Controlling complexity in individual-based models of aquatic vegetation and fish communities

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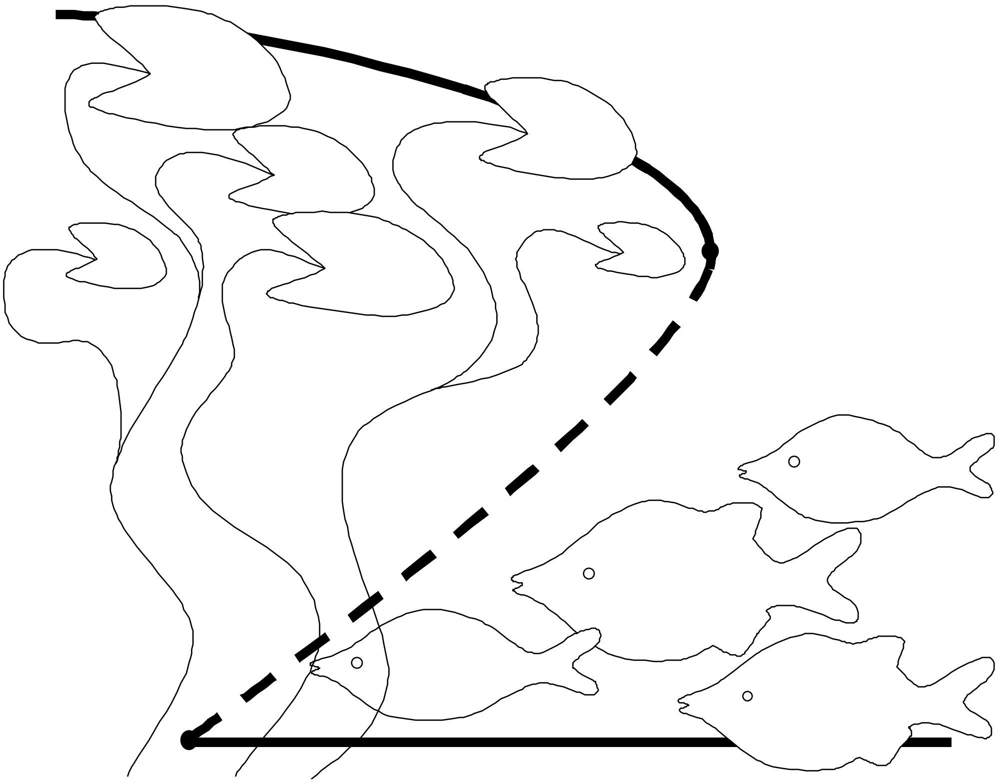

Chapter 1
A strategy to improve the contribution of complex simulation models to ecological theory

Egbert H. van Nes & Marten Scheffer

Abstract

Large models are commonly used for simulations of past results or future scenario's of ecosystems. However, such models have been criticized by many authors, mainly because the causes of their results are hard to understand. Simple abstract models have contributed much more to the development of ecological theory. However, simple models also have their deficits: these models often are hard to test empirically and many essential ecological aspects such as individual variability are hard to include. Moreover, minimal models focus on one single mechanism only, while in reality there are often many simultaneously operating mechanisms that cause an ecological phenomenon.

In this paper we present a strategy which we have found useful for improving our understanding of the way in which complex models generate their results. The strategy consists of three phases: 'scrutinizing', 'simplifying' and 'synthesizing'. The first step is a thorough analysis of the model behavior with respect to a selected set of parameters ('scrutinizing'). Secondly, similar analyses are done with several simplified versions of the model ('simplifying'). In this step, relationships between state variables or species that may potentially cause incomprehensible behavior, are replaced by fixed values or highly simplified relations. The last step is to explain the differences between the full and the simplified versions and to discuss the results in the light of the existing ecological theory, field patterns or other models ('synthesizing'). We argue that this way of combining analyses of simple and more elaborate models is a powerful way to gain understanding of complex systems.

Introduction

In the 1970s expectations about the contribution of complex simulation models to prediction and understanding of ecosystems were high. The model CLEAN (Bloomfield et al., 1974) is an example of the complex models developed in this period. It describes the dynamics of a full aquatic food web, including phytoplankton, zooplankton and fish, by means of 28 coupled differential equations. Later, this approach has been criticized mainly because such models are hard to develop, hard to communicate and hard to understand (Scheffer and Beets, 1994; Grimm, 1994). Nonetheless, large complex models are still being developed and have proven to be suited for simulation purposes, for example in water quality management or risk assessment procedures of chemicals (see review of: Koelmans et al., 2001).

