the scientist should first try to reduce observation and/or process error as much as possible. If both errors remain important, then model selection is most reliable if both observation error fit and process error fit select the same model. Parameter estimates obtained by these methods are characterized by large coefficients of variation. The data should also exhibit dynamics of much higher amplitude than the errors in the data. This can be obtained either by low initial conditions in laboratory experiments or by perturbation of natural systems.

Acknowledgements

We thank Jean Coursol and Brian Dennis for helpful and clarifying discussions on the errors-in-variables problem. We also thank Eric Walter for useful comments on identifiability and distinguishability. This research was supported by the Swiss National Science Foundation (grant 31-43440.95 to RA) and by the French ‘Programme Environnement, Vie et Société’ (CNRS).

Appendix

7.A Calculating the derivatives of the state variables with respect to the parameters

For the Levenberg-Marquart method as well as for calculating the error function CB_1 and CB_2 arises the problem of differentiating the solution of an ordinary differential equation with respect to a parameter. We have applied the following method (see, e.g., Pavé 1994). Let $y(t)$ be the solution of the differential equation

$$\frac{dy(t)}{dt} = f(y(t), a), \quad y(t_0) = y_0$$

where f depends on a parameter a . We are looking for $\xi(t) := \frac{dy(t)}{da}$. Applying the chain rule and changing the order of derivation, we obtain

$$\begin{aligned} \frac{d}{da} \frac{dy(t)}{dt} &= \frac{d}{dt} \xi(t) \\ &= \frac{df(y, a)}{dy} \frac{dy}{da} + \frac{df(y, a)}{da} \\ &= \frac{df(y, a)}{dy} \xi(t) + \frac{df(y, a)}{da} \end{aligned}$$

and, therefore, by solving the following coupled differential equations,

$$\begin{aligned} \frac{dy(t)}{dt} &= f(y(t), a) \\ \frac{d\xi(t)}{dt} &= \frac{df(y, a)}{dy} \xi(t) + \frac{df(y, a)}{da} \\ y(t_0) &= y_0 \\ \xi(t_0) &= 0 \end{aligned}$$

we find the required derivative $\xi(t)$ by numerical integration. If a is the initial condition y_0 then $\frac{df(y, a)}{da} = 0$ and $\xi(t_0) = 1$. This concept can easily be extrapolated to vector valued $y(t)$ (dimension m). In this case, dy/dt , dy/da , f , df/da , ξ and $d\xi/da$ are vectors of dimension m and df/dy is an $m \times m$ matrix, the total derivative.

Chapter 8

From pattern to process: identifying predator-prey models from time-series data

Christian Jost, Roger Arditi

Abstract

Fitting time-series to nonlinear models is a technique of increasing importance in population ecology. In this paper we apply it to detect predator dependence in the predation process by comparing two equally complex predator-prey models (one with and one without predator dependence) to predator-prey time-series. Stochasticities in such data come either from observation error or from process error or from both. We discuss how these errors have to be taken into account in the fitting process and we develop eight different model-selection criteria. Applying these to laboratory data of protozoan and arthropod predator-prey systems shows that they have little predator dependence, with one interesting exception. Field data are more ambiguous (either selection depends on the particular criteria or no significant differences can be detected) and we show that both models fit reasonably well. We conclude that simple systems in homogeneous environments show in general little predator dependence. More complex systems show significant predator dependence more often than simple ones, but the data are also often inconclusive. Predictions for such systems based on simulation analyses should rely on several models to reduce mathematical artefacts in these predictions.

Les techniques d'ajustement de modèles non linéaires à des séries temporelles prennent une importance croissante en écologie. Dans le présent travail, nous les appliquons à la détection d'un éventuel effet de l'abondance des prédateurs sur le processus de prédation en comparant deux modèles proie-prédateur d'égale complexité (l'un avec et l'autre sans prédateur-dépendance) à des séries temporelles d'abondances de proies et de leurs prédateurs. La variabilité des données provient d'erreurs d'observation, d'erreurs de processus, ou des deux. Nous discutons la façon dont il faut tenir compte de ces erreurs lors de l'ajustement de modèles, et nous développons huit critères différents de sélection de modèle. L'ajustement des modèles à des données sur des systèmes proie-prédateur de laboratoire (protozoaires et arthropodes) montre, à une exception près, que l'abondance des prédateurs a peu d'influence. Les données de terrain sont plus ambiguës (soit la sélection dépend du critère de sélection retenu, soit la qualité de l'ajustement n'est pas significativement différente pour les deux modèles), mais les deux modèles s'ajustent correctement. Nous concluons que des systèmes simples en environnement homogène présentent en général peu de prédateur-dépendance. Des systèmes plus complexes présentent plus souvent une prédateur-dépendance significative que les systèmes simples, mais les données ne permettent souvent pas de trancher. Il convient donc de baser d'éventuelles prédictions fondées sur des simulations sur plusieurs modèles afin de réduire les risques d'artefacts mathématiques dans ces prédictions.

8.1 Introduction

The relation between predator-prey theory and real population time-series has been the subject of many studies since the early publication of the Lotka-Volterra equations or the Nicholson-Bailey model. The studied systems range from protozoan organisms (Gause, 1935; Luckinbill, 1973; Veilleux, 1979) over arthropod systems (Utida, 1950; Huffaker, 1958; Begon et al., 1996b) and microtine systems (Hanski & Korpimäki, 1995) to the whole plankton community of lakes (Scheffer, 1998). Traditionally, model validation is done by comparing the data to the model either qualitatively (stable or cyclic dynamic behaviour, length of cycles, amplitudes, etc.) or quantitatively (estimating parameters in the field, calibrating the model ‘by hand’ to obtain a good fit to the data). Recent computer power combined with powerful global optimisation algorithms enable researchers to fit rather complex mechanistic nonlinear models to time-series data. Such fits serve not only for model validation, but also for the detection of chaos (Turchin & Taylor, 1992; Dennis et al., 1997; Turchin & Hanski, 1997), the testing of hypothesis (Berryman, 1996; Turchin & Ellner, 2000) or model selection (Morrison et al., 1987; Carpenter et al., 1994; Harrison, 1995; Morris, 1997). See Shea (1998) for a review of general uses in population ecology.

In this paper we use model fitting as a criterion for model selection. The particular functional form of a predator-prey model can have implications in fisheries management and conservation biology (Yodzis, 1994), on persistence of populations (Myerscough et al., 1996) or on spatial distributions of predators (van der Meer & Ens, 1997). We address the question of detecting predator dependence in the functional response (e.g., due to interference amongst searching predators). The functional response links prey and predator dynamics in all models that follow the conservation of mass principle (Rosenzweig & MacArthur, 1963; Ginzburg, 1998). In this large general framework, many different expressions for the functional response can be found in the literature (see May (1976b) and Michalski et al. (1997) for inventories). The most widely used forms (Lotka-Volterra, Holling type I, II and III) are functions of the prey abundance only (prey-dependent, termed “laissez-faire” by Caughley (1976)) and do not depend on predator abundance. Expressions that include predator dependence become usually more complex (Hassell & Varley, 1969; Beddington, 1975; DeAngelis et al., 1975) which renders parameterization or theoretical analysis more tedious. In practice this often results in the use of (simpler) prey-dependent functional responses. The discussion on the importance of predator dependence has been revived by the introduction of the ratio-dependent concept (Arditi & Ginzburg, 1989) which offers a theoretical framework for modelling predator-prey systems (but also food chains or whole food webs) with a functional response that inherently includes predator dependence while preserving the simplicity of the traditional Holling-type functions. While prey-dependent predator-prey models rest essentially on top-down mechanisms (Oksanen et al., 1981), ratio-dependent models can reflect both bottom-up and top-down relations (Arditi & Ginzburg, 1989; Poggiale et al., 1998).

The two views have mostly been tested by comparing equilibrium population abundances along a gradient of enrichment or by reanalyzing data of published functional response experiments (see next section). Fitting models to time-series data of populations that are not in an equilibrium and applying goodness-of-fit as a criterion approaches the

problem from a dynamic point of view. The way how models should be fit to time-series depends on the source of errors in the data (Solow, 1995; Hilborn & Mangel, 1997). If the underlying process is stochastic and there is no error due to imperfect sampling (observation error), then predictions are only possible for a limited time into the future, e.g., to the next data point (1-step-ahead fitting). On the other side, if the underlying process is deterministic and there is only observation error, then we can fit the population trajectory (as determined by the model, its parameters and the initial population size) over the whole length of the time-series (see Figure 8.1). We will adopt Pascual & Kareiva's (1996) terminology for these two types of fitting, calling the first **process-error-fit** and the second **observation-error-fit**. In the literature one may also find the terms **s-step-ahead fitting** (Ellner & Turchin, 1995) for process-error-fit and **trajectory fitting** for observation-error-fit.

A process-error-fit approach was used by Carpenter et al. (1994) for 7 years of freshwater plankton data in two North American lakes (Paul Lake and Tuesday Lake), one of them having been manipulated during the experiment (addition and removal of fish). These authors fitted alternative prey- and ratio-dependent discrete models (difference equations) assuming the (non-manipulated) parameters to be the same over the whole 7 years. They showed in a simulation study that model selection should be possible with the data of the manipulated system, but the actual real data analysis yielded little interpretable results. One problem in their study is that plankton dynamics are more correctly modelled by a continuous system (large populations and overlapping generations) and taking the time between measurements as the prediction time step is an arbitrary choice. Furthermore, parameters might change from one year to the next.

Another study (Harrison, 1995) used an observation-error-fit approach and compared several continuous predator-prey models (differential equations) by fitting them to the protozoan data of Luckinbill (1973). Working with laboratory data, the author assumed stochastic influences to be negligible compared to observation error. A major problem in this study is that Luckinbill did not provide any information on measurement error in his data and therefore criteria that take model complexity into account (e.g. Akaike's information criterion, see Hilborn & Mangel (1997)) were not used by Harrison. Unsurprisingly, the model with the largest number of parameters gave the best fit.

The two described methods of fitting, i.e., process-error-fit and observation error fit, are statistically correct only if there is either no measurement error or no process stochasticity respectively. Methods that account for both errors simultaneously exist, but they require independent estimation of one of the errors or of their relative size (Clutton-Brock, 1967; Reilly & Patino-Leal, 1981; Schnute & Richards, 1995; Pascual & Kareiva, 1996). Since this information is often not available or hard to obtain, the "practical decision usually involves choosing between the two fitting procedures" and "the two assumptions are expected to provide two extremes in a range of likely parameter estimates" (quoted from Pascual & Kareiva (1996), who make an extensive discussion of statistical properties of the two types of fitting).

In this paper, we use the method of fitting alternative models to time-series data in order to address the biological problem of detecting predator dependence in the functional response. This will be done by fitting a prey-dependent and a ratio-dependent continuous predator-prey model with the same number of parameters (analogously to the treatment

of Carpenter et al. (1994) with discrete time models) to a large number of real population time-series and applying goodness-of-fit as a criterion. These time-series come from simple protozoan batch cultures, spatially more complex laboratory arthropod systems and complex lake plankton systems. Since such data contain both observation and process errors, we will apply systematically both process-error-fit and observation-error-fit, assuming that selection of the same model with both types of fits indicates a more reliable result. This reliability is further extended by not using least squares only but also robust techniques (to detect artifacts caused by outliers in the data) and by the use of bootstrapping to test whether the differences found in the goodness-of-fit or the predictive power are significant. Since all time-series analysed here have the characteristics of a continuous system (large populations, overlapping generations), we fit the differential equations and not their discretised analogues. We will work with data found in the literature (including the data of the studies mentioned above) and original plankton data from Lake Geneva that all give reasonable fits with both types of fitting. We will reanalyze Carpenter et al.'s data with continuous models and by fitting each year separately. Since seasonal plankton dynamics are often explained by deterministic models of the type used here (Scheffer, 1998), it will also be interesting to see how such models perform when confronted with real data. Harrison's analysis will partially be redone with models of the same complexity only (thus permitting direct comparison) and by testing his observation-error-fit results against process error fit results. Based on all these fits we will also discuss some of the advantages and disadvantages of either process-error-fit or observation-error-fit.

The time-series being used are characterised by a small size [10 - 50 data triplets (time, prey, predator)] and by rather large measurement errors with coefficients of variation (CV) of up to 50 %. For these reasons, a good fit of some model does not necessarily mean that the used formalism describes the biological processes correctly. This was demonstrated convincingly for the case of logistic population growth already very early in the history of mathematical population biology, namely by Feller (1939). Besides Verhulst's logistic function, he also considered two other mathematical models that are S-shaped and that have the same number of parameters and showed that the two forms fit equally well to the real data that were then considered to be the "proof" that the logistic model has the character of a physical law. This example illustrates that obtaining a good fit of a model to data is not a proof of the biological correctness of the chosen mathematical formalism. Or, in the words of Cale et al. (1989), 'multiple process configurations can produce the same pattern'.

These serious problems of model fitting can be addressed by following May's (1989) advice by 'generating pseudo-data for imaginary worlds whose rules are known, and then testing conventional methods for their efficiency in revealing these known rules'. Following this advice and Carpenter et al.'s example, we tested the distinguishability of the two models under consideration in a simulation study (see chapter 7). This study showed that the tested models can reliably be identified by goodness-of-fit from predator-prey time-series (that reach an equilibrium after at least one large amplitude oscillation) with 20 data triplets and moderate errors (CV of 10%).

8.2 The alternative models

Based on the principles of mass conservation and decomposition of the dynamics of a population into birth and death processes we write the canonical form of a predator-prey model as

$$\begin{aligned}\frac{dN}{dt} &= f(N)N - g(N, P)P \\ \frac{dP}{dt} &= eg(N, P)P - \mu P,\end{aligned}\tag{8.1}$$

where N and P are prey and predator abundances respectively, f is the prey growth rate in the absence of a predator, μ the predator mortality rate in the absence of prey and e the conversion efficiency. Predation is represented in these equations by the functional response g (Solomon, 1949), which in general depends on both prey and predator abundances.

In order to fit model (8.1) to data, we have to formulate f and g explicitly. For the recruitment function f , we use a standard logistic growth,

$$f(N) = r\left(1 - \frac{N}{K}\right),$$

with intrinsic growth rate r and carrying capacity K . For the functional response two models will be considered, a prey-dependent one and a ratio-dependent one:

$$\frac{aN}{1 + ahN} \longleftarrow g(N, P) \longrightarrow \frac{\alpha N/P}{1 + \alpha hN/P},\tag{8.2}$$

where a is the searching efficiency, h the handling time and α an overall searching efficiency for all predators. The dynamics of the resulting predator-prey systems can be, with both functional responses, stable coexistence, unstable coexistence (limit cycles) or extinction of the predator. The ratio-dependent model also offers extinction of both prey and predator (Jost et al., 1999). These dynamics are also observed in the time-series with which we shall compare the models by a goodness-of-fit criterion. For this comparison to be possible, even in the absence of exact knowledge about data quality (type of error, standard deviations), the models must have the same number of parameters. As mentioned in the Introduction, there exist various models with various degrees of predator dependence. The two above are taken as examples at the two extremes (8.2). We chose the Holling type II model because it is the most widely used predator-independent (= prey-dependent) functional response. The ratio-dependent model is the simplest predator-dependent functional response that has the same number of parameters as Holling's model and that offers comparable dynamics. Alternative predator-dependent models with comparable dynamics (Beddington, 1975; DeAngelis et al., 1975; Hassell & Varley, 1969) have more parameters.

The ratio-dependent model was originally proposed as a simple hypothesis that accounts for predator dependence (Arditi & Ginzburg, 1989). The fact that it was justified with empirical and phenomenological arguments has aroused some controversy (Abrams, 1994; Ruxton & Gurney, 1994; Akçakaya et al., 1995; Abrams, 1997) but mechanisms

leading to ratio dependence have now been demonstrated (Poggiale et al., 1998; Cosner et al., 1999). However, it should be noted that in highly complex systems, such as lakes, there can be too many important processes at work to incorporate them all in a mechanistically-derived model (spatial aggregation, defence mechanisms, refuge, etc.). In such situations, we consider that phenomenological models whose predictions correspond to global empirical patterns are reasonable options.

The two contrasting hypotheses have mainly been tested indirectly, by comparing equilibrium properties in relation to enrichment, based on empirical evidence for positive correlation between trophic level abundances in freshwater lakes (McCauley et al., 1988; Arditi et al., 1991a; Mazumder & Lean, 1994; Mazumder, 1994; McCarthy et al., 1995). There is also experimental evidence that spatial heterogeneity induces predator dependence in the functional response (Beddington et al., 1978; Arditi & Saïah, 1992). Analysis of direct measurements of the functional response at the behavioural level has revealed many cases of predator dependence with some cases agreeing with ratio dependence (Arditi & Akçakaya, 1990). Predator dependence seems thus to be a common occurrence in natural populations. Ratio dependence is just one particular way to include predator dependence, but it does so in a parsimonious way and allows for direct comparison with prey-dependent types of the functional response. Therefore, a better fit of the ratio-dependent model over the prey-dependent model cannot be interpreted as a proof that this model is correct, but only that it better approximates the actual occurrence of predator dependence.

We have avoided so far the term “density dependence”. There is some confusion in the literature about the use of this term in the context of predator-prey models since density can refer to prey or predator abundance. We agree with Ruxton and coworkers who equate density dependence with predator dependence (Ruxton & Gurney, 1992; Ruxton, 1995), because the functional response is intrinsically bound to the predator and also because density dependence indicates in its usual sense a detrimental effect of density on its own population’s growth rate. However, some authors refer to prey density when using the term ‘density-dependent predation’. We consider this to be an incorrect usage of the term, but to avoid any confusion, we will refrain from this term.

8.3 Materials and methods

8.3.1 Time-series

Two kinds of time-series data are analysed: data retrieved from the published literature and unpublished original data of phyto- and zooplankton dynamics in Lake Geneva. Only data with strong dynamics (sustained or damped oscillations) and allowing reasonable fits with both process-error-fit and observation-error-fit are considered. Since the difference between the two functional responses we compare is in the influence of predator abundance, we request that the range of variation of predator abundance over time is such that the CV is greater than 50%. See Table 8.1 for a listing of all data taken from the literature. The data were usually obtained by scanning the graphics and extracting the data with the software *DataThief* (Macintosh). This process introduces unavoidably some

error, but this error is of minor importance compared to the final residuals in the fits. The data for Paul and Tuesday Lake (Carpenter et al., 1993) were given directly in tabulated form within the publication, and some missing data points were obtained from the authors. One data set of Luckinbill (1973) was also obtained directly from the author. Most of these data sets were originally given with no indication on the observation error, or it was measured once and assumed to be similar for all data points (Carpenter et al., 1994; Huffaker, 1958). Therefore, the calculated likelihoods (see below) cannot have an absolute meaning, and will only serve to reject fits if the model becomes too unlikely.

Table 8.1: Sources for data are: 1) Gause (1935), 2) Gause et al. (1936), 3) Luckinbill (1973), 4) Veilleux (1979), 5) Flynn & Davidson (1993), 6) Wilhelm (1993), 7) Huffaker (1958), 8) Huffaker et al. (1963), 9) Carpenter & Kitchell (1994), 10) CIPEL reports (1986-1993). Numbers or letters separated by comma refer to further data sets with the same basic name, e.g. gause1,-3 refer to data sets gause1 and gause3. Usually these numbers refer to the figures or tables within the cited publication, except for plankton data where they refer to the year the data have been collected.

Name of data set	source	prey	predator	type of data
gause1,-3,-4	1	<i>Paramecium caudatum</i>	<i>Didinium nasutum</i>	batch culture (#individuals)
gauset2a,-c,-d,-e,-f	2	<i>Aleuroglyphus agilis</i>	<i>Cheyletus eruditus</i>	batch culture (#individuals)
luckin2a,-2b,-3,-4a,-4b,-5	3	<i>Paramecium aurelia</i>	<i>Didinium nasutum</i>	batch culture (#individuals)
veill8, -10	4	<i>Paramecium aurelia</i>	<i>Didinium nasutum</i>	batch culture (#individuals)
flynn1b,-1c,-2b,-2c	5	<i>Isochrysis galbana</i>	<i>Oxyrrhis marina</i>	batch culture (#cells)
wilh4.2,-4.4,-5.27,-5.28,-5.29,-5.30	6	<i>Escherichia coli</i>	<i>Tetrahymena thermophila</i>	batch culture (biovolume)
huff11,-12, ... ,-18	7	<i>Eotetranychus sexmaculatus</i>	<i>Typhlodromus occidentalis</i>	laboratory (#individuals)
huff63-3,-63-4	8	<i>Eotetranychus sexmaculatus</i>	<i>Typhlodromus occidentalis</i>	laboratory (#individuals)
paul84,-85, ... ,-90, tues84,-85, ... ,-90	9	edible phytoplankton	zooplankton	whole lake data (biomass)
edPhy86,-87, ... ,-93	10	edible phytoplankton	herbivorous zooplankton	whole lake data (biomass)
totPhy86,-87, ... ,-93	10	total phytoplankton	herbivorous zooplankton	whole lake data (biomass)

The data on Lake Geneva were collected as part of the lake monitoring program of the International Commission for Protection of Lake Geneva Against Pollution (CIPEL). The sampling methods are described in annual reports, e.g. CIPEL (1995). A short description can also be found in Gawler et al. (1988). Phytoplankton was sampled with a Pelletier bell-shaped integrating sampler from 0 to 10 m water depth. Zooplankton was

sampled by vertical tows from a depth of 50 m with coupled nets. Plankton biomass was calculated from abundance and estimated biovolume. Phytoplankton with length $< 50 \mu\text{m}$ and biovolume $< 10^4 \mu\text{m}^3$ was considered edible phytoplankton. Herbivorous zooplankton was identified by species and age class: cladocerans (mainly *Daphnia* and *Bosmina*), calanoides (*Eudiaptomus*) and cyclopoids for the age classes nauplii to copepodites stage 3 (higher age classes were considered carnivorous). The samples were taken at the station SHL2, at the centre of the lake, midway between Evian and Lausanne (lake depth 309 m). Plankton was usually sampled twice a month. The observation error was not measured, but the collecting scientists estimate the *CV* to be in the range of 10-20 % for an individual sample as in Carpenter et al. (1994). However, there are important heterogeneities in the lake, and the *CV* between several samples in the same area at the same time can be much larger (N. Angeli, pers. comm.). For this reason, we use in the fitting a prudent *CV* of 50 %, which is considered realistic for zooplankton but somewhat pessimistic for phytoplankton.

8.3.2 Error functions

As explained in the Introduction, we consider two types of errors, measurement error (imprecise sampling) and dynamic noise (due to environmental stochasticities, differences between the biological process and its mathematical description and, to a lesser extent in our data, demographic stochasticity). Figure 8.1 illustrates the resulting difference between observation-error-fit and process-error-fit. The prediction horizon with process-error-fit is traditionally one time step ahead (e.g., Carpenter et al. 1994, Dennis et al. 1995). For the reasons detailed in Ellner & Turchin (1995), we predict the dynamics s time steps ahead, with s chosen in such way that the autocorrelation with the predictor drops under 0.5. The main argument for this choice is to detect the nonlinear dynamics in the time-series. On smaller prediction horizons, standard statistical linear regression models might be more powerful than our mechanistic nonlinear models. See Ellner & Turchin (1995) for a more detailed justification.

We will assume that the (observation or process) error in the densities is of a multiplicative type (lognormal), with a constant *CV* (stationarity). This type of distribution is typical for population data in general (Dennis et al., 1997; Hilborn & Mangel, 1997). It was used and justified for plankton in particular by Carpenter et al. (1994). For protozoan and arthropod data also, this choice seems reasonable (Wilhelm, 1993; Huffaker, 1958). In general, the true nature of the error can be intermediate between normal and lognormal. This was assumed in the regression analysis of Harrison (1995) performed with Luckinbill's data, but this approach requires another parameter that Harrison determined empirically. For reasons of parsimony, we refrained from such an approach, and the lognormal error type seems on the whole better suited to the kind of data we analysed. Cases in which model selection might be biased by using lognormal error are discussed specifically. Uncertainties in the time measurements are considered to be small in comparison with the errors in abundances and are neglected in this study.

To formalise these ideas, consider a simple differential equation $dy/dt = f(y, \theta)$ with time-series data $(t_i, Y_i)_{1 \leq i \leq m}$, where t_i is the time at which the population y is observed to have density Y_i , m is the number of data points [for predator-prey models y has to be

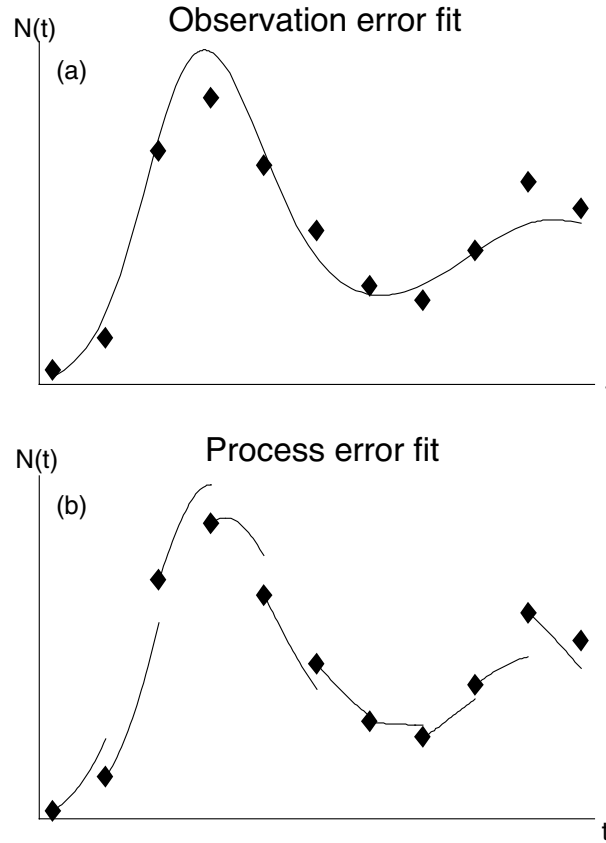


Figure 8.1: Fitting a differential equation to a time-series. In (a) all error is assumed to be measurement error and the whole trajectory is fitted at once (observation-error-fit), while in (b) all error is assumed to be process error and each data point serves as an initial condition to predict the next data point (process-error-fit).

replaced by the couple (N, P) and θ is a vector of q parameters. Let \hat{y}_i be the unknown real population density at time t_i , and $y(t_i) = y(t_i, \theta)$ the deterministic solution of the differential equation at time t_i with parameters θ . If there is only observation error in the data, then the whole trajectory is fit and there is only one initial condition, $y(t_0) = \hat{y}_0$, that is treated like a free parameter. If there is only process error then the initial condition is different for each predicted data point and defined as the data point s steps previously, $y(t_{i-s}) = Y_{i-s}$, $s \geq 1$. With these notations and with $\Delta t_i = t_i - t_{i-s}$, the process can be written as

observation error only $\hat{y}_i = y(t_i, \theta)$ $Y_i = \hat{y}_i \omega$ $y(t_0) = \hat{y}_0$	process error only $\hat{y}_i = y(t_i, \theta) \nu(\Delta t_i, f, \theta)$ $Y_i = \hat{y}_i$ $y(t_{i-s}) = Y_{i-s}$
--	--

Process error ν and observation error ω are considered to be lognormal random variates with constant coefficients of variation CV_ν and CV_ω respectively. However, note that the process error ν depends in general on the time interval between measurements and on the underlying process f with parameters θ .

The log-transformed data are assumed to be Gaussian with expectation $\log(\hat{y}_i)$ and

standard deviation σ_k ($= \sqrt{\log(CV_k^2 + 1)}$), $k = \nu, \omega$ (Carpenter et al., 1994). We define the residual as

$$d_i = \log(Y_i) - \log(y(t_i)).$$

The fitting procedure minimises the sum of squared residuals weighted by the variances,

$$X_k^2 = \min_{\theta} \sum_{i=1+s}^m \frac{d_i^2}{\sigma_k^2}, \quad k = \nu, \omega \quad (X_k^2)$$

(with $s = 0$ for $k = \omega$). This least squares regression with the described statistical model is equivalent to maximum likelihood (Press et al., 1992).

While the proportionality between population size and standard deviation of measurement or process error is generally accepted, there may be considerable doubt about the normality of the log-transformed values. Regression with criterion X_k^2 is very sensitive to outliers (data points that are farther away from their real value than would be expected with a normal distribution) with respect to parameter estimation and model selection (Linhard & Zucchini, 1986). We therefore used as a second criterion the Laplacian (or double exponential) error function,

$$X_k^L = \min_{\theta} \sum_{i=1+s}^m \frac{|d_i|}{\sigma_k}, \quad k = \nu, \omega \quad (X_k^L)$$

which is more robust against such outliers (Press et al., 1992).

8.3.3 Simulation study, numerical methods and bootstrapping

The power of error function X_k^2 for selecting the correct model from time-series data has been tested in a simulation study (see chapter 7): we parameterized the two models (8.1 and 8.2) randomly to create deterministic dynamics that resemble the observed dynamics in a lake (reaching a stable equilibrium after one or two large amplitude oscillations) and simulated stochastic data (20 data points) containing both process error and observation error (both of a multiplicative type and with $CV = 0.1$, comparable to the ones found in lakes). Both models were fitted to these artificial time-series with error functions X_k^2 in a 3-step-procedure: (a) computing upper and lower limits of the parameters from the time-series data, (b) finding starting values of the parameters with a genetic algorithm and (c) computing the optimal parameters with the standard simplex method coupled with simulated annealing (Press et al., 1992). In this regression scheme we use only the available time-series data to estimate the parameters and with them the discrepancy between model and data. Only logical constraints such as positivity of parameters are applied. This simulation study showed that either observation-error-fit or process error fit alone detect the correct model with more than 95% confidence if we require that the goodness-of-fit for each model (as estimated by X_ω^2 or X_ν^2) differ by more than 5%. More importantly, in only 1% of all fits was the wrong model identified with both criteria simultaneously.

All real time-series in this study are fitted with error functions X_k^2 and X_k^L by the same 3-step-procedure that was used in the simulation study, with process-error-fit and observation-error-fit. In a further analysis we estimate the expectation $E(X_k^2)$ by residual bootstrapping as described in Efron & Tibshirani (1993). Based on the bootstrap fits we calculate the improved estimate of prediction error $IEPE$ (Efron & Tibshirani, 1993) to compare the predictive power of the two models. See the Appendix for a detailed technical description of these methods. As a by-product, the bootstrapping permits to estimate for each time-series the variation in the estimated parameters.

8.3.4 Model comparisons

Model selection will be based on the goodness-of-fit according to criteria X^2 , X^L or $E(X^2)$ and the prediction error criterion $IEPE$ detailed above. The likelihood ℓ of the model (given the data) can be calculated approximatively with X^2 and the degrees of freedom DF [number of predicted data points minus number of parameters, i.e., $DF = 2(m-s)-q$] by the formula

$$\ell = \Gamma \left(\frac{X^2}{2}, \frac{DF}{2} \right), \quad (8.3)$$

where Γ is the incomplete gamma function (Press et al., 1992). We could not derive such a function for the likelihood in case of Laplacian error. Therefore, the same function is used to get at least an order of magnitude of the likelihood.

Note that equation (8.3) is absolutely correct for linear models only (Press et al., 1992). To know what likelihood levels should be expected with our nonlinear models we have to rely on the likelihoods computed in the simulation analysis (chapter 7) that ranged from 0.01 to 0.9 (that is, likelihood ℓ after fitting the model that was originally used to simulate the artificial data). Assuming a larger discrepancy between the theoretical model and the real process we accept all fits with a likelihood above 0.001 (calculated with a ‘prudent’ CV of 0.5), otherwise model selection is considered nonsignificant. While X^2 and X^L must differ by at least 5% between the two models to be considered significantly different (see previous section), $E(X^2)$ and $IEPE$ (obtained by bootstrapping) are compared directly with a standard t-test ($\alpha = 0.05$) and model selection is accepted as significant if the likelihood of $E(X^2)$ is also above the limit 0.001. The discussion will be based solely on the significant fits that are indicated in Table 8.4 by a \dagger or \ddagger . The \ddagger indicates strongly significant fits ($\ell > 0.001$ with $CV = 0.1$).

The comparison between the qualitative dynamic behaviour of the data and the (winning) fitted model is used as a second criterion for the adequacy of the model. These qualitative dynamics are classified into strongly stable equilibria (ss) when the trajectory converges to the equilibrium after at most one oscillation, stable equilibria (st) if there is more than one oscillation before stabilisation, limit cycles (l), extinction of the predator only (pe) and extinction of both populations (e). See Figure 8.2 for an illustration of the different types.