Simple models, on the other hand, have been used in ecology since the beginning of the 20th century. These models, describing an ecological problem in few differential equations, have contributed much to ecology theory (e.g., May, 1981). However, it has been recognized that minimal models have severe deficiencies as well. For instance, individual variability and spatial heterogeneity, which are essential for the dynamics of many systems, are usually neglected. This has recently led to a revival of more complex theoretical models, particularly individual-based models (Huston et al., 1988; Judson, 1994). Although in the late 1980's there was great optimism about the contribution of these models to ‘unify ecological theory’ (Huston et al., 1988), the contribution of these models to ecological theory over the first 10 years of their existence has been disappointing (Grimm, 1999).

Here, we give a brief review of the specific advantages and problems of both modeling strategies; subsequently we present a strategy that we have found useful as a way to extend the use of complex models, not only as a simulation tool, but also as a tool for enhancing our understanding of complex ecological systems. The approach allows one to have the best of both different modeling styles.

Large versus small models, the pro's and con's

Large complex models

The main critique for complex simulation models is that their results are so incomprehensible that theoreticians cannot learn much from them (Grimm, 1994). Indeed, complex models are often not primary aimed at understanding nature, but meant as an engineering tool aimed at making predictions (Caswell, 1976). However, Scheffer and Beets (1994) argue that if one is not able to understand the reasons of the behavior of complex models, predictions produced with these models are of limited use, and maybe even not much better than those produced with much cheaper statistical black box models, as both can only produce valid predictions within a relatively narrow operation domain (Van Straten, 1998).

Another problem is that even a very good fit on an independent data set is no guarantee for a correct model formulation. It can often be achieved with very different (unrealistic) parameter settings and even with very different model formulations (Simons and Lam, 1980). Hence, if one does not understand why the model produces its results, it is hard to tell whether it is for the correct reason (Rykiel, 1996).

A related problem is that complex models are difficult to communicate and therefore the scientific soundness is hard to judge by other researchers. Results of a complex model can not be reproduced by others; they can only be believed (Lorek and Sonnenschein, 1999). This is certainly true for individual-based models, which do not have a formal notation like a set of differential equations. Quite serious is the problem that the software implementation is usually complex, and consequently prone to software bugs, which may remain unnoticed, and significantly affect the results. Indeed, for large models it is extremely difficult to verify that the ideas are transformed correctly into computer code, possessing the desired behavior under all circumstances (Rykiel, 1996).

As complex models are often used for policy and decision making, there is a need for quality control, which unfortunately still is no common practice (Scholten and Udink ten Cate, 1999). An important stage in improving the quality of models is model validation. Therefore, much attention has been devoted to the question how complex models should be validated (e.g., Rykiel, 1996; Van der Molen, 1999). Some authors maintain that models can never be properly validated (Oreskes et al., 1994). Rykiel (1996), however, using a more modest definition of validation: “validation means that the model is acceptable for its intended use”, comes to an extensive list of tests that should be part of the validation process. Unfortunately, ecological and environmental models are in practice often validated only by comparison with empirical data. As mentioned before the ability to predict independent data or future data alone does not mean that the model adequately describes the cause and effect relations of the real system (Rykiel, 1996). If the causes of the model behavior are at least understandable, it can be made clear which assumptions lead to the model behavior. Only then, the model can truly produce hypotheses that can be tested in independent studies.

Various Monte-Carlo methods exist to calculate how the uncertainty of parameter estimates affects the predictions of complex models (Fedra, 1983). However, it is generally acknowledged that this procedure gives an under-estimation of the uncertainty (Reichert and Omlin, 1997), as it does not account for the uncertainty in the model formulations (Scheffer and Beets, 1994). The methods of uncertainty analysis are based on the assumption that parameter values may be uncertain but the model is correct. This assumption is far from valid in ecological models, where the uncertainty in the model structure is usually very large, and there is usually not one single generally accepted model formulation (Reichert and Omlin, 1997). Also, the uncertainty in the initial and boundary conditions is usually neglected (Van der Molen, 1999). Despite these problems, uncertainty analysis is a useful technique to show the propagation of errors in complex models, as long as the results are presented as a minimum estimate of uncertainty. In abstract simplified models such analysis is of little use, as there are too many processes neglected.