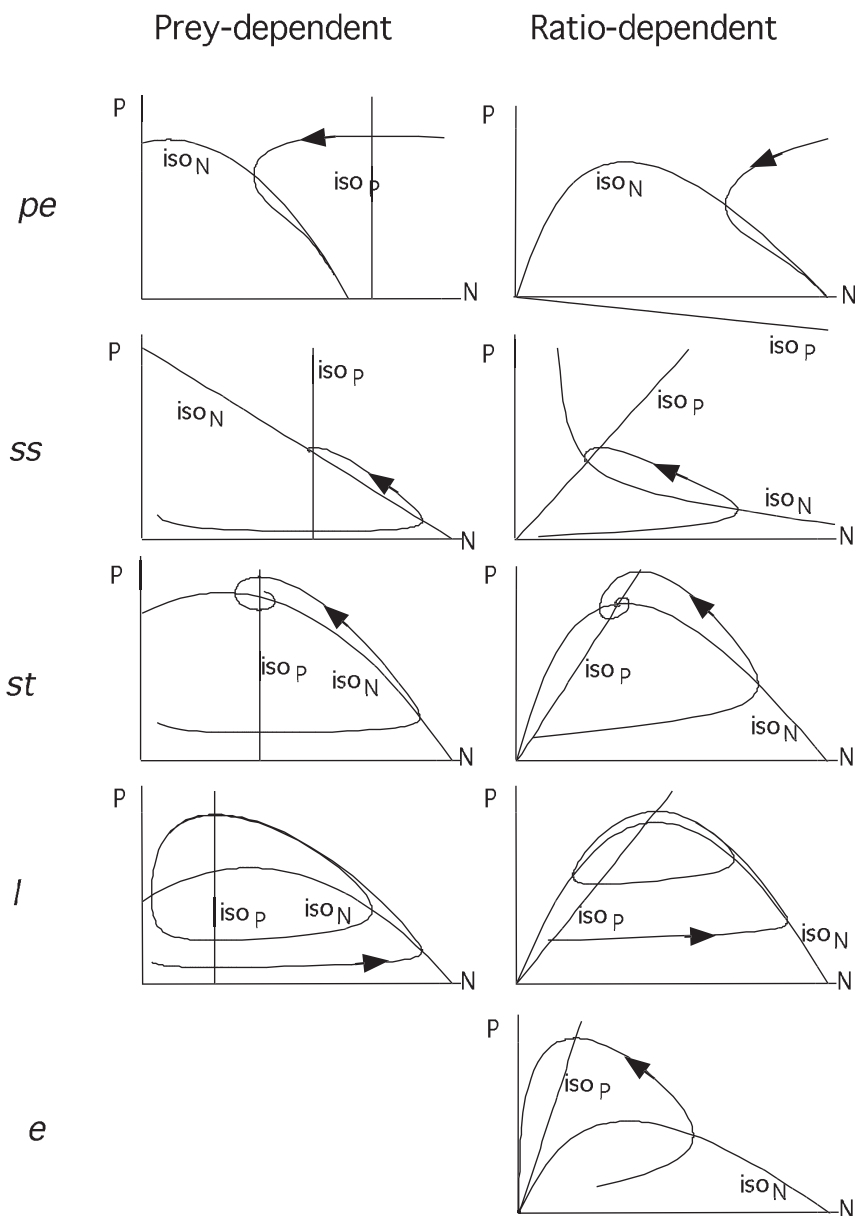


Figure 8.2: The different dynamic behaviours that are distinguished in the data and in the fitted models. Each graph shows the phase space with isoclines of prey (iso_N) and predator (iso_P) and an example trajectory. *pe* designates extinction of the predator only, *ss* strongly stable systems, *st* stable ones, *l* limit cycles, and *e* extinction of both populations (only possible in the ratio-dependent model).

8.4 Results

The detailed fitting results (model selection per type of fitting and per criterion) with additional information on each time-series (size and apparent dynamics) are summarised in Table 8.4 (see legend for more details). To facilitate their interpretation the essential model selection results are condensed in Table 8.2 applying the following rules: for each time-series a “winning” model is selected if all significant fits with both types of fitting and with the four different criteria identify the same model, otherwise the time-series is marked as ambiguous. For the lake data the same procedure is also applied separately for both types of fitting. Furthermore, we indicate if the qualitative dynamics (Figure 8.2) of the significant fits correspond to the apparent dynamics of the timeseries. Since extinction is not possible in the prey-dependent model we assume correct detection of the qualitative behaviour if the fit shows limit cycle behaviour (the closest to extinction that this model can produce).

Table 8.2: Summary of model selections: the first part of the table lists for each group of time-series the number of times each model was selected by both fitting types, with the number of correct qualitative dynamics in parentheses. The number of ambiguous model selections are listed in the last column. The second part of the table treats process-error-fit (PEF) and observation-error-fit (OEF) separately for lakes.

data	prey-dep.		ratio-dep.		ambiguous	
Gause	6 (3)		1 (1)		1	
Luckinbill, Veilleux	6 (1)		0		2	
Flynn and Davidson	0		4 (4)		0	
Wilhelm	2 (0)		2 (2)		2	
Huffaker	6 (5)		0		4	
Paul Lake	2 (2)		2 (0)		3	
Tuesday Lake	4 (2)		0		3	
Lake Geneva (edible)	2 (1)		4 (2)		2	
Lake Geneva (total)	5 (2)		1 (0)		2	
	PEF	OEF	PEF	OEF	PEF	OEF
Paul Lake	2 (2)	3 (3)	2 (0)	2 (0)	3	2
Tuesday Lake	2 (1)	6 (3)	1 (1)	0	4	1
Lake Geneva (edible)	4 (3)	2 (1)	1 (0)	6 (3)	3	0
Lake Geneva (total)	2 (2)	6 (2)	3 (1)	1 (0)	3	1

8.4.1 Protozoan data (simple batch cultures)

The protozoan data of Gause, Luckinbill, Flynn & Davidson, and Veilleux were the easiest to fit and they gave the most significant results. Of Gause’s eight data sets, six are prey-dependent, one ratio-dependent and one nonsignificant. The latter data set has less than 10 data triplets (time, prey, predator); it may simply be too short for a reliable model identification. In most cases the dynamic behaviour is also correctly detected by

the winning model. We can therefore conclude that Gause's data do not indicate any significant predator-dependence in the functional response. This is confirmed by Luckinbill's and Veilleux's data (both with similar organisms), in which six prey-dependent time-series are identified and two are ambiguous. However, the observed limit cycle was only detected once by process-error-fit. The regression resulted mostly in dynamics with a stable equilibrium. One data set of Veilleux fits significantly better to the ratio-dependent model with observation-error-fit: these data show fast convergence to a sustained stable limit cycle with minima far above zero, a pattern that cannot be produced with the prey-dependent model. However, the ratio-dependent fit does not resemble the data very much either. We think that this limit cycle should rather be explained by delayed effects, and the significant ratio-dependent fit is also due to the lognormal error structure that gives more importance to points closer to zero. When repeating the regression assuming a Gaussian error the fit becomes indeed significantly prey-dependent.

An interesting exception to this prey-dependent predominance in protozoan systems are the data of Flynn & Davidson (1993) which are all strongly significantly ratio-dependent for all criteria and both types of fitting. These data are those of static batch cultures without aeration, stirred every day before sampling. It is therefore likely that heterogeneities developed between stirrings. The data sets 'flynn1b', 'flynn2b' and 'flynn2c' are shortened from their Figures 1b, 2b and 2c respectively because there was an obvious change of parameters during the experiment, detectable by an abrupt change in dynamics and described by the authors as the onset of strong cannibalism amongst predators. The data sets consist of the data before the change.

The data of Wilhelm (1993) are the least conclusive: two data sets are prey-dependent, another two are ratio-dependent and two are ambiguous. The pre-equilibrium dynamics in the time-series (always one large amplitude cycle followed by a long time of stable coexistence) are probably too short for a reliable model identification.

The variation in the estimated parameters is rather high (medians of the CV 's ranging from 0.16 to 0.78) but they are smaller than with the other time-series (see below). Observation-error-fit gives slightly smaller CV 's than process-error-fit.

8.4.2 Arthropod data (spatially complex laboratory systems)

Huffaker's data fit rather badly to both models (low likelihoods), but the few significant results are always prey-dependent observation error fit. Process-error-fit confirms this result with the exception of two significant ratio-dependent fits with Laplacian error (equation X_k^L). However, these two fits are qualitatively wrong (stable dynamics instead of limit cycles or extinction). The data themselves are always unstable with oscillations and coming close to extinction, although the populations seem very often to recover shortly before termination of the experiment. These dynamics are correctly reproduced with both models and observation-error-fit. Interestingly the prey-dependent model retains these unstable dynamics with s -step-ahead fitting, while the ratio-dependent model mostly converges to a stable system. This is a further indication that the prey-dependent model is closer to the real dynamics. The medians of the CV 's of the estimated parameters range from 0.09 to 1.91 (again with smaller ones in observation-error-fit).

8.4.3 Plankton data (complex lake plankton systems)

In general these data are very noisy and it is not clear if there are well defined dynamic patterns or only noise. However, the algorithms seemed to find dynamic patterns in some cases.

With observation-error-fit, Paul Lake gives five times a significant fit, of which three are prey-dependent. Process-error-fit gives four significant fits, also with two prey-dependent ones. In three cases, the two types of fitting are contradictory. Carpenter et al. (1994) had not found any significant result for this lake with discrete predator-prey models and process-error-fit (one-step-ahead fitting), which agrees with our finding. The results are rather different in manipulated Tuesday Lake. Observation-error-fit selects the prey-dependent model in six of the seven time-series, with one ambiguity. Process-error-fit is less conclusive, with two prey-dependent time-series, one ratio-dependent, three non-significant and one ambiguity. Interestingly, Carpenter et al. found for this lake a good fit to the ratio-dependent model. We do not know if this discrepancy comes from the fact that we look at seasonal dynamics or because we use continuous models.

For Lake Geneva, we the phytoplankton either with edible algae only or with total algal biomass. Observation-error-fit gives the clearest trends: ratio-dependent (6 vs. 2) for edible phytoplankton, prey-dependent (6 vs. 1) for total phytoplankton. With process-error-fit the trends are less distinct but seem to contradict the previous results: prey-dependent (4 vs. 1) with edible phytoplankton, ratio-dependent (3 vs. 2) with total phytoplankton. Ambiguities between results from the two types of fitting appear in four cases.

Regarding qualitative behaviour, observation-error-fit often results in transient dynamics without reaching an equilibrium state or the dynamics are in some cases true limit cycles, while process-error-fit nearly always results in stable systems. Especially the ratio-dependent model shows often strongly stable dynamics (a pattern termed “limited predation” by Arditi & Ginzburg (1989), see Figure 8.2). The medians of the *CV*’s of the estimated parameters cover a wide range from 0.4 to 2.4 (again with smaller ones in observation-error-fit).

8.5 Discussion

We have compared predator-prey time-series (that contain both process and observation error) to two alternative predator-prey models with the objective to detect predator dependence in the functional response. The goodness-of-fit was estimated by fitting the models to the time-series assuming that there is either observation error only or process error only, an assumption made necessary by the insufficient quantitative information about the actual errors in the data. Looking at the proportion of ambiguous model selection due to a small difference between the two goodness-of-fit values (marked with a • in Table 8.4), we see that observation-error-fit was only half as much ambiguous as process-error-fit (in all analysed systems). It seems therefore that observation-error-fit is a more efficient tool than process-error-fit to select models (this difference was also noted by Harrison 1995). However, since the data contain both types of error, the most

reliable selection is possible if both types of fitting are used and if their selection results are not contradictory. Actually, model selection is less limited by the type of fitting than by the dynamic variation in relation to errors in the time-series. When there are strong dynamics over the whole length of the time-series (Gause's, Luckinbill's, Veilleux's, Flynn and Davidson's and Huffaker's data) then both types detect the same winning model and few ambiguous results due to small differences in goodness-of-fit are obtained. Only if there is little dynamic variation (one large initial oscillation as in Wilhelm's data) or if the dynamics are hidden behind strong observation errors as in lakes such ambiguous results become more frequent.

A number of technical problems with both types of fitting are worth discussing. The strongest limitation for observation-error-fit is that it works only for relatively short time-series because process error accumulates with time even in well controlled laboratory systems (Harrison, 1995). Process-error-fit is questionable with respect to the choice of s (time steps ahead prediction, see discussion in Ellner & Turchin 1995). Furthermore, when predicting s steps ahead, one implicitly also predicts $s - 1$, $s - 2$, \dots , 1 steps ahead, and there is currently no statistical solution as to how this information should be properly incorporated into the fitting process. For future research in this direction, we need more quantitative information about observation or process error in the time-series data. This would permit to select between models of different complexity (by using information criteria such as Akaike's information criterion, see Hilborn & Mangel 1997) and the use of regression techniques that account for both observation and process error (Reilly & Patino-Leal, 1981; Schnute & Richards, 1995; Ellner & Turchin, 1995). However, these methods are computationally very expensive especially for fitting continuous systems. Bootstrapping one single data set can take a full week of computing time on a couple of workstations (Peter Turchin, personal communication). For such reasons simpler regressions as done in this paper will remain a useful tool in ecology, especially since extensive simulations with artificial data (May, 1989) are often the only possibility to test whether the available data can answer the question at hand.

The main subject of this study, detecting predator dependence in the functional response, yields interesting and unexpected results. The most significant results are obtained with the protozoan data. Most systems are either closer to prey dependence or the samples are too small to detect reliably predator dependence. However, there is one predator-prey system with four time-series (Flynn & Davidson, 1993) that shows significant predator dependence. The predators in this system can show strong cannibalism at low prey-densities (pers. comm. with the authors). Although such cannibalism was not observed in the analysed data, this suggests that the predators are capable of strong interference when they encounter one another. Since these batch cultures were stirred only once every 12 h, it is possible that heterogeneities developed between stirrings. Both factors have been shown to lead to predator dependence. To our knowledge this is the first example of a protozoan system with monospecific prey and predator that exhibits so strong predator dependence that the ratio-dependent model fits better. This example demonstrates that the biology of the system must dictate the model being built, and that traits like potential cannibalism can indicate that a model with predator dependence is more appropriate.

Luckinbill and Veilleux obtained in their experiments several population cycles before

extinction by reducing the predator attack rate (thickening of the medium with methyl cellulose) and by reducing prey carrying capacity and growth rate [using poorer nutrition (half strength cerophyl mixture) for the prey in time-series 'luckin5']. Qualitatively, these parameter changes can stabilise both the prey-dependent and the ratio-dependent model. Only by a direct quantitative comparison of the data with the two models can we exclude predator dependence to be an important trait in these systems. The stable limit cycles obtained by Veilleux (1979) (with a refinement of Luckinbill's technique) differ qualitatively from both models, indicating that either a model with intermediate predator dependence or other mechanisms such as delayed effects are important. Harrison (1995) obtained drastically improved fits to Luckinbill's data upon incorporating these two traits (predator mutual interference and a delayed numerical response in the form of nutrient storage).

It appears that simple homogeneous and monospecific predator-prey systems are often better described by a prey-dependent model. Kaunzinger & Morin (1998) studied a three-level protozoan food chain (bacteria - *Colpidium striatum* - *Didinium nasutum*) and demonstrated that enrichment changes equilibria and system stability in a way that agrees better with prey-dependent theory (Rosenzweig, 1971; Oksanen et al., 1981). Bohannan & Lenski (1997) compared dynamics and equilibria of a bacteria-bacteriophage system (in a chemostat setup, with two different nutrient inflow concentrations) qualitatively with a complex prey-dependent model (dividing bacteria into susceptible and resistant strains) and with a simple aggregated ratio-dependent model (only one state variable to describe bacteria). They found that the qualitative results (destabilization with increasing nutrient inflow, both bacteria and bacteriophage equilibria increase with the higher nutrient inflow) were better predicted by the prey-dependent model. However, the comparison is statistically unsatisfactory, since the number of parameters were not taken into account (11 in the prey-dependent model and 7 in the ratio-dependent model).

There also seems to be no predator dependence in Huffaker's arthropod data. In most cases the prey-dependent model fits better, and in the two cases with process-error-fit where the ratio-dependent model fits better this fit is qualitatively wrong (stable equilibrium instead of a limit cycle, see Table 8.4). Two other aspects are important for the fits to these data: (1) quantitatively the models fit rather badly to the data, the experimental systems showing larger variation than can be reproduced by our simple models and (2) observation-error-fit gives with both models qualitatively correct fits (see Figure 8.3). The first point might be explained by Huffaker's experimental setup, food for prey being dispersed in a 2- or 3-dimensional structure and the prey colonising this food in a fairly heterogeneous manner. Such a laboratory system is structurally more complex than the protozoan batch cultures of the previous paragraph. The second point indicates that the used models can nevertheless be used for qualitative analysis; only quantitative conclusions should be interpreted with care.