Minimal models

Minimal models are simple abstract models that are developed for the purpose of gaining understanding of a single aspect of a system, based on clear assumptions. This kind of models is also called 'strategic' (Levins, 1966) or sometimes 'conceptual' (Grimm, 1994). It excludes simple empirical models, which describe a phenomenon with statistically derived equations. Minimal models typically focus on one specific explanation of a phenomenon and consist usually of few equations. They often generate a hypothesis about a possible cause of a phenomenon that would not easily be achieved intuitively (Scheffer and Beets, 1994). Instead of re-creating the complexity of real ecosystems, these models aim to find a possible explanation of a phenomenon which can serve as a search image for studies of the real system. Obviously, the comparison with the real system is a critical and difficult step. Even irrealistic patterns produced by simple models may puzzle scientists for many years and contribute to the understanding of nature. The 'paradox of enrichment' (Rosenzweig, 1971) for instance is a model artifact, but by studying it, we learn that there must be important stabilizing mechanisms in nature (Scheffer and De Boer, 1995).

The number of parameters of simple models should be low enough to be able to explore the behavior of the models completely. There are several well-tested software tools available to implement such models without the necessity for the modeler to program in a basic computer language. Furthermore, there are sophisticated tools to analyze the behavior of these models in a large part of their parameter space. Bifurcation analysis (viz., the analysis of modes of asymptotic behavior of simple models) has become an independent branch of applied mathematical science (Kuznetsov, 1995). Moreover, a subset of the simplest minimal models can be analyzed analytically. Disadvantage is that these approaches may set artificial constraints to the level of abstraction, not dictated by nature but by the available mathematical analysis tools.

Importantly, minimal models are aimed to be generic, describing a theoretical concept, and not a specific situation. Grimm (1994) notes that there is a trade-off between generality and the ability to produce testable predictions. Due to the complex nature of ecology, the abstractions are usually more far-reaching than in other exact sciences such as physics (DeAngelis, 1988), therefore there has been some discussion about the question whether ecological problems are not too complex to be described in a highly simplified way (Onstad, 1988). Most theoretical ecological models are based on few famous equations (logistic equation, Lotka-Volterra and Ricker curves). These basic equations only have been tested with laboratory experiments often even with an amazingly poor fit (Hall, 1988). Hall (1988) criticized minimal models for this reason. Moreover, many essential aspects of natural species dynamics are usually neglected in simple models, such as seasonal changes (e.g., Scheffer, 1998). Consequently, minimal ecological models are usually very hard to test and to validate with empirical data. This may explain why the popularity of abstract models is marginal among many practical ecologists (Scheffer and Beets, 1994) and policy makers. Uncertainty analysis is of little use in these models, because there are too many processes neglected and the whole behavior of the model can be explored in detail.

Important aspects such as heterogeneity and individual variability, which cannot be included in minimal models, can be handled by individual-based models (Judson, 1994;

Grimm, 1999). Most of these models, however, are much more complex and less generic than minimal models (Grimm, 1999), having the same drawbacks as other large models.

Another more fundamental problem with minimal models is that these models usually focus on one cause of a phenomenon only, whereas in ecology causation is often complicated (Scheffer and Beets, 1994). A single ecological phenomenon can be caused by several mechanisms that act simultaneously. Although one of the mechanisms will often dominate, the dominant mechanism may differ from case to case. The positive effect of vegetation on the turbidity of shallow lakes is an example of such phenomenon. There is broad consensus about the fact that vegetation enhances water turbidity, though there are many ideas about the cause responsible for this (Scheffer, 1998). In such case, the question is not whether a mechanism may cause an observed phenomenon, but rather how important it is, relatively to the other mechanisms. The latter question typically cannot be answered by means of a minimal model.

How to bring these worlds closer together?