The fits to phyto- and zooplankton data are the most difficult to interpret. The easiest conclusion would be that either the data are too noisy for this kind of model identification or that both models are too simple for lake dynamics. The first interpretation is supported by the qualitative nature of the process-error-fits (mostly stable or strongly stable systems) that might mean that the best prediction is not obtained by dynamic nonlinear modelling but rather by simply using some mean abundance of prey and predator. Despite these

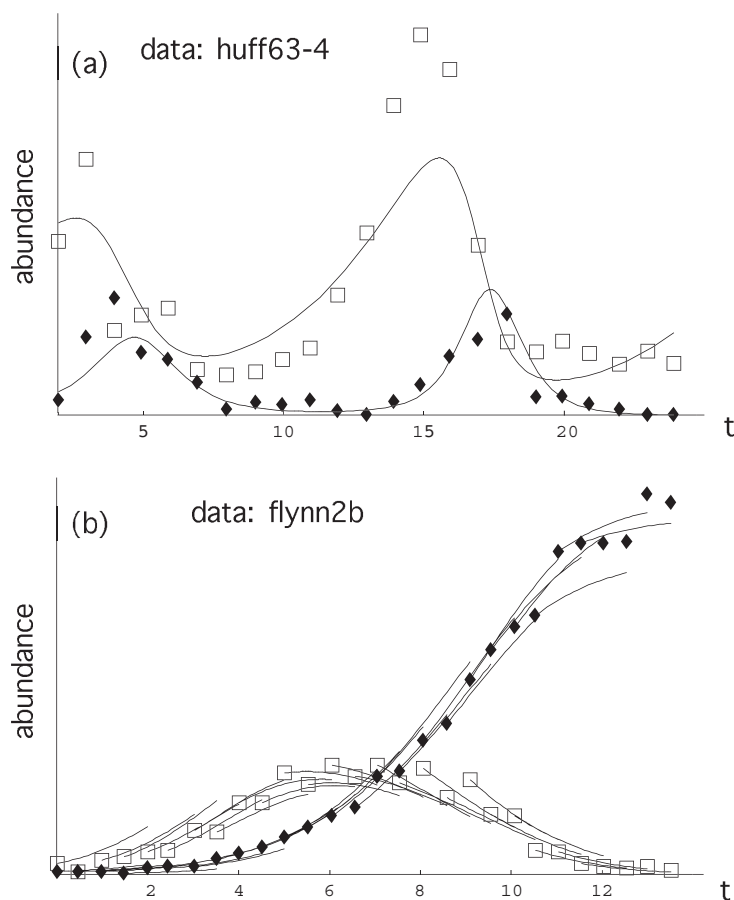


Figure 8.3: Two examples illustrating (a) observation-error-fit with a prey-dependent model to Huffaker's data and (b) process-error-fit ($s = 4$) with a ratio-dependent model to Flynn and Davidson's data.

reservations, many significant model identifications were obtained with observation-error-fit, showing that long term dynamic patterns are present. These significant fits are of both types (prey-dependent and ratio-dependent) with tendencies for some lakes: Tuesday lake being mostly prey-dependent, the system with edible phytoplankton in Lake Geneva rather ratio-dependent and the system with inedible algae more prey-dependent. However, these tendencies are not sufficiently clear to give recommendations as to which model might be more appropriate. Brett & Goldman (1997) argued that phytoplankton displays strong bottom-up influence while zooplankton is more sensitive to top-down control. The phytoplankton-zooplankton interaction itself (that is studied in this paper) is subject to both forces, which might also explain the ambiguity in model identification.

We can conclude that these heterogeneous systems with multispecies prey and predator levels show both types of functional responses or intermediate types. Or, in the words of Yodzis (1994) who studied relations between predator dependence in the functional response and fisheries management, "it remains frustratingly difficult to say just which functional form is the appropriate one for a given population". As a consequence, we should base population management decisions on the predictions of several competing models, building up confidence in each model by constant comparison of its predictions

with actual observations. Decision making then results from the predictions of all these models and on the current confidence level in them (similarly to weather forecast). For lake management in particular, other models could use sigmoid functional responses since alternative prey exist [the ‘inedible’ algae can be consumed to some extent (Davidowicz et al., 1988; Gliwicz, 1990; Bernardi & Giussani, 1990)]. Simple linear forms of the functional response are another reasonable choice in the context of process-error-fit and short term prediction (Carpenter et al., 1994). A very good example of this multi-model approach is given by Sherratt et al. (1997), who analyse four completely different models (reaction-diffusion equations, coupled map lattices, deterministic cellular automata and integrodifference equations) to study invasion patterns in space. Since a common feature emerges from all models, it can be regarded as a highly likely real feature. Working with at least two models can help identify model artifacts and direct further research.

With respect to detection of predator dependence, one might also suggest to consider an intermediate model that can be predator-dependent or predator-independent depending on the value of a specific parameter (as done in Arditi & Akçakaya (1990) for functional response data) and then directly estimate this parameter. However, looking at the uncertainty of the estimated parameters in this study makes it unlikely to obtain more information about predator dependence by this intermediate approach. Bayesian approaches to estimate posterior distribution functions of this parameter were also proposed (Stow et al., 1995), but they require sophisticated multidimensional integration techniques and little is known about the robustness of these methods when confronted with ecological data of the type used here.

One basic support for the Holling type II function comes from an analogy with the Michaelis-Menten enzyme kinetics and Monod’s work on bacterial growth (Monod, 1942). Monod’s function of microbial growth is structurally equivalent to the Holling type II function and it has been used with enormous success during the last 60 years. However, other functions have been discussed in microbiology and, most interestingly for this study, Contois published already in 1959 a growth function for microorganisms that is equivalent to the particular ratio-dependent model used in this study. Many authors have used Contois’ function without comparison to Monod’s function and they obtained good fits to their data (mostly sewage and fermentation processes) (Bala & Satter, 1990; Tijero et al., 1989; Lequerica et al., 1984; Pareilleux & Chaubet, 1980; Ghaly & Echiegu, 1993). Table 8.3 lists studies that compared several functions to data according to a single selection criterion. While Contois’ function often fitted better than Monod’s function, model selection was also often ambiguous (as in the present work). Many of these results deal with systems in which the prey or the predator are sets of many species. While monospecific systems seem to be better approximated by Monod’s model (Grady Jr. et al., 1972), just as we saw in our analysis with Gause’s, Huffaker’s and Luckinbill’s data, multispecies systems as cited above and in Table 8.3 seem to favour predator-dependent models (Grady Jr. & Williams, 1975; Elmaleh & Ben Aim, 1976; Daigger & Grady Jr., 1977).

To summarise, systems with monospecific prey and predator show, in general, little predator dependence in the functional response except in cases where predators have a strong potential to interfere with each other (e.g., cannibalism). More complex systems such as plankton in freshwater lakes show a multitude of patterns. We found no indicators

Table 8.3: Collection of studies that compared Contois' function quantitatively with other functions. The models tested are noted in the third column with the best fitting model, if there was one, in capitals. References are: (1) Chiu et al. (1972), (2) Ashby (1976), (3) Morrison et al. (1987), (4) Dercová et al. (1989), (5) Wilhelm (1993).

ref.	system	tested functions
(1)	microbial sewage	Moser, Monod, Contois
(2)	protozoa feeding on bacteria	Contois, ASHBY (Monod's function divided by predator density)
(3)	nutrient limited phytoplankton growth	Monod, CONTOIS, LOGISTIC
(4)	growth and glucose consumption of yeast	CONTOIS, Monod
(5)	protozoa feeding on bacteria	Contois, Monod and 9 others *

*best fits were obtained with functions that are sigmoid with respect to substrate concentration, either Contois or Monod type

in these systems that tell whether predator dependence in the functional response should be included or not. We conclude that whenever predictions must be done by model simulation, at least two different models should be used to distinguish robust features from model-dependent features. Parameters of such models should be estimated as well as possible by direct measurements in the field, with nonlinear regression being used only for fine-tuning. The fitting itself should account for stochasticities in the observed data, but the techniques used in this study (observation-error-fit and process-error-fit) leave much room for further improvement.

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Table 8.4: Results for fitting time-series data. The data sets are described by their length m and their apparent dynamic behaviour (in parenthesis if difficult to decide): st for stable non trivial equilibrium, ss for strongly stable equilibrium, l for limit cycle, e for extinction of both populations, pe for extinction of the predator only and t for transient trajectory. For each type of fitting (process-error-fit or observation-error-fit) the better fitting model is indicated (p for prey-dependent and r for ratio-dependent) with criteria X^2 , X^L (both with the dynamic behaviour of the selected model with the fitted parameters), expectation E_{X^2} and improved estimate of prediction error (IE). s is the prediction horizon in process-error-fit. Significance of model selection is indicated by a \dagger or by a \ddagger ; \bullet indicates non-significance due to a low difference between the fits to each model; the absence of a superscript indicates non significance due to a low likelihood (see the text for the employed definition of significance).

data characteristics			process-error-fit					observation-error-fit			
name	m	dyn.	s	X_ν^2	X_ν^L	E_{X^2}	IE	X_ω^2	X_ω^L	E_{X^2}	IE
gause1	18	st	2	r st	p \dagger st	r \bullet	p \bullet	p \dagger st	p \dagger st	p \dagger	p \dagger
gause3	18	l	2	p \dagger st	p \dagger l	p \dagger	p \dagger	p \dagger l	p \dagger l	p \dagger	p \dagger
gause4	19	l	2	p \dagger st	p \dagger st	p \dagger	p \dagger	p \dagger l	p \dagger l	p \dagger	p \dagger
gauset2a	10	e	1	p l	p \bullet l	p	p	p l	p \dagger l	p \dagger	p \dagger
gauset2c	10	e	1	p l	p \dagger st	r	r	p \dagger l	p \dagger l	p \dagger	p \dagger
gauset2d	10	e	1	p l	p \dagger l	p	p	p l	p \dagger l	p \dagger	p
gauset2e	9	e	1	p l	p l	p	r	p l	p l	r \bullet	p
gauset2f	9	e	1	r e	r \dagger st, e	r \bullet	r \bullet	r \dagger e	r \bullet e	r \bullet	r \dagger
luckin1a	35	l	3	p st	p \dagger st	p	p	p l	p \dagger l	p \dagger	p \dagger
luckin1b	24	l	3	p st	p \dagger st	p \dagger	p \dagger	p \dagger l	p \dagger l	p \dagger	p \dagger
luckin3a	16	l	3	r \dagger st	p \dagger st	p \dagger	p \dagger	p \dagger l	p \dagger l	p \dagger	p \dagger
luckin4a	27	l	3	p st	p \dagger st	p \dagger	p \dagger	p l	p \dagger l	p \dagger	p \dagger
luckin4b	21	l	3	p l	p \dagger l	p \dagger	p \dagger	p \dagger l	p \dagger l	p \dagger	p \dagger
luckin5	62	l	3	p st	p \dagger st	p	p	p \dagger l	p \dagger l	p \dagger	p \dagger
veill8	87	l	3	p \dagger st	p \dagger st	p \dagger	p \dagger	r \dagger l	r \bullet l	r \dagger	r \dagger
veill10	20	l	3	p l	p \dagger st	p \dagger	p \dagger	p \dagger l	p \dagger l	p \dagger	p \dagger
flynn1b	14	t	4	r \ddagger t	r \dagger t	r \ddagger	r \ddagger	r \dagger t	r \dagger t	r \dagger	r \dagger
flynn1c	21	st, e	4	r \dagger e	r \dagger e	r \dagger	r \dagger	r \dagger e	r \dagger e	r \ddagger	r \ddagger
flynn2b	28	st, e	4	r \dagger e	r \dagger e	r \dagger	r \dagger	r \dagger e	r \dagger e	r \dagger	r \dagger
flynn2c	28	st, e	4	r \dagger e	r \dagger e	r \dagger	r \dagger	r \dagger e	r \dagger e	r \dagger	r \dagger
wilh4.2	16	st, e	4	r st	r \dagger e	r	p	p st	p \dagger ss	p \dagger	p \dagger
wilh4.4	17	st, e	3	r \dagger ss	r \bullet ss	r \bullet	r \dagger	r \dagger st	r \bullet st	r \bullet	r \bullet
wilh5.27	17	e	4	p st	r \bullet ss	r	p	p st	r \dagger e	p	p
wilh5.28	22	st, e	5	r \bullet e	r \bullet e	r \bullet	r \bullet	p \dagger pe	p \dagger t	p \dagger	p \dagger
wilh5.29	19	st	3	p \dagger ss	r \dagger ss	p \dagger	p \dagger	r \bullet st	p \dagger ss	p \bullet	p \bullet
wilh5.30	18	st, e	4	p \bullet pe	r \bullet ss	r \bullet	p \bullet	p \dagger t	p \dagger t	p \dagger	p \dagger

huff11	12	e, l	3	$r\ st$	$r\ st$	r	p	$r\ st$	$r\ st$	r	r
huff12	13	e	3	$p\ l$	$r\ e$	p	p	$p\ l$	$p^\dagger l$	p	p
huff13	10	e	2	$p\ l$	$p^\dagger l$	p	p	$p^\dagger l$	$p^\dagger l$	p^\dagger	p^\dagger
huff14	10	e	2	$p\ l$	$p^\dagger l$	p^\dagger	p^\dagger	$p^\dagger l$	$p^\dagger l$	p^\dagger	p^\dagger
huff15	11	e, l	3	$r\ st$	$p\ l$	r	p	$r\ st$	$p^\dagger l$	r	r
huff16	11	e, l	3	$p\ l$	$p\ l$	p	p	$p^\dagger l$	$p^\dagger l$	p^\dagger	p^\dagger
huff17	12	e	3	$r\ st, e$	$r^\dagger st$	r	p	$p\ l$	$p^\dagger l$	p	p
huff18	35	l	4	$r\ st$	$r\ st$	r	r	$p\ l$	$p\ l$	p	p
huff63-3	58	l	4	$p\ st$	$p^\bullet st$	p	p	$p\ st$	$p^\dagger st$	p	p
huff63-4	23	l	3	$p\ l$	$r^\dagger st$	r	p	$p^\dagger l$	$p^\dagger l$	p^\dagger	p^\dagger
paul84	13	(st)	2	$r^\bullet ss$	$r^\bullet ss$	r^\bullet	r^\bullet	$p^\bullet st$	$r^\dagger t$	r^\dagger	p^\bullet
paul85	17	st	2	$p\ st$	$p^\dagger ss$	p	p	$p\ ss$	$p^\dagger st$	p	p
paul86	14	(st)	2	$p^\bullet st$	$p^\bullet st$	p^\dagger	p^\dagger	$p^\bullet st$	$r^\dagger t$	p^\bullet	r^\dagger
paul87	15	(st)	2	$p\ st$	$p^\bullet st$	r	p	$p^\dagger st$	$p^\dagger st$	p^\dagger	p^\dagger
paul88	15	(l)	2	$r^\bullet ss$	$r^\bullet ss$	r^\bullet	r^\bullet	$r^\dagger t$	$p^\dagger st$	r^\bullet	r^\dagger
paul89	13	l	2	$p\ ss$	$r^\dagger st$	p	p	$= st$	$p^\dagger l$	$=$	$=$
paul90	16	(l)	2	$p\ st$	$r^\dagger ss$	p	r	$r\ st$	$r^\bullet st$	r	r
tues84	11	st	2	$p\ ss$	$r^\bullet ss$	p^\bullet	r^\bullet	$p^\dagger st$	$r^\bullet t$	p^\dagger	p^\dagger
tues85	13	st	2	$r\ e$	$r^\bullet e$	p	p	$p\ l$	$p^\dagger t$	p^\dagger	p^\dagger
tues86	14	(l)	2	$r^\dagger st$	$r^\bullet st$	p^\dagger	p^\dagger	$p^\dagger l$	$r^\bullet t$	p^\dagger	p^\dagger
tues87	15	(l)	2	$p\ st$	$p^\bullet pe$	p	p	$p^\dagger l$	$r^\bullet t$	p^\dagger	p^\bullet
tues88	13	(l)	2	$p^\dagger st$	$p^\dagger st$	p^\dagger	p^\dagger	$p^\dagger st$	$p^\dagger st$	p^\dagger	p^\dagger
tues89	11	st	2	$p^\bullet st$	$p^\bullet st$	r^\bullet	p^\dagger	$p^\dagger st$	$r^\dagger st$	p^\bullet	p^\bullet
tues90	19	(st)	2	$p\ ss$	$r^\bullet ss$	r^\bullet	r^\dagger	$p^\dagger l$	$p^\dagger t$	p^\dagger	p^\dagger
edPhy86	14	(l)	2	$r\ ss$	$p^\bullet ss$	r	p	$p\ st$	$r^\dagger ss$	p	p
edPhy87	13	(st)	2	$p\ st$	$p^\dagger st$	p^\dagger	p^\dagger	$p^\dagger st$	$p^\bullet st$	p^\dagger	p^\bullet
edPhy88	13	(st)	2	$p\ st$	$p^\bullet l$	p^\dagger	p^\dagger	$p^\dagger st$	$p^\dagger t$	p^\dagger	p^\dagger
edPhy89	13	(l)	2	$p\ ss$	$r^\bullet st$	p^\dagger	r^\bullet	$r^\bullet st$	$r^\dagger t$	r^\bullet	r^\bullet
edPhy90	14	(st)	2	$r^\bullet ss$	$r^\bullet ss$	r^\bullet	r^\bullet	$r^\dagger st$	$r^\dagger st$	r^\dagger	r^\dagger
edPhy91	12	(st)	2	$r\ ss$	$p^\bullet ss$	r^\bullet	r^\bullet	$r^\dagger st$	$r^\dagger st$	r^\dagger	r^\dagger
edPhy92	11	st	2	$p\ ss$	$p^\dagger ss$	p	r	$r\ st$	$r^\dagger st$	r^\dagger	p^\bullet
edPhy93	12	st	3	$r\ st, e$	$r^\dagger e$	r^\dagger	r^\dagger	$r^\dagger t$	$r^\dagger t$	r^\dagger	r^\dagger
totPhy86	14	(st)	3	$p\ t$	$r^\dagger ss$	p	r	$r\ t$	$r^\dagger t$	r	r
totPhy87	13	(st)	2	$p\ ss$	$p^\dagger ss$	p^\bullet	p^\dagger	$p\ st$	$p^\bullet t$	p^\dagger	r^\bullet
totPhy88	15	(l)	2	$p\ ss$	$r^\bullet ss$	p	r	$p\ st$	$p^\dagger st$	p	p
totPhy89	14	(l)	2	$p\ st$	$r^\bullet ss$	p^\bullet	r^\bullet	$p^\dagger st$	$p^\dagger st$	p^\dagger	p^\dagger
totPhy90	14	st	2	$p^\dagger st$	$r^\bullet ss$	p^\dagger	p^\dagger	$p^\dagger st$	$p^\dagger st$	p^\dagger	p^\dagger
totPhy91	16	(l)	2	$p\ ss$	$p^\bullet ss$	p^\bullet	r^\bullet	$p^\dagger st$	$r^\bullet st$	p^\bullet	p^\dagger
totPhy92	16	(l)	2	$r^\dagger ss$	$r^\bullet ss$	r^\dagger	r^\dagger	$p^\bullet t$	$p^\bullet l$	r^\dagger	p^\dagger
totPhy93	16	(l)	2	$r^\dagger ss$	$r^\dagger ss$	r^\dagger	r	$p^\dagger l$	$p^\bullet l$	p^\dagger	p^\bullet

Appendix

8.A Residual bootstrapping and *IEPE*

We use the same notation as introduced in the section ‘Error functions’. The algorithm described below is of the type residual bootstrapping (Efron & Tibshirani, 1993). This approach assumes that the used model is correct and the parameters obtained by minimising equation X_k^2 are used to construct the bootstrap time-series.

Fitting the whole trajectory (with initial condition as a free parameter or nuisance parameter) is related to simple non-linear curve fitting and the following algorithm is taken from Efron & Tibshirani (1993). For process-error-fit the same algorithm can be used with slight modifications that are indicated. Let $\hat{\theta}$ be the best fitting solution to the original data, obtained by minimising equation X_k^2 , with the residuals

$$\hat{\epsilon}_i = \log(Y_i) - \log\left(y(t_i), \hat{\theta}\right), \quad 1 + s \leq i \leq m$$

and total error \hat{e} ($s = 0$ for observation-error-fit). These residuals represent the empirical distribution function of the residuals. Now the bootstrap estimates are created by the following algorithm:

1. (for process-error-fit only) Fix initial values $y_i^* = Y_i$, $1 \leq i \leq s$.
2. Calculate the bootstrap data $(y_i^*)_{1+s \leq i \leq m}$ by

$$\log(y_i^*) = \log(y(t_i), \hat{\theta}) + \epsilon_i^* \quad 1 \leq i \leq m$$

where the ϵ_i^* are a random sample with replacement from the $(\hat{\epsilon}_k)_{1+s \leq k \leq m}$ (for predator-prey data, all residuals are thrown in the same pool). For process-error-fit $s \geq 1$ and the bootstrap data are calculated recursively.

3. Estimate $\hat{\theta}^*$ from the bootstrap data by minimising equation X_k^2 , with final error e^* .
4. Go to second item and repeat the loop B times ($B = 50$).

Efron & Tibshirani (1993) suggest that $B = 50 - 200$ is in general sufficient for a reliable bootstrap estimate. Since regression of a differential equation to data is already quite costly we used the lower value ($B = 50$), thus allowing to bootstrap on average 1-4 time-series per day. Mean and standard deviation of the error are now calculated in the usual way from the B estimates e^* .

The method of the improved estimate of prediction error (*IEPE*) is described in Efron & Tibshirani (1993) (chapter 17). Let $e_{\hat{\theta}^*}$ be the error with the original data obtained

using the fitted bootstrap parameters $\hat{\theta}^*$. The difference $e_{\hat{\theta}^*} - e^*$ is in general positive and called the ‘optimism’. The improved estimate of prediction error is now calculated by

$$IEPE = \frac{1}{m - s} \left[\hat{e} + \frac{1}{B} \sum_{i=1}^B (e_{\hat{\theta}^*, i} - e_i^*) \right]$$

($s = 0$ in case of observation-error-fit) and its standard deviation is taken to be the standard deviation of the optimism’s scaled by the number of predicted data points. This estimation of prediction error is independent of the estimated residual variance and the number of parameters fitted, so it is less model dependent than alternatives such as C_p and BIC statistics (Efron & Tibshirani, 1993).

Appendix A

Collection of predator-prey models

Following the two principles ‘conservation of mass’ and ‘decomposition of any growth process into birth and death processes’ leads to the general equations for a predator-prey model:

$$\begin{aligned}\frac{dx}{dt} &= F(x) - g(x, y)y \\ \frac{dy}{dt} &= h((g(x, y)))y - \mu(y)y\end{aligned}$$

where $F(x)$ is the prey growth function, $g(x, y)$ the functional response, $h(\dots)$ the numerical response (predators produced in terms of numbers or biomass as a function of the consumption) and $\mu(y)$ is a predator mortality rate. The terms functional and numerical response were introduced by Solomon (1949).

Predator-prey models that do not follow the ‘conservation of mass’ principle are not considered in this collection. Popular predator-prey models of this type go back to an initial idea of Leslie & Gower (1960) who studied the model

$$\begin{aligned}\frac{dx}{dt} &= r\left(1 - \frac{x}{K}\right)x - axy \\ \frac{dy}{dt} &= cy\left(1 - d\frac{y}{x}\right).\end{aligned}$$

The obvious modification of replacing the Lotka-Volterra predation term axy by a bounded Holling type II functional response $ax/(1 + ahx)$ has been proposed, analysed and published by both Tanner (1975) and May (1975).

Whenever power laws are used (e.g., x^m), dimensional problems can occur. They could in principle be remedied by inserting a ‘dummy’ parameter u that is of the same dimension as the used state variable (e.g., replace x^m by $\left(\frac{x}{u_x}\right)^m u_x$), but this more complicated notation is never used in practice (see also section 1.2).

A.1 The prey growth function

Often $F(x)$ is decomposed into $F(x) = xf(x)$ where f is called intrinsic growth rate or per capita growth rate. Following these scheme three types of growth may be identified:

- constant $f(x)$ (exponential or Malthusian growth) or linear decrease of $f(x)$ with increasing x (logistic growth),
- maximal intrinsic growth rate at intermediate density (Allee effect),
- nonlinear hyperbolic decrease of the intrinsic growth rate (Gompertz Law, a popular model in clinical oncology).

Possible mathematical forms of these growth functions (and others) are listed in table A.1.

A.2 The functional response

The functional response (prey eaten per predator per unit of time) has found different functional expressions in the literature. Tables A.2 and A.3 list a little collection of the different types with their origin.

Table A.1: Simple growth functions found in the literature

source	$F(x)$	remarks
Malthus (1798)	rx	exponential or Malthusian growth, considered like a 'growth-law'
Verhulst (1838)	$r(1 - \frac{x}{K})x$	logistic growth equation
Goel et al. (1971), Gilpin et al. (1976), Richards (1959)	$r(1 - (\frac{x}{K})^\theta)x$	theta logistic growth
Rosenzweig (1971)	$r((\frac{K}{x})^g - 1)x$	$1 \geq g > 0$
Smith (1963)	$r \frac{K-x}{K+\epsilon x} x$	
von Bertalanffy (1951)	$px^m - qx$	often $m = 2/3$ is used by an allometric relationship with the organisms weight
Szathmáry (1991), Eigen & Schuster (1979)	kx^2	hyperbolic growth for sexual reproduction, the population reaches infinity in finite time (solution $x(t) = (\frac{1}{x(0)} - kt)^{-1}$)
Szathmáry (1991), Zielinski & Orgel (1987)	$\alpha + k\sqrt{x}$	subexponential growth (found in enzyme-free replication)
Allee (1931), Edelstein-Keshet (1988)	$(r - a(x - b)^2)x$	the condition $b < \sqrt{r/a}$ must be fulfilled
Volterra (1938)	$(kx - d - \delta x^2)x$	incorporating the Allee effect in sexually reproducing organisms
Allee (1931), Bazykin (1985)	$r(1 - \frac{x}{K})x(\frac{x}{\epsilon} - 1)\frac{K}{K-\epsilon}$	inverse density dependence at low densities
Philip (1957), Sza- thmáry (1991)	$(k(x) - d(x))x - kxe^{-\beta x}$	$1 - e^{-\beta x}$ is the probability of a female being fertilized and corresponds to Volterra's $kx - \delta x^2$, $(k(x) - d(x))$ corresponds to Verhulst's $r(1 - x/K)$.
Gompertz (1825)	$-\alpha x \ln(x)$	equivalent to $\lambda e^{-xt}x$
Gompertz (1825)	$r \ln(\frac{K}{x})x$	
Gutierrez (1992)	$(a(1 - e^{-\frac{b}{x}}) - c)x$	
Schoener (1978)	$(\frac{I_E}{Y+x} - m)x$	mechanistic derivation, m is outwash, equivalent to Smith (1963) and to Getz (1984)

Table A.2: Functional responses that depend on the prey density (x) only

source	$g(x)$	remarks
Lotka-Volterra (Nicholson (1933) in discrete form)	ax	linear functional response without saturation
Maynard Smith (1975) (Thompson (1924) in discrete form)	b	constant response, destabilising
Gause (1934)	$c\sqrt{x}$	less efficient predator than Lotka-Volterra
Rosenzweig (1971)	cx^l ($0 < l \leq 1$)	approx. type II, but without saturation
Holling (1959a)	$\frac{ax}{1+ahx}$	type II (disc equation), equivalent to the Monod type function
Ivlev (1961)	$b(1 - e^{-\frac{a}{b}x})$	type II
Watt (1959)	$b(1 - e^{-cx^2})$	type III, may be generalised by replacing 2 by n
Real (1977)	$\frac{bx^n}{c+x^n}$	type III for $n > 1$. Studied with $n = 2$ by Takahashi (1964)
Jost et al. (1973)	$\frac{bcx^2}{b+dx+cx^2}$	multiple saturation model, type III, also proposed by Hassell et al. (1977)
Arditi (1980)	$\frac{ba(x+cx^2)}{b+a(x+cx^2)}$	type III, slope at the origin not 0
Andrews (1968)	$\frac{bx}{c+x+dx^2}$	Monod-Haldane equation, growth inhibition at high densities
Tostowaryk (1972)	$\frac{adx}{d+a(x+cx^3)}$	type II at low densities, decline at high densities
Sokol & Howell (1981)	$\frac{ax}{1+bx^2}$	<i>Daphnia</i> feeding on ('inedible') filamentous algae, simplified Monod-Haldane equation

Table A.3: Functional response models that depend on prey (x) and predator (y) density

source	$g(x, y)$	remarks
Hassell & Varley (1969)	pxy^{-m}	modification of Lotka-Volterra or Nicholson
Gomatam (1974)	$px \frac{\log y}{y}$	no saturation, inspired by Gompertz (1825)
Strebel & Goel (1973)	$cx^l y^{-m}$	modification of Rosenzweig (1971), no saturation
Hassell & Rogers (1972)	$\frac{pbxy^{-m}}{b+px}$	combination of Hassell & Varley (1969) with disc equation, affects saturation level
Rogers & Hassell (1974)	$g_1(x) \frac{y_s}{y}$	$g_1(x)$ is any function from Table A.2. Affects saturation level. y_s is the solution of $my_s^2 + (1-m)y_s - y = 0$.
Crowley & Martin (1989)	$\frac{ax}{1+ahx} \frac{1}{1+\beta y}$	derived from the behavioral ‘pre-emption’ model
Harrison (1995)	$g_1(x) \frac{1}{1+\beta y}$	$g_1(x)$ is any function from Table A.2.
Beddington (1975)	$\frac{px}{1+ahx+m(y-1)}$	generalisation of the disc equation
DeAngelis et al. (1975)	$\frac{px}{1+cx+my}$	equivalent to the preceding for $y \gg 1$.
Arditi & Akçakaya (1990), (Sutherland, 1983)	$\frac{\alpha x y^{-m}}{1+\alpha h x y^{-m}}$	combines completely Hassell & Varley (1969) with Hollings disc equation
Arditi & Michal-ski (1995), Contois (1959)	$\frac{\alpha x}{y+\alpha h x}$	type II like ratio-dependent, equivalent to preceding model for $m = 1$.
Watt (1959)	$b \left(1 - e^{-\frac{p}{b} x y^{-m}} \right)$	modification of Ivlev (1961)
Watt (1959)	$b \left(1 - e^{-c x^2 y^{-m}} \right)$	type III
Arditi et al. (1978)	$\begin{cases} p \frac{x}{y} & \text{if } xp < ya \\ a & \text{if } xp > ya \end{cases}$	type I ratio-dependent form with saturation
Aiba et al. (1968)	$\alpha \frac{x}{K_s+x} e^{-ky}$	
Fukaya et al. (1996)	$\frac{\alpha x^m}{y+\alpha h x^m}$	used in fermentation processes

A.3 The numerical response

The numerical response is usually considered to be proportional to the functional response, $h(g(x, y)) = eg(x, y)$, with ecological efficiency e and any $g(x, y)$ from Tables A.2 or A.3. Other forms are possible but rarely used in the literature (e.g., Arditi et al. (1978), a ratio-dependent model with a ‘hunger phase’ at low ratios x/y).

A.4 Predator mortality

Formulations of the predator mortality are summarized in table A.4. See Edwards & Brindley (1996) for a discussion and references to these forms.

Table A.4: Predator mortality functions

source	$\mu(y)$	remarks
	μ	constant mortality rate, used since the Lotka-Volterra predator prey model
Steele & Henderson (1981)	μy	results in a slanted predator isocline (no paradox of enrichment), justified with increased predation by higher predators
Steele & Henderson (1992)	$\frac{\mu y}{b+y}$	more realistic response to increased higher predation
DeAngelis et al. (1975), Bazykins model	$s + \mu y$	

Appendix B

Data from Lake Geneva

These are the detailed time-series from Lake Geneva that were used in chapter 8. The data have been provided by J. P. Pelletier and G. Balvay from the hydrological station at Thonon, INRA. The temperature and phosphorous data were not directly used in the fitting but are added here for completeness.

Observed state variables and their units are the following:

State variable	abbreviation	unit
Nano phytoplankton	NanP	mg/m^3 fresh weight
Total phytoplankton	TotP	mg/m^3 fresh weight
Herbivorous zooplankton	HerbZ	mg/m^3 fresh weight
Temperature at 5m water depth	T5	$^{\circ}C$
Dissolved Phosphorous PO ₄ at 5m water depth	PO4	$\mu g/l$

Plankton dynamics year 1986

Date	NanP	TotP	HerbZ	T5	PO4
21-Jan-86	131.6	380.6	334	5.9	50
18-Feb-86	89.7	415.4	146	5.2	61
3-Mar-86	28.7	180.7	176	5	64
17-Mar-86	361.8	444.5	316	5.3	59
8-Apr-86	438.1	494.1	370	5.6	58
21-Apr-86	521.1	556.6	458	5.8	59
5-May-86	1053.0	1063.8	1122	7.9	46
20-May-86	661.4	675.5	2568	9.6	3
2-Jun-86	101.0	139.1	4906	13.8	13
16-Jun-86	50.1	62.8	798	12.8	32
7-Jul-86	805.9	825.1	6518	16.9	10
21-Jul-86			980	16	8
4-Aug-86	1522.3	3046.4	1746	20	2
18-Aug-86	762.8	1887.9	1184	20.1	3
8-Sep-86	1712.0	2225.0	1076	17.9	4
23-Sep-86	2015.6	2129.6	2740	17.3	2
6-Oct-86	621.6	685.7	2044	14.5	4
6-Nov-86	239.0	346.7	614	11.4	15
17-Nov-86	317.3	497.4	190	10.7	10
8-Dec-86	225.1	329.3	476	9	22