Over the past years we have developed and analyzed various complex ecological models. In our efforts to understand each aspect of the behavior of these models, we have gradually converged to a strategy, which is characterized by three phases: ‘scrutinizing’, ‘simplifying’ and ‘synthesizing’ (Fig. 1.1). These phases may be applied in several cycles. The first step is a thorough analysis of the model behavior, in which the behavior of the model with respect to a selected set of parameters is analyzed in depth (‘scrutinizing’). Secondly, similar analyses are done with simplified versions of the model (‘simplifying’). The last step is to explain the differences between the full and the simplified versions and to discuss the results in the light of the existing ecological theory, field patterns or other models (‘synthesizing’).

The order of the first two phases can also be reversed. We found this particularly useful during the construction of very complex models that are hard to calibrate. By starting to calibrate simplified versions and subsequently increasing the complexity in a stepwise fashion, the calibration of the complex model is kept manageable.

Scrutinizing

The purpose of this phase is to scan the behavior of the model in a large part of the parameter space spanned by the most relevant parameters. We first need to identify a manageable number of relevant parameters. Large models often have hundreds of parameters, of which the effect on the results obviously cannot be analyzed in detail.

One way to select the most relevant parameters is to use the results of a Monte-Carlo sensitivity analysis. The standard sensitivity analysis, in which all parameters are varied randomly, produces a sensitivity matrix, in which for all model outputs, sensitivity coefficients ($s_{i,j,t}$) of each parameter i are produced. These sensitivity coefficients give the relative change of in the model results of the model output j at time t ($M_{j.t}$) as a consequence of changing the parameters over a range of Δp_i

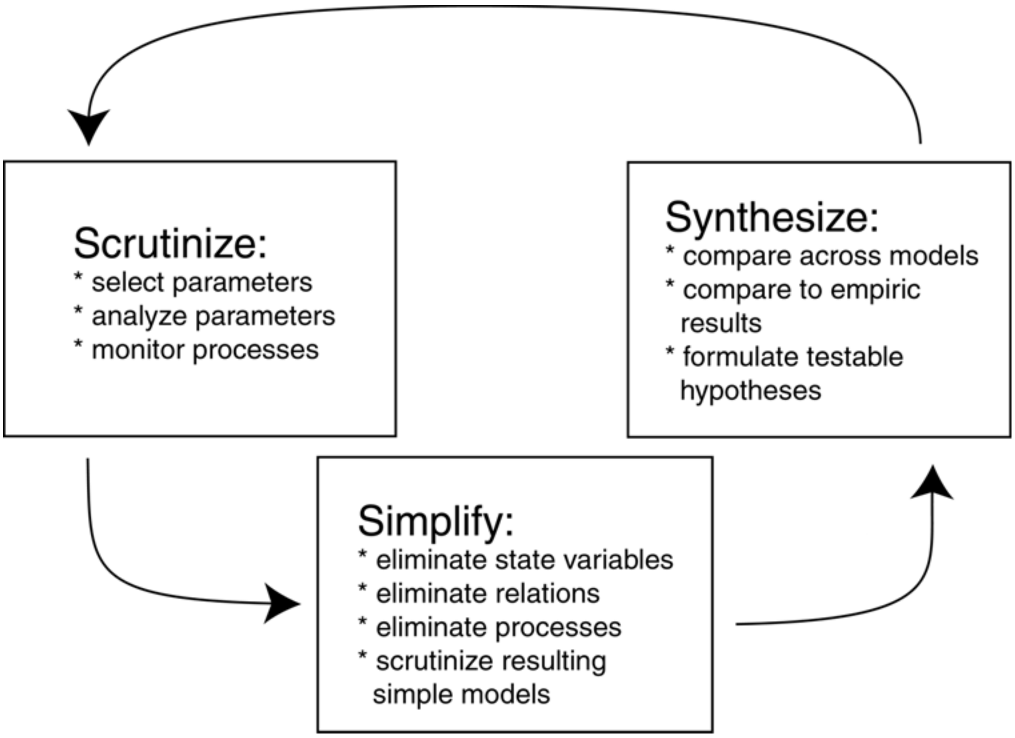

Fig. 1.1. *An overview of the proposed* s^3 *strategy of model analysis and adjustment*

$$s_{i,j,t} = \frac{\partial M_{j,t}}{\partial p_i} \frac{\Delta p_i}{M_{j,t}} \tag{1.1}$$