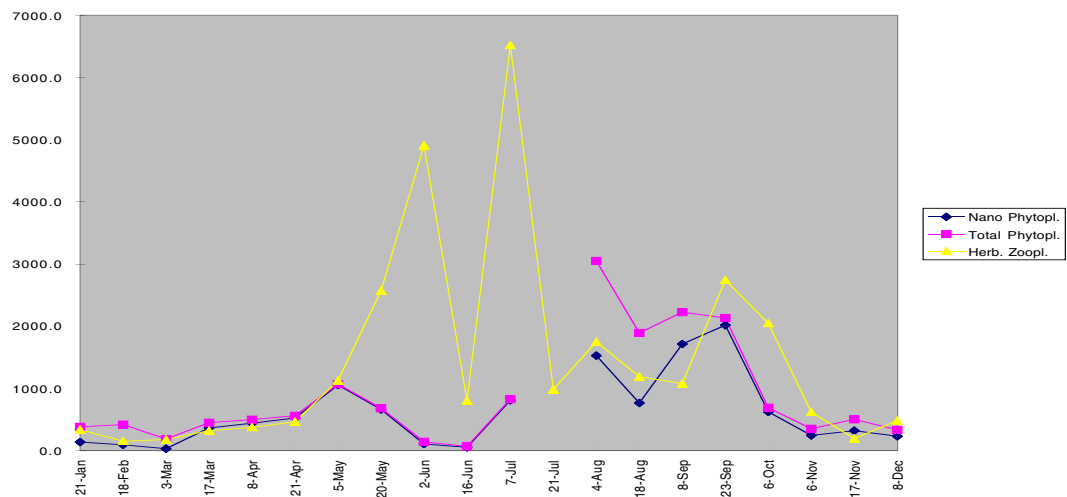


Figure B.1: Plankton dynamics year 1986

Plankton dynamics year 1987

Date	NanP	TotP	HerbZ	T5	PO4
26-Jan-87	184.7	257.6	170	5.4	50
9-Feb-87	157.1	217.5	96	5.1	56
2-Mar-87	101.5	132.1	388	5.4	52
17-Mar-87	123.0	299.9	244	5.2	54
6-Apr-87	581.6	934.6	196	5.4	52
21-Apr-87	2264.6	3289.8	324	8.2	35
11-May-87	2359.6	3281.5	264	8.8	34
18-May-87	3547.1	4185.1	538	9.8	12
2-Jun-87	948.8	991.7	340	11.1	4
22-Jun-87	129.1	236.2	2548	14	20
6-Jul-87	861.1	2288.8	406	13.1	6
22-Jul-87	337.5	2014.0	1276	16.7	9
3-Aug-87	620.2	7568.7	666	19.1	8
18-Aug-87	503.0	2125.5	498	16.3	3
7-Sep-87	851.4	1626.4	2242	19.9	3
22-Sep-87	846.1	1191.5	2172	20.5	5
5-Oct-87	542.7	846.2	182	15	2
20-Oct-87	633.2	849.3	992	13.2	2
2-Nov-87	588.0	692.3	288	12.9	1
16-Nov-87	248.8	310.2	336	11.2	8
7-Dec-87	191.1	256.6	208	9	18

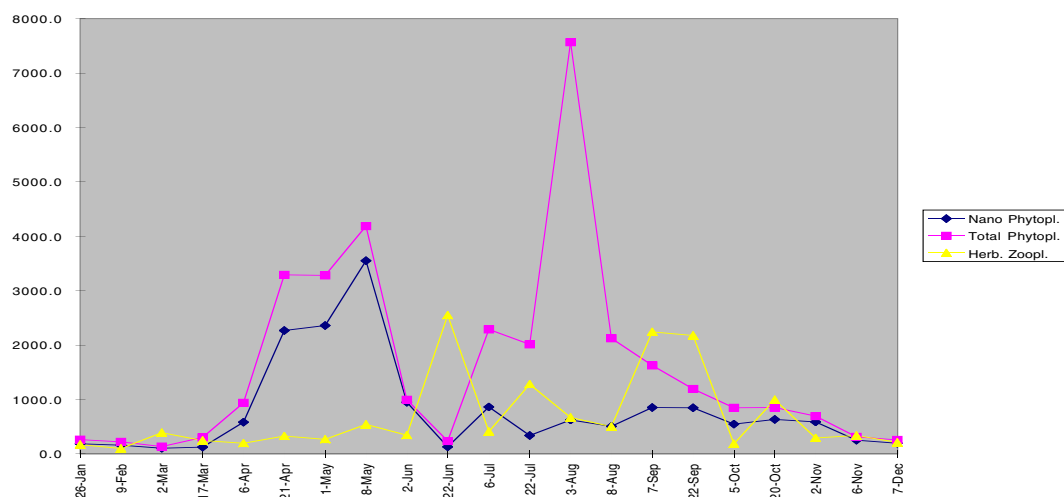


Figure B.2: Plankton dynamics year 1987

Plankton dynamics year 1988

Date	NanP	TotP	HerbZ	T5	PO4
11-Jan-88	142.4	300.2	92	7.2	34
15-Feb-88	322.5	495.2	214	6.2	42
14-Mar-88	171.9	291.0	152	5.6	44
29-Mar-88	50.4	149.9	110	6.1	46
11-Apr-88	676.6	3087.9	120	7.3	20
25-Apr-88	1350.5	2993.4	310	9.6	18
9-May-88	1636.7	1757.6	476	12.8	5
24-May-88	109.1	160.6	1106	13.1	3
8-Jun-88	56.3	83.2	1528	14.3	4
20-Jun-88	327.7	814.1	774	17.6	2
5-Jul-88	241.0	562.0	1146	18.5	3
19-Jul-88	311.6	3529.5	534	20.4	3
3-Aug-88	849.5	1909.4	170	21.6	3
16-Aug-88	395.1	2187.7	262	16.2	1
5-Sep-88	224.1	3716.2	274	18.8	2
20-Sep-88	185.4	2997.8	584	16.2	4
4-Oct-88	227.1	2608.5	74	15	2
17-Oct-88	229.5	1696.7	210	14.6	4
9-Nov-88	128.2	433.4	154	11.3	11
28-Nov-88	208.4	619.2	244	8.8	22
12-Dec-88	198.7	332.8	284	7.8	26

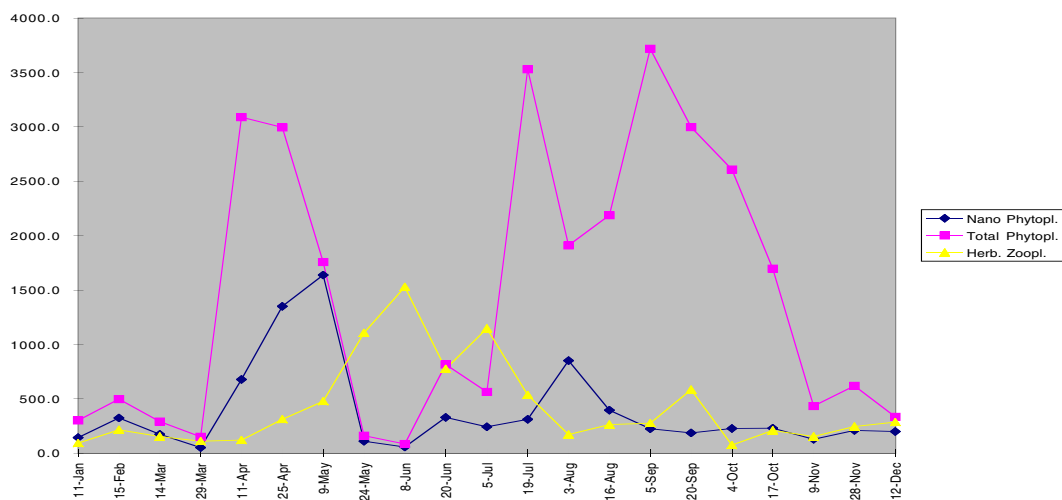


Figure B.3: Plankton dynamics year 1988

Plankton dynamics year 1989

Date	NanP	TotP	HerbZ	T5	PO4
16-Jan-89	34.1	150.7	76	6.7	32
13-Feb-89	26.4	94.9	104	6.1	42
6-Mar-89	46.6	297.3	266	6.4	36
20-Mar-89	99.1	630.5	290	6.8	34
10-Apr-89	458.0	843.9	160	7.7	24
24-Apr-89	2376.8	3533.8	610	9	3
9-May-89	1270.0	1443.1	434	10.5	3
22-May-89	1206.3	1225.2	1066	11.7	6
5-Jun-89	134.8	180.1	3032	16.6	0
19-Jun-89	749.8	869.0	1370	16.4	0
5-Jul-89	522.0	1042.5	1934	17	2
24-Jul-89	353.5	1624.5	540	17.7	1
7-Aug-89	271.0	2329.1	322	21.1	2
21-Aug-89	389.4	1486.1	592	22.5	2
11-Sep-89	363.0	902.6	380	18	3
19-Sep-89	1460.9	1820.7	1688	18.5	5
2-Oct-89	421.8	698.6	2086	15.5	3
16-Oct-89	436.8	690.4	818	13.2	3
6-Nov-89	139.5	169.2	982	12.8	3
20-Nov-89	281.4	388.8	132	10.5	7
11-Dec-89	58.9	138.5	30	6.9	35

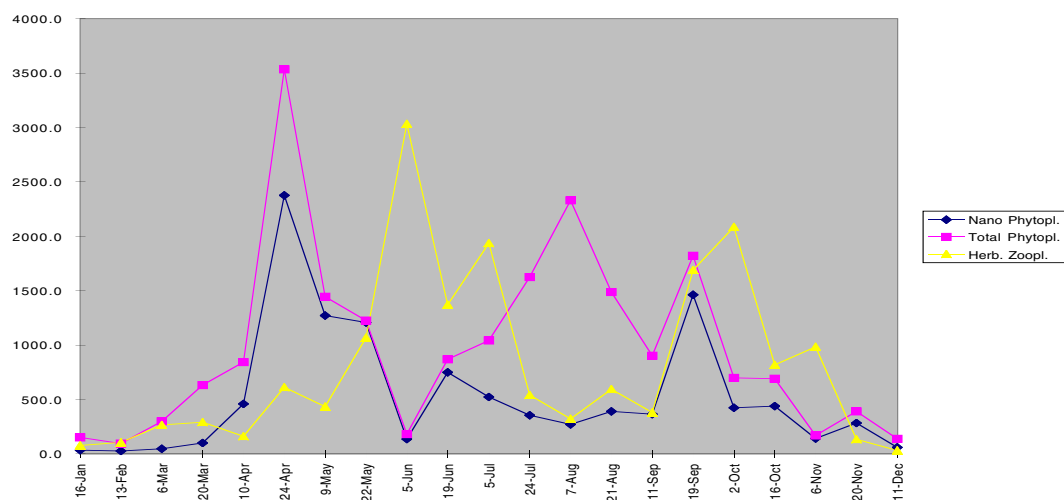


Figure B.4: Plankton dynamics year 1989

Plankton dynamics year 1990

Date	NanP	TotP	HerbZ	T5	PO4
15-Jan-90	216.5	282.2	68	7	25
20-Feb-90	212.9	388.9	162	6.9	29
5-Mar-90	177.5	416.2	80	6.6	33
2-Apr-90	689.8	1060.6	104	7.2	27
12-Apr-90	1179.1	1483.5	258	7.3	21
25-Apr-90	3541.4	3702.2	498	8.8	16
9-May-90	1847.2	1894.2	958	14.6	6
21-May-90	243.7	271.6	1994	16	3
6-Jun-90	399.6	771.1	1690	16.6	5
18-Jun-90	655.3	1135.0	612	17.3	3
9-Jul-90	474.2	1381.3	562	19.4	2
25-Jul-90	481.1	1689.0	518	16	0
6-Aug-90	478.3	1455.6	396	22.2	3
20-Aug-90	226.9	1050.9	414	21.9	2
3-Sep-90	389.1	1589.7	432	19.8	4
18-Sep-90	296.3	1437.5	616	18.7	3
1-Oct-90	110.8	329.8	474	17.1	3
15-Oct-90	119.7	220.2	1044	15.4	3
13-Nov-90	179.2	229.0	288	11.4	6
26-Nov-90	122.9	196.3	314	10.3	7
17-Dec-90	174.2	281.2	174	7.5	21

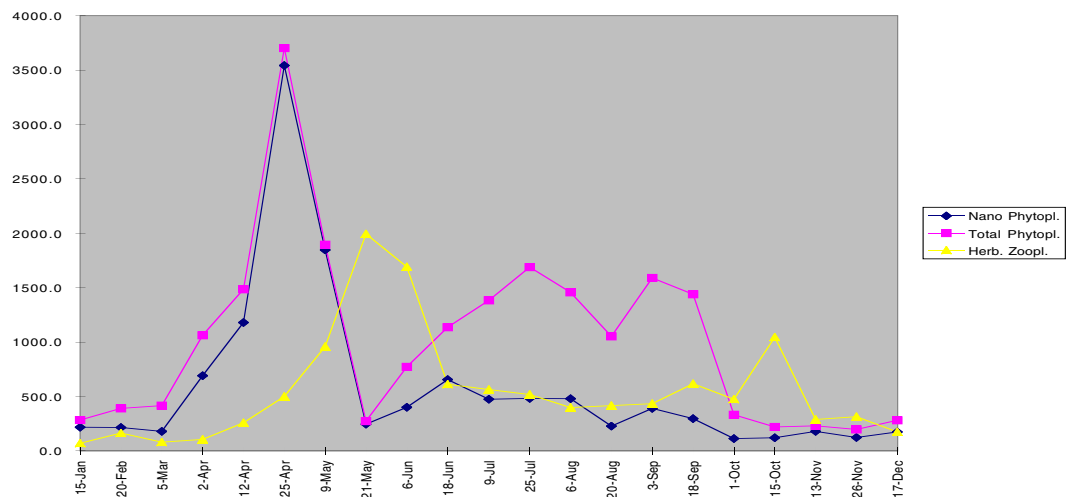


Figure B.5: Plankton dynamics year 1990

Plankton dynamics year 1991

Date	NanP	TotP	HerbZ	T5	PO4
23-Jan-91	130.5	224.0	150	6.5	28
18-Feb-91	78.4	142.7	110	5.9	34
4-Mar-91	1097.2	1220.9	128	6	29
18-Mar-91	312.0	431.4	272	7.3	8
8-Apr-91	1874.0	1929.0		7.2	8
22-Apr-91	1246.4	1270.8	780	7.1	16
14-May-91	2631.5	2643.8	994	8.9	13
27-May-91	694.6	705.5	618	10.9	6
10-Jun-91	293.0	336.2	2280	15.7	16
24-Jun-91	537.8	630.7	1044	15.9	5
8-Jul-91	540.0	935.6	376	20	2
22-Jul-91	636.7	2377.0	136	20.3	3
5-Aug-91	788.2	1222.7	132	21.3	4
26-Aug-91	225.7	1101.2	256	22.9	6
9-Sep-91	160.1	508.1	292	19.5	5
25-Sep-91	204.6	723.6	510	18.7	4
8-Oct-91	368.8	662.1	228	15.7	3
29-Oct-91	342.5	1389.0	370	11.3	3
18-Nov-91	144.7	398.7	410	10.2	7
16-Dec-91	282.5	397.1	62	7	22

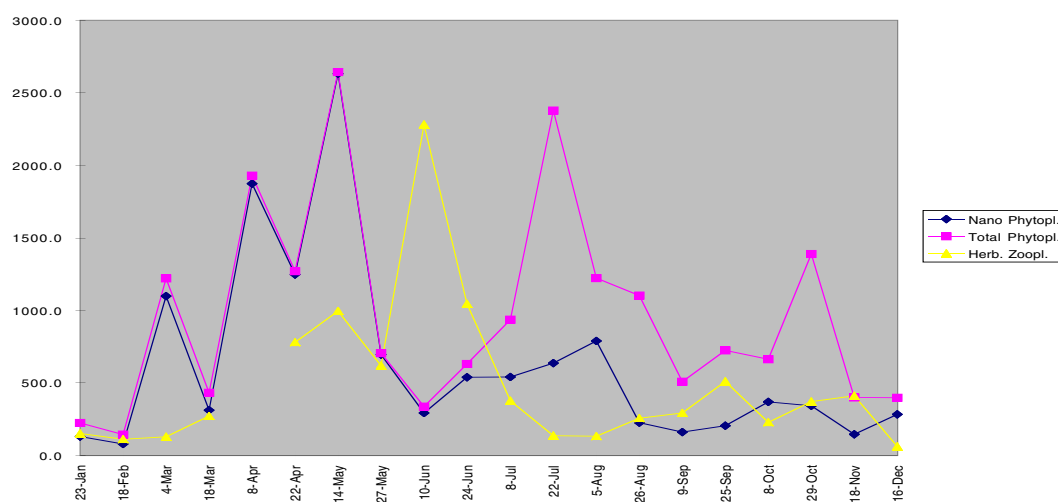


Figure B.6: Plankton dynamics year 1991

Plankton dynamics year 1992

Date	NanP	TotP	HerbZ	T5	PO4
15-Jan-92	151	209	158	6.39	25
24-Feb-92	124	177	272	5.6	24
2-Mar-92	253	494	218	6.17	23
17-Mar-92	282	354	438	6.17	23
7-Apr-92	705	754	270	6.45	18
21-Apr-92	601	683	512	7.5	27
4-May-92	1890	1929	856	9.83	4
20-May-92	2117	2181	620	9.32	1
1-Jun-92	193	292	1822	15.45	5
15-Jun-92	932	978	1030	15.5	4
6-Jul-92	562	1190	1058	17.5	3
20-Jul-92	216	634	410	19.1	2
3-Aug-92	348	2425	322	16.52	3
17-Aug-92	1028	3334	334	21.58	3
7-Sep-92	72	1265	450	18.37	3
22-Sep-92	328	2887	442	19.12	3
14-Oct-92	204	1445	586	14.73	2
27-Oct-92	60	1946	236	11.7	1
9-Nov-92	81	1091	228	10.97	3
23-Nov-92	132	988	244	9.79	10
14-Dec-92	68	214	328	8.42	13

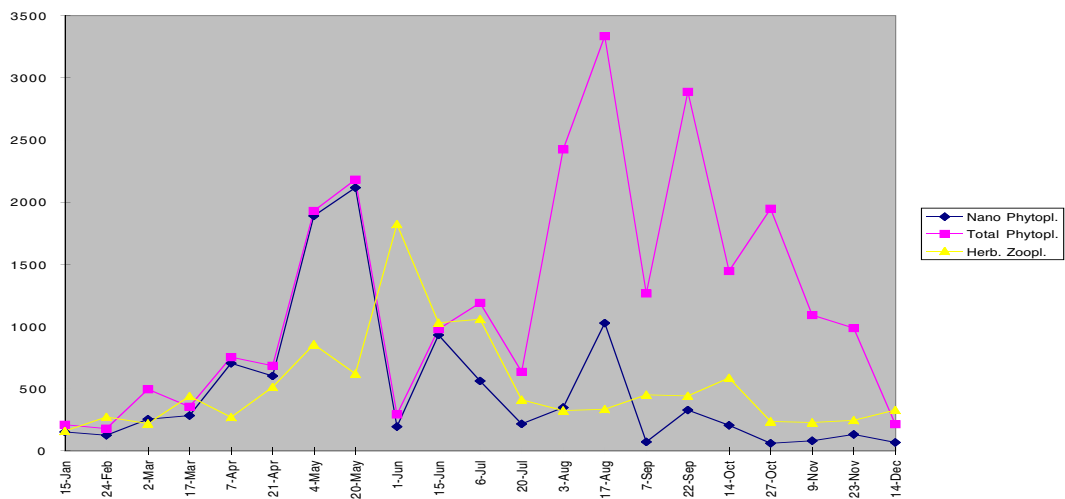


Figure B.7: Plankton dynamics year 1992

Plankton dynamics year 1993

Date	NanP	TotP	HerbZ	T5	PO4
14-Jan-93	232.9	445.2	364		
2-Mar-93	194.9	708.4	170		
15-Mar-93	387.9	591.7	232		
5-Apr-93	571.4	777.2	210		
19-Apr-93	2985.6	3315.8	164		
3-May-93	2780.0	2983.0	1366		
17-May-93	2063.0	2155.6	2000		
7-Jun-93	858.5	935.1	1278		
21-Jun-93	341.7	590.0	572		
5-Jul-93	493.5	909.8	350		
26-Jul-93	208.1	3685.1	374		
2-Aug-93	85.2	3289.3	368		
23-Aug-93	63.7	1404.0	442		
6-Sep-93	122.4	2485.0	242		
21-Sep-93	110.9	1243.0	592		
4-Oct-93	149.8	2173.5	528		
3-Nov-93	405.9	1513.6	128		
8-Nov-93	848.6	1679.0	114		
24-Nov-93	159.1	382.0	482		

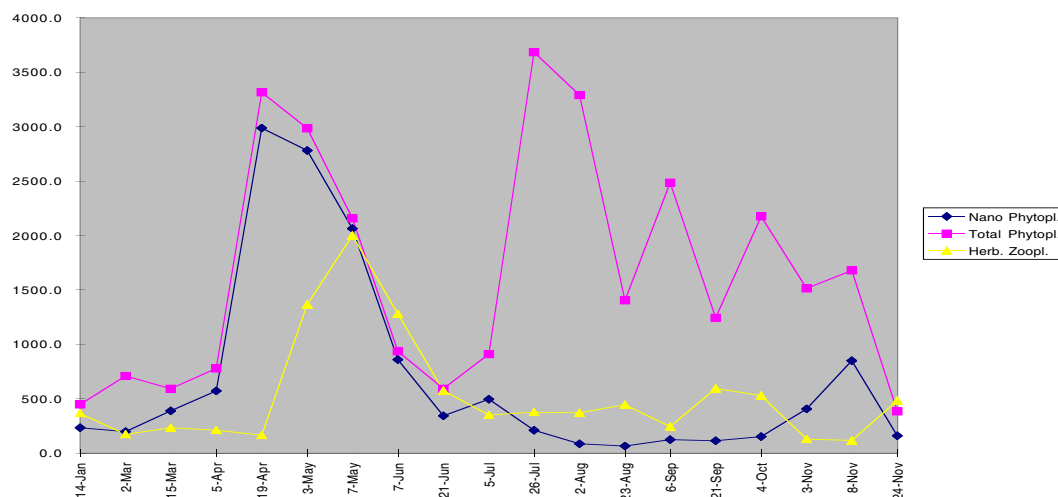


Figure B.8: Plankton dynamics year 1993

Appendix C

Distinguishability and identifiability of the studied models

C.1 Distinguishability

Let us first define what we mean by distinguishability (sensu Walter & Pronzato (1997)): if there are two models, $M(\Phi)$ and $\hat{M}(\hat{\Phi})$, with their vector of parameters Φ and $\hat{\Phi}$ respectively, we say $M(\cdot)$ is structurally distinguishable from $\hat{M}(\cdot)$ if for almost any realization Φ of parameters for $M(\cdot)$ there is no realization $\hat{\Phi}$ for $\hat{M}(\cdot)$ such that $M(\Phi) = \hat{M}(\hat{\Phi})$.

Consider we have a set of non-zero parameters for the prey-dependent model. Equating the prey equations of both models we get

$$r\left(1 - \frac{N}{K}\right)N - \frac{aNP}{1 + ahN} = \rho\left(1 - \frac{N}{\kappa}\right)N - \frac{\alpha NP}{P + \alpha\beta N} \quad \forall N \neq 0, P \neq 0.$$

Multiplying both sides by $(1 + ahN)(P + \alpha\beta N)$ we get a polynomial equation in N and P . The coefficients of a polynomial are unique, therefore the coefficients belonging to any $N^i P^j$ must be the same on the left and on the right side. Since the term aP^2 has no counterpart on the right side this is only possible for $a = 0$ in violation of the assumption of non-zero parameters. We may therefore conclude that the two models are distinguishable.

C.2 Identifiability

Of the various methods described in (Walter, 1987) we will apply here the Taylor series expansion for the case of exact observations without error. The latter hypothesis enables us in principle to calculate successive derivatives of the population abundances, thus expressions like $\dot{N}(0)$ or $\ddot{N}(0)$ may be considered as known constant values.

In the Taylor series expansion approach the outputs (abundances in time, trajectories) are developed in a Taylor series about $t = 0^+$ of which the successive terms can be calculated and can be expressed as functions of the unknowns. Thus we can obtain a sufficient number of equations that can be solved for the unknown parameters.

C.2.1 Predator-prey model with prey-dependent functional response

Consider the model

$$\begin{aligned}\dot{N} &= r\left(1 - \frac{N}{K}\right)N - \frac{aN}{1+ahN}P, & N(0) &= N_0 \\ \dot{P} &= e\frac{aN}{1+ahN}P - \mu P, & P(0) &= P_0.\end{aligned}$$

This model has 6 parameters that need to be estimated, so we will need at least 6 equations.

$$\frac{\dot{N}}{N} = r\left(1 - \frac{N}{K}\right) - \frac{aP}{1+ahN} =: \eta \quad (\text{C.1})$$

$$\frac{\dot{P}}{P} = e\frac{aP}{1+ahN} - \mu =: \beta \quad (\text{C.2})$$

$$\partial_t \eta = \frac{\ddot{N}N - \dot{N}^2}{N^2} \stackrel{(\dot{N}=\eta N, \dot{P}=\beta P)}{=} -\frac{\eta r N}{K} + \frac{a^2 h \eta N P}{(1+ahN)^2} - \frac{a\beta P}{1+ahN} =: \gamma \quad (\text{C.3})$$

$$\partial_t \beta = \frac{\ddot{P}P - \dot{P}^2}{P^2} \stackrel{(\dot{N}=\eta N, \dot{P}=\beta P)}{=} \frac{ea\eta N}{(1+ahN)^2} =: \delta \quad (\text{C.4})$$

$$\partial_{tt} \eta = -\frac{(\eta^2 + \gamma)rN}{K} - \frac{2a^3 h^2 \eta^2 N^2 P}{(1+ahN)^3} + \frac{a^2 h N P (2\eta\beta + (\eta^2 + \gamma))}{(1+ahN)^2} - \frac{aP(\beta^2 + \delta)}{1+ahN} \quad (\text{C.5})$$

$$\partial_{tt} \beta = ae \left(\frac{(\eta^2 + \gamma)N}{(1+ahN)^2} - \frac{2ah\eta^2 N^2}{(1+ahN)^3} \right) \quad (\text{C.6})$$

The last two equations were simplified using the relations $\ddot{N} = N(\gamma + \eta^2)$ and $\ddot{P} = P(\delta + \beta^2)$ (see equations (C.3) and (C.4)). We can further simplify equations (C.3, C.5, C.6) by using relation (C.4): $\frac{1}{(1+ahN)^2} = \frac{\delta}{ea\eta N}$. Since μ only appears in equation (C.2) we can solve the remaining five equations for the remaining parameters and calculate μ at the end.

$$\frac{\dot{N}}{N} = r\left(1 - \frac{N}{K}\right) - \frac{aP}{1+ahN} =: \eta \quad (\text{C.7})$$

$$\partial_t \eta = -\frac{\eta r N}{K} + \frac{ahP}{e} \delta - \frac{a\beta P}{1+ahN} =: \gamma \quad (\text{C.8})$$

$$\partial_t \beta = \frac{ea\eta N}{(1+ahN)^2} =: \delta \quad (\text{C.9})$$

$$\begin{aligned}\partial_{tt} \eta &= -\frac{(\eta^2 + \gamma)rN}{K} - \frac{2a^2 h^2 \eta N P}{(1+ahN)e} \delta \\ &\quad + \frac{ahP(2\eta\beta + (\eta^2 + \gamma))}{\eta e} \delta - \frac{aP(\beta^2 + \delta)}{1+ahN} =: \epsilon\end{aligned} \quad (\text{C.10})$$

$$\partial_{tt} \beta = \frac{(\eta^2 + \gamma)}{\eta} \delta - \frac{2ah\eta N}{1+ahN} \delta =: \phi \quad (\text{C.11})$$

Evaluating all five new equations at $t = 0$ we obtain five equations with five unknown parameters and can now test if there exists a unique positive solution for them. This

involves algebraic manipulations which can be done in any software such as Mathematica or Maple, so here only the main steps will be described, not the intermediate results.

The parameters r and K only appear in equations (C.7,C.8) and (C.10). Solve the first two equations for r and K and insert the (unique) solution into equation (C.10). Now solve equation (C.9) for h (there will be only one solution that is positive) and insert it into (C.11) and into the updated version of (C.10), which build now a system of two equations in the unknowns e and h . Solve now the updated version of (C.11) for e , plug it into (C.10), which will thus become a polynomial of first degree in a . Therefore, there exists a unique solution that can be positive in all parameters. Finally, plug the solutions for a and h back into (C.2) to obtain μ .

C.2.2 Predator-prey model with ratio-dependent functional response

Consider the model

$$\begin{aligned}\dot{N} &= r\left(1 - \frac{N}{K}\right)N - \frac{\alpha N}{P + \alpha h N}P, & N(0) &= N_0 \\ \dot{P} &= e\frac{\alpha N}{P + \alpha h N}P - \mu P, & P(0) &= P_0.\end{aligned}$$

We will proceed in the same manner as in the last section. The six basic equations become:

$$\frac{\dot{N}}{N} = r\left(1 - \frac{N}{K}\right) - \frac{\alpha P}{P + \alpha h N} =: \eta \quad (\text{C.12})$$

$$\frac{\dot{P}}{P} = e\frac{\alpha P}{P + \alpha h N} - \mu =: \beta \quad (\text{C.13})$$

$$\partial_t \eta = \frac{\ddot{N}N - \dot{N}^2}{N^2} \stackrel{(\dot{N}=\eta N, \dot{P}=\beta P)}{=} -\frac{\eta r N}{K} + \frac{\alpha^2 N P h (\eta - \beta)}{(P + \alpha h N)^2} =: \gamma \quad (\text{C.14})$$

$$\partial_t \beta = \frac{\ddot{P}P - \dot{P}^2}{P^2} \stackrel{(\dot{N}=\eta N, \dot{P}=\beta P)}{=} \frac{e\alpha NP}{(P + \alpha h N)^2} =: \delta \quad (\text{C.15})$$

$$\begin{aligned}\partial_{tt} \eta &= -\frac{(\eta^2 + \gamma)rN}{K} - \frac{2\alpha P(\alpha \eta h N + \beta P)^2}{(P + \alpha h N)^3} - \frac{\alpha P(\beta^2 + \delta)}{P + \alpha h N} \\ &\quad + \frac{2\alpha \beta P(\alpha \eta h N + \beta P) + \alpha P(\alpha h (\eta^2 + \gamma)N + (\beta^2 + \delta)P)}{(P + \alpha h N)^2}\end{aligned} \quad (\text{C.16})$$

$$\partial_{tt} \beta = \frac{\alpha e NP(\gamma - \delta)}{(P + \alpha h N)^2} - \frac{\alpha e NP(\eta - \beta)^2(P - \alpha h N)}{(P + \alpha h N)^3}. \quad (\text{C.17})$$

The last two equations were simplified using the relations $\ddot{N} = N(\gamma + \eta^2)$ and $\ddot{P} = P(\delta + \beta^2)$ (see equations (C.14) and (C.15)). We can further simplify equations (C.14, C.16, C.17) by using relation (C.15): $1/(P + \alpha h N)^2 = \delta/(e\alpha NP(\eta - \beta))$. Since μ only appears in equation (C.13) we can solve the remaining five equations for the remaining

parameters and calculate μ at the end.

$$\frac{\dot{N}}{N} = r\left(1 - \frac{N}{K}\right) - \frac{\alpha P}{P + \alpha h N} =: \eta \quad (\text{C.18})$$

$$\partial_t \eta = -\frac{\eta r N}{K} + \frac{\alpha h}{e} \delta =: \gamma \quad (\text{C.19})$$

$$\partial_t \beta = \frac{e \alpha N P (\eta - \beta)}{(P + \alpha h N)^2} =: \delta \quad (\text{C.20})$$

$$\begin{aligned} \partial_{tt} \eta = & -\frac{(\eta^2 + \gamma) r N}{K} - \frac{2(\alpha \eta h N + \beta P)^2}{(P + \alpha h N) e N (\eta - \beta)} \delta - \frac{\alpha P (\beta^2 + \delta)}{P + \alpha h N} \\ & + \frac{2\beta(\alpha \eta h N + \beta P) + \alpha h (\eta^2 + \gamma) N + (\beta^2 + \delta) P}{e N (\eta - \beta)} \delta =: \epsilon \end{aligned} \quad (\text{C.21})$$

$$\partial_{tt} \beta = \frac{(\gamma - \delta)}{(\eta - \beta)} \delta + \frac{(\eta - \beta)(P - \alpha h N)}{P + \alpha h N} \delta =: \phi \quad (\text{C.22})$$

Evaluating all five new equations at $t = 0$ we obtain five equations with five unknown parameters and can now test if there exists a unique positive solution for them.

Solve equations (C.18) and (C.19) for parameters r and K and insert the solutions into equation (C.21). Solve now equation (C.20) for h (there is at most one positive solution) and insert it into equation (C.22) and into the updated version of equation (C.21). Now solve this new version of equation (C.22) for e and insert it into (the new) equation (C.21). This has now finally become a polynomial of first degree in α and thus there exists at most one positive solution of the equations (C.12) to (C.17).

Appendix D

Transient behavior of general 3-level trophic chains

In a general food chain of length n the rate of change of each state variable depends both on lower and higher state variables:

$$\begin{aligned}\dot{x}_1 &= f_1(x_1, x_2) \\ &\vdots \\ \dot{x}_i &= f_i(x_{i-1}, x_i, x_{i+1}) \quad 2 \leq i < n \\ &\vdots \\ \dot{x}_n &= f_n(x_{n-1}, x_n).\end{aligned}$$

Bernard & Gouzé (1995) presents a method for determining the possible succession of maxima and minima of the state variables in a food chain where the rate of change of each state variable only depends on itself and the next higher state variable. With slight modifications (personal communication with the authors of Bernard & Gouzé (1995)), this method may be applied to food chains, defined as above, and thus one can determine the possible succession of maxima and minima. This method is applied to study general prey-dependent and ratio-dependent 3-level food chains with regard to their ability to describe the succession of events in the PEG-model (Sommer et al., 1986).

D.1 The method

The method is based on studying the sign-transitions (i.e. changes of the sign of the derivative) of state variables in the velocity space instead of the phase space. Let

$$z_i(t) := \dot{x}_i(t) = f_i(x_{i-1}, x_i, x_{i+1}),$$

(in a physical analogy, if $x(t)$ is abundance at time t , $z(t)$ is the velocity of the abundance at time t), then we can calculate the acceleration

$$\dot{z}_i(t) = t_i z_{i-1} + d_i z_i + s_i z_{i+1}$$

with $t_i = \partial_{x_{i-1}} f_i$, $d_i = \partial_{x_i} f_i$ and $s_i = \partial_{x_{i+1}} f_i$. If the state variable x_i is at an extremum, then $z_i = 0$ and with knowledge of the signs of the velocities before the extremum (i.e. if z_{i-1} and z_{i+1} were positive or negative) and knowledge of the signs of t_i and s_i we may determine if x_i changed from a negative slope to a positive slope (x_i at minimum) or vice versa. Therefore we can create all possible successions of extrema of our system and compare them with real data in order to reject the model if it cannot predict the observed pattern.