The overall effect of each parameter ($s_{tot,i}$) on all model results can be determined by summing the sensitivity coefficients as follows:

$$s_{tot,i} = \sqrt{\left(\sum_{j,t} \left(s_{i,j,t} \right)^2 \right)} \tag{1.2}$$

Because complex models usually have both many model outputs and many parameters, this analysis produces a huge sensitivity matrix, which can be hard to understand. Klepper (1989; 1997) developed an elegant method to perform a multivariate analysis on these sensitivity coefficients. The purpose of this analysis is to create clusters of parameters that have an equal (or opposite) qualitative effect on the model outcomes. Selecting one parameter of each cluster creates a more manageable and relevant set of parameters. The parameter with the maximum total effect ($s_{tot,i}$) of each cluster is a reasonable choice. Of course, the generated parameter set can be supplemented with parameters that are of particular interest to the model user.

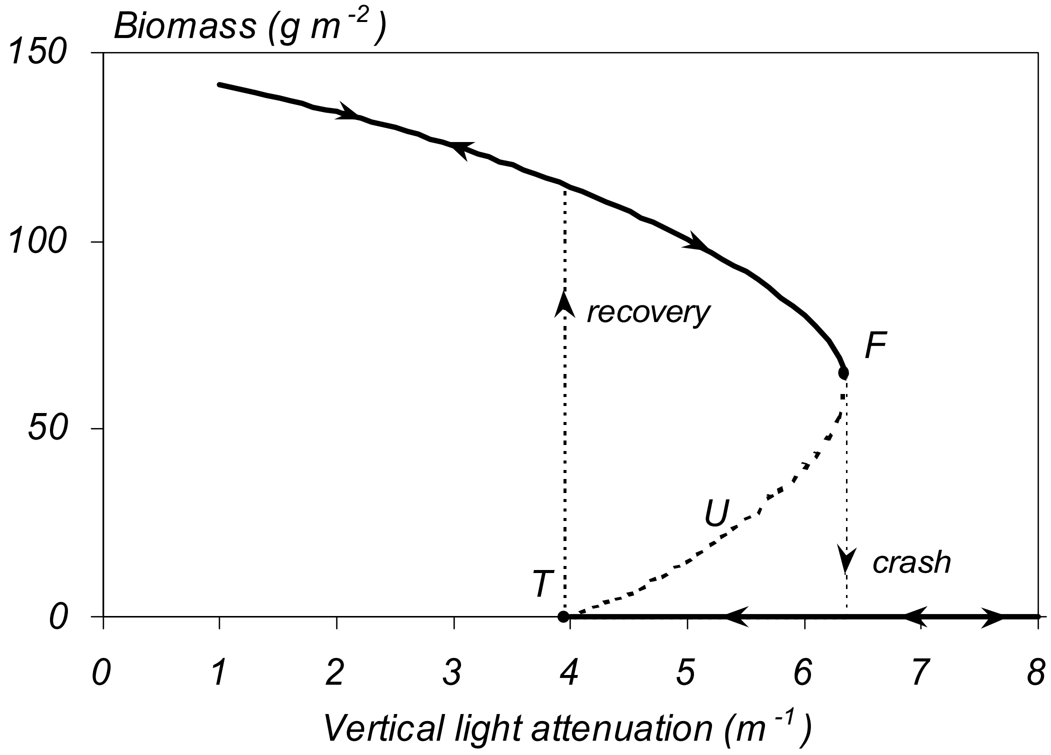

Fig. 1.2 *Example of a brute force analysis to find equilibria and bifurcations of a relatively complex vegetation model (Chapter 4), using an efficient parameter scanning technique (see text). The figure shows the summer biomass of the plant Chara aspera after long runs. The unstable equilibrium (U) was found by scanning the behavior for large numbers of different initial conditions in the vicinity of the unstable equilibrium. The fold (F) and transcritical bifurcations (T) are catastrophic.*

The next step consists of scanning the selected parameters in discrete steps, plotting a general 'currency' of the model, analogously to the currencies of simple models. Examples of such general 'currencies' are the asymptotic behavior (viz. the model behavior after long runs, loosely referred to as 'equilibria'), return time, resilience, variability of a time series, extinction time and persistence. These currencies can be used to answer general questions like "Does the model have alternative equilibria under certain conditions?" (Chapter 4), "Under what conditions is the extinction risk of a species minimal?" (Uchmański, 2000) and "What are the resilience and resistance of a lake ecosystem, before and after biomanipulation" (Carpenter et al., 1992).