We won't dwell here on the mathematical details, but simply mention a necessary condition in addition to the ones given in Bernard & Gouzé (1995):

- The set of trajectories such that two state variables admit at the same time an extremum is of zero measure.

For the trophic chains that we will consider here this and the other conditions Bernard & Gouzé (1995) are always fulfilled.

D.2 The 3-level trophic chains and the PEG-model

Consider the model

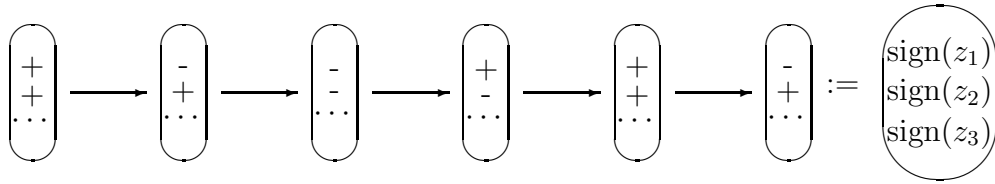
$$\begin{aligned}\dot{x}_1 &= f_1(x_1, x_2) = r\left(1 - \frac{x_1}{K}\right)x_1 - g_1(x_1, x_2)x_2 \\ \dot{x}_2 &= f_2(x_1, x_2, x_3) = e_1 g_1(x_1, x_2)x_2 - g_2(x_2, x_3)x_3 \\ \dot{x}_3 &= f_3(x_2, x_3) = e_2 g_2(x_2, x_3)x_3 - \mu x_3\end{aligned}$$

where g_1 and g_2 are either prey-dependent (left) or ratio-dependent (right) functional responses,

$$\begin{aligned}g(x_1) &\longleftarrow g_1(x_1, x_2) \longrightarrow g\left(\frac{x_1}{x_2}\right) \\ g(x_2) &\longleftarrow g_2(x_2, x_3) \longrightarrow g\left(\frac{x_2}{x_3}\right).\end{aligned}$$

In general, g_1 and g_2 are positive, monotonically increasing, concave functions of their respective arguments, $g_i(y) > 0$, $\dot{g}_i(y) > 0$ and $\ddot{g}_i(y) < 0$ for $y = x_i$ or $y = \frac{x_i}{x_{i+1}}$ (for a justification of this assumption see Arditi & Ginzburg (1989)) and $g_i(0) = 0$.

In the context of the PEG-model x_1 is the phytoplankton, x_2 the herbivorous zooplankton and x_3 carnivorous zooplankton or planktivorous fish. Succession of maxima and minima are given for the phytoplankton and herbivorous zooplankton: both populations start with increasing abundances ($z_1(0) > 0, z_2(0) > 0$), phytoplankton shows the first maximum, followed by a zooplankton maximum, the phytoplankton shows the spring depression (clear water phase), followed by a minimum in the zooplankton. Then phytoplankton reaches the next maximum again before the zooplankton. If the signs of the z_i are written in a vertical box, this succession may be written as



D.2.1 Analysis of the prey-dependent model

We have the following signs in the jacobian:

$$\begin{aligned}
 t_1 &= \partial_{x_3} f_1 = 0 \\
 t_2 &= \partial_{x_1} f_2 = e_1 x_2 \partial_{x_1} g_1(x_1) > 0 \\
 t_3 &= \partial_{x_2} f_3 = e_2 x_3 \partial_{x_1} g_1(x_1) > 0 \\
 s_1 &= \partial_{x_2} f_1 = -g_1(x_1) < 0 \\
 s_2 &= \partial_{x_3} f_2 = -g_2(x_2) < 0 \\
 s_3 &= \partial_{x_1} f_3 = 0
 \end{aligned}$$

Therefore, the possible transitions of the z_i , depending on the signs of z_{i-1} and z_{i+1} , are shown in figure D.1. If $z_1 * z_3 > 0$ then z_2 can evolve in both ways (marked as p for ‘possible’ in the transition graph in figure D.2).

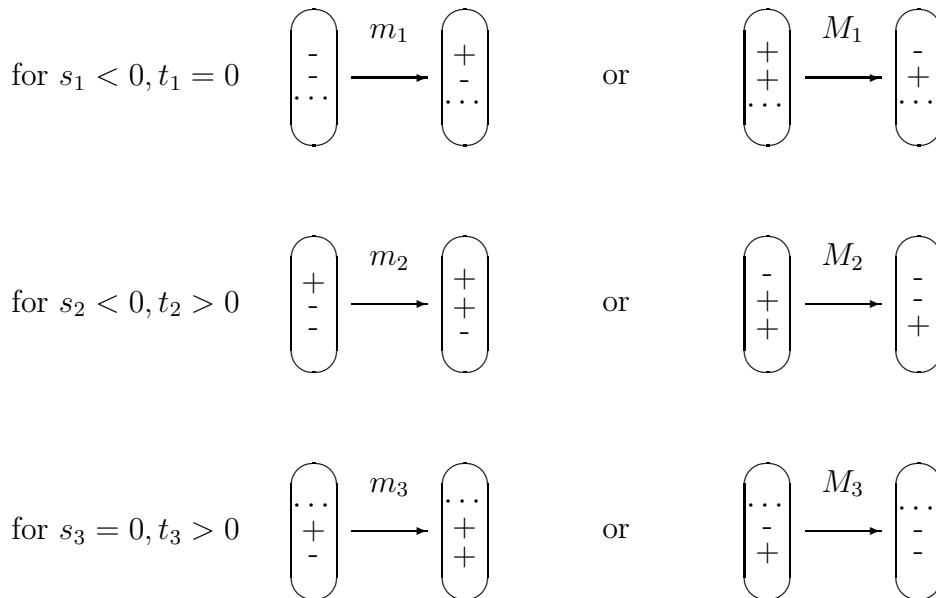


Figure D.1: The possible transitions between extrema for the prey-dependent and the ratio-dependent model.

We may now study all possible transitions of the whole system (see figure D.2). We can conclude that our model can predict the succession of events in the PEG-model.

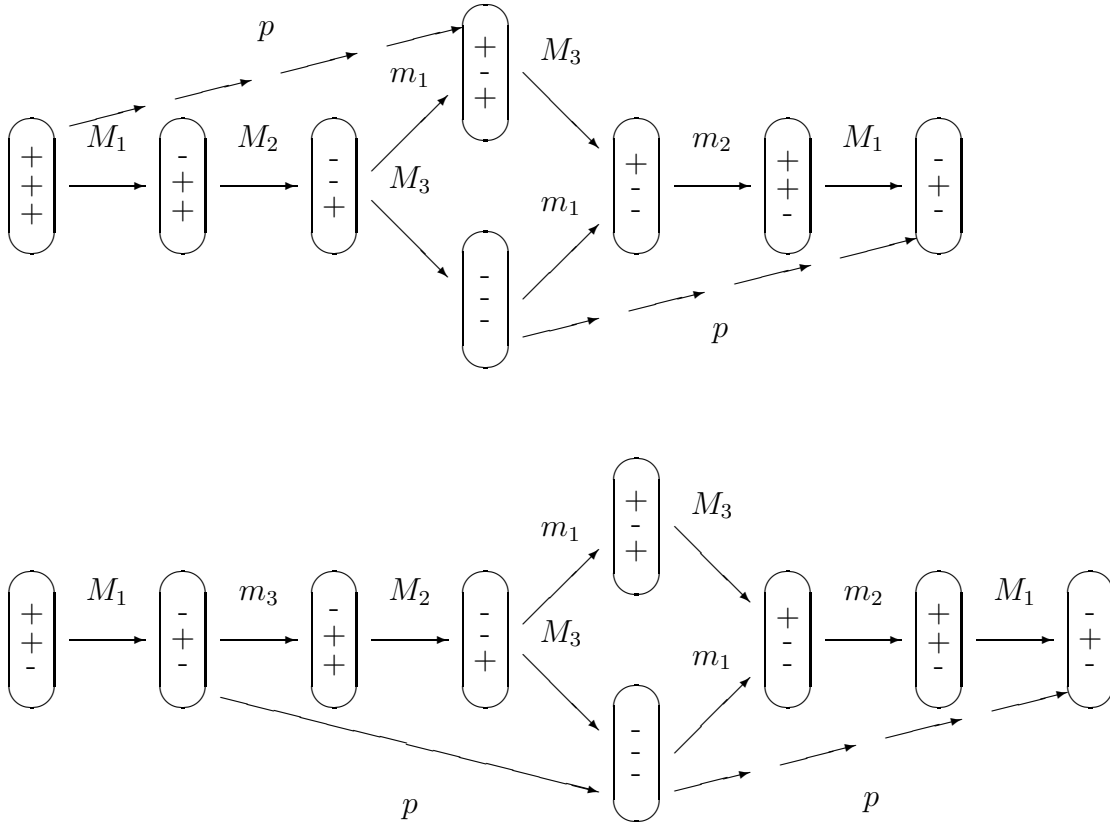


Figure D.2: The possible transitions for the prey- and ratio-dependent model. The straight arrows refer to transitions consistent with the PEG-model, while the dashed arrows refer to other transitions. A p indicates alternative possibilities.

D.2.2 Analysis of the ratio-dependent model

We have the following signs in the jacobian:

$$\begin{aligned}
 t_1 &= \partial_{x_3} f_1 = 0 \\
 t_2 &= \partial_{x_1} f_2 = e_1 g_1 \left(\frac{x_1}{x_2} \right) > 0 \\
 t_3 &= \partial_{x_2} f_3 = e_2 g_2 \left(\frac{x_2}{x_3} \right) > 0 \\
 s_1 &= \partial_{x_2} f_1 = - \left(-g_1 \left(\frac{x_1}{x_2} \right) \frac{x_1}{x_2} + g_1 \left(\frac{x_1}{x_2} \right) \right) < 0
 \end{aligned} \tag{D.1}$$

$$s_2 = \partial_{x_3} f_2 = - \left(-g_2 \left(\frac{x_2}{x_3} \right) \frac{x_2}{x_3} + g_2 \left(\frac{x_2}{x_3} \right) \right) < 0 \tag{D.2}$$

$$s_3 = \partial_{x_1} f_3 = 0.$$

Inequalities (D.1) and (D.2) hold because of the Mean Value Theorem (see below). Since all the signs are the same as in the prey-dependent model the transitions will be the same as in figure D.1 and in figure D.2 and so the ratio-dependent model may also predict the

events of the PEG-model.

Proof of inequalities (D.1) and (D.2) Let f be a strongly concave function ($\ddot{f} < 0$) on the interval $I := [0, \infty)$ with $f(0) = 0$. The Mean Value Theorem states that for any $x, y \in I$, $x < y$ there exists a $\xi \in (x, y)$ such that $f(y) - f(x) = (y - x)\dot{f}(\xi)$. Since f is concave, $\dot{f}(\xi) > \dot{f}(y)$ and so we get the inequality

$$f(y) > f(x) + (y - x)\dot{f}(y) \stackrel{x=0}{=} y\dot{f}(y).$$

With $f = g_i$ and $y = \frac{x_i}{x_{i+1}}$ this proves inequalities (D.1) and (D.2).

q.e.d.

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Titel: En qualitative und quantitative Vergleich zwüschet Räuber-Beute Model und ökologische Ziiitriehene

Zämefassig

Di vorligendi Dissertation vergliicht zwei Räuber-Beute Model mit Ziiitriehene, entweder us em Labor oder vo Feld-Studie. S'erschi Model nimmt a dass d'Konsumfunktion nume vo de Beute Dichti abhanget. So n'es Model zeigt charakteristike vo n'ere vo-obe-duraab Kontrolle. S'anderi Model nimmt a dass d'Konsumfunktion vom Verhältnis Beute pro Räuber abhanget. Die Ahnahm hätt zur Folg dass das Model nöd nume vo-obe-duraab Kontrolle zeigt, sondern au vo-une-duruuf Kontrolle. Di mathematisch Analyse vo dem Verhältnis-abhängige Model zeigt e richi Grenz-Dünamik mit mehrere Attraktore. Eine vo dene Attraktore isch de Ursprung (das heisst beidi populatione stärke us). De hauptsächlich Unterschiid zwüsched dene zwei Model isch ihri Reaktion zu n'ere Beriicherig vo de Umwelt: s'erschi Model verlürt sini Stabilität und nume de Räuber profitiert vom Riichtum, wohingege s'zweiti Model gliich stabil bleibt und beidi, de Räuber und d'Beute, profitiered vom Riichtum. De Vergleich vo dene beide Model mit em verbale PEG-Model (beobachteti Dünamik vo Plankton i Süesswasser See i de gmässigte Klima-Zone) zeigt dass beidi Model die Dünamik chönd erkläre falls sich ein oder zwei vo de Model Parameter mit de Saison verändered. Di maximale Ähnlichkeit isch s'statistische Werkzeug zum die beide Model quantitativ mit Ziiitriehene vo verschidene Tüpe vo Räuber-Beute Syschtem z'vergliche. Einzeller- und Insekte-Date (beidi us em Labor) passed generell besser zum erschte (nume Beute-abhängige) Model, wohingege d'Plankton Date mit beidn'e Model übereinstimmed ohni ei's vo de Model z'bevorzüche. I dem Fall isch es nützlich beidi Model z'Bruuche, erschtens, zum usefinde welli Vorhersage empfindlich uf de Unterschiid zwüsched dene zwei Model reagiered, und zweitens, zum wiiteri Forschige inschpiriere.

Title: Comparing predator-prey models qualitatively and quantitatively with ecological time-series data

Abstract

This thesis compares two predator-prey models with the temporal dynamics observed in laboratory or field predator-prey systems. The first model assumes that the functional response is a function of prey density only, resulting in a model with top-down characteristics. In contrast, the second model considers this function to depend on the ratio prey per predator, resulting in a model with both top-down and bottom-up characteristics. The mathematical analysis of this ratio-dependent model reveals rich boundary dynamics with multiple attractors, one of them being the origin (extinction of both populations). The major difference between the two models is in the predictions in response to enrichment, which acts as a destabilizing factor and increases the predator equilibrium only in the prey-dependent model, but which is neutral with respect to stability and increases both prey and predator equilibria in the ratio-dependent model. The comparison of both models to the verbal PEG-model (observed plankton dynamics in freshwater lakes) shows that they both can explain these dynamics if seasonality is added to one or several model parameters. The maximum likelihood concept is used to compare the two models quantitatively with predator-prey time series of several types. Protozoan and arthropod (laboratory) data are generally better described by the prey-dependent model. For the phytoplankton-zooplankton interaction, both models are valid and none is better than the other. In this case, using both models can help detecting predictions that are sensitive to predator dependence and direct further research if necessary.

Discipline : Ecology

Keywords : predator-prey models, predator-prey dynamics, nonlinear regression, model-selection, time series, ratio dependence, PEG-model, Contois model

Titre: Comparaison qualitative et quantitative de modèles proie-prédateur à des données chronologiques

Résumé

La présente thèse compare deux modèles proie-prédateur avec les dynamiques temporelles de systèmes observés en laboratoire ou sur le terrain. Le premier modèle suppose que la réponse fonctionnelle dépend uniquement de la densité des proies, et présente donc les caractéristiques des modèles où les abondances sont contrôlées “de haut en bas”. Au contraire, le second modèle considère que la réponse fonctionnelle dépend du ratio entre densité de proies et densité de prédateurs, et inclut donc une régulation des abondances “de bas en haut”. L’analyse mathématique de ce modèle ratio-dépendant fait apparaître des dynamiques de bord riches avec de multiples attracteurs, dont l’un est l’origine (extinction des deux populations). La différence majeure entre les deux modèles réside dans leurs prédictions sur la réponse d’un système à l’enrichissement: déstabilisation, et augmentation de l’abondance à l’équilibre du prédateur uniquement dans le modèle proie-dépendant, stabilité inchangée et augmentation de l’abondance à l’équilibre des proies et des prédateurs dans le modèle ratio-dépendant. La comparaison de ces deux modèles avec le modèle verbal PEG (décrivant la dynamique planctonique dans les lacs) montre que tous deux peuvent rendre compte de cette dynamique si des changements saisonniers sont introduits dans les valeurs d’un ou plusieurs paramètres. Nous comparons quantitativement les deux modèles avec différents types de séries temporelles de systèmes proie-prédateur par la méthode du maximum de vraisemblance. Les données concernant des protozoaires ou des arthropodes (en laboratoire) sont en général mieux décrites par le modèle proie-dépendant. Pour l’interaction phytoplancton-zooplancton, les deux modèles conviennent aussi bien l’un que l’autre. Le fait d’utiliser les deux modèles peut alors permettre de détecter parmi les prédictions celles qui sont sensibles à la prédateur-dépendance et, éventuellement, d’orienter des recherches supplémentaires.

Title: Comparing predator-prey models qualitatively and quantitatively with ecological time-series data

Abstract: see preceding page

Discipline : Ecologie

Mots-Clés : modèles proie-prédateur, dynamiques proie-prédateur, regression nonlinéaire, sélection de modèle, séries chronologiques, ratio-dépendance, modèle de Contois, modèle PEG