As an example, we describe a relatively efficient procedure to scan for alternative equilibria (Chapter 4). One starts with a parameter setting at which there is only one equilibrium, for instance a situation with clear water and vegetation (Fig. 1.2). The model is stabilized by simulating a sufficient number of years till the same pattern is repeated each year (i.e., the 'equilibrium' is reached). Thereafter, one parameter, for instance the vertical light attenuation, is increased with a small step. Without resetting the model, the new equilibrium is found by simulation. This procedure is continued at least till a catastrophical bifurcation is reached (*F* in Fig. 1.2, the water then is too turbid for vegetation). After this point the model goes to the alternative equilibrium. After this alternative equilibrium is reached, this equilibrium is continued in the opposite direction, by changing the same parameter in the opposite direction in small steps, where after each step the equilibrium is found by simulation. When the second catastrophical bifurcation (*T*) is reached, the model will go to the first equilibrium again. In the example of Fig. 1.2 the vegetation recolonizes the lake at this point. This method visualizes the hysteresis that occurs with alternative equilibria. The scanning of parameters can also be done in pairs to construct two-dimensional plots. For example, to construct a bifurcation plot in two dimensions of the parameter space, the above-described scanning procedure is repeated for several values of a second parameter (Fig. 1.3).

To get a first impression about the important mechanisms that generate simulated patterns it can also be useful to simply monitor the relations and processes in the full model in depth. For instance, information on the mortality causes of preys and the 'stomach' content of predators can help to clarify the relations between predators and preys more than just monitoring the population densities (Chapter 7). The drawback of this method is that it can create an unmanageable database of results as the number of relationships increases exponentially with the number of species. Still this method is particularly useful in cases where different mechanisms may contribute to cause one phenomenon simultaneously.

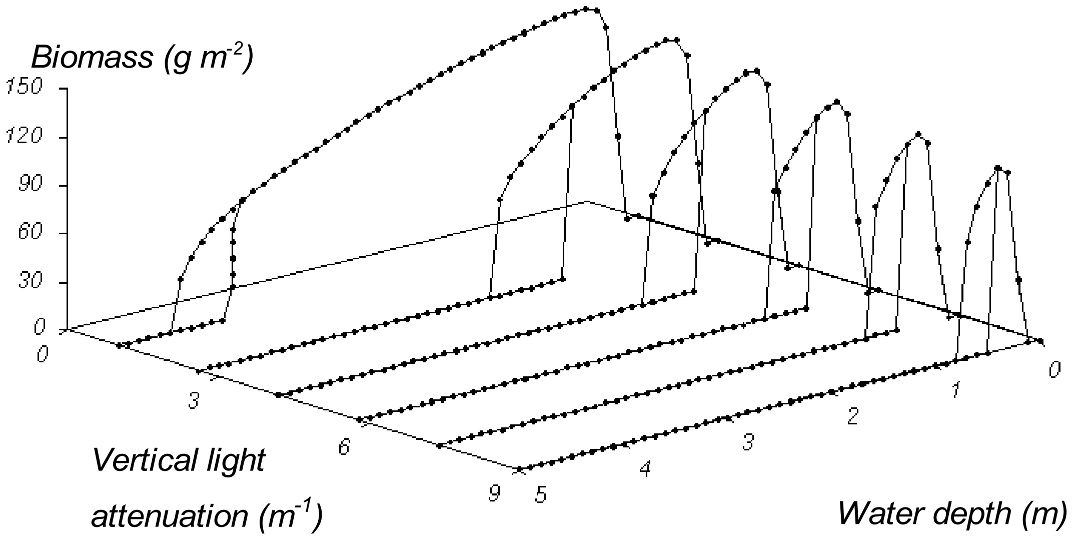

Fig. 1.3 *An example of a two dimensional analysis of equilibria and bifurcations with a relatively complex vegetation model (Chapter 4). Both the water depth and the vertical light attenuation are changed. At each vertical light attenuation value, the water depth is changed in two directions to find alternative equilibria. The points where vegetation disappears and reappears are the catastrophical bifurcations that are dependent on both environmental parameters.*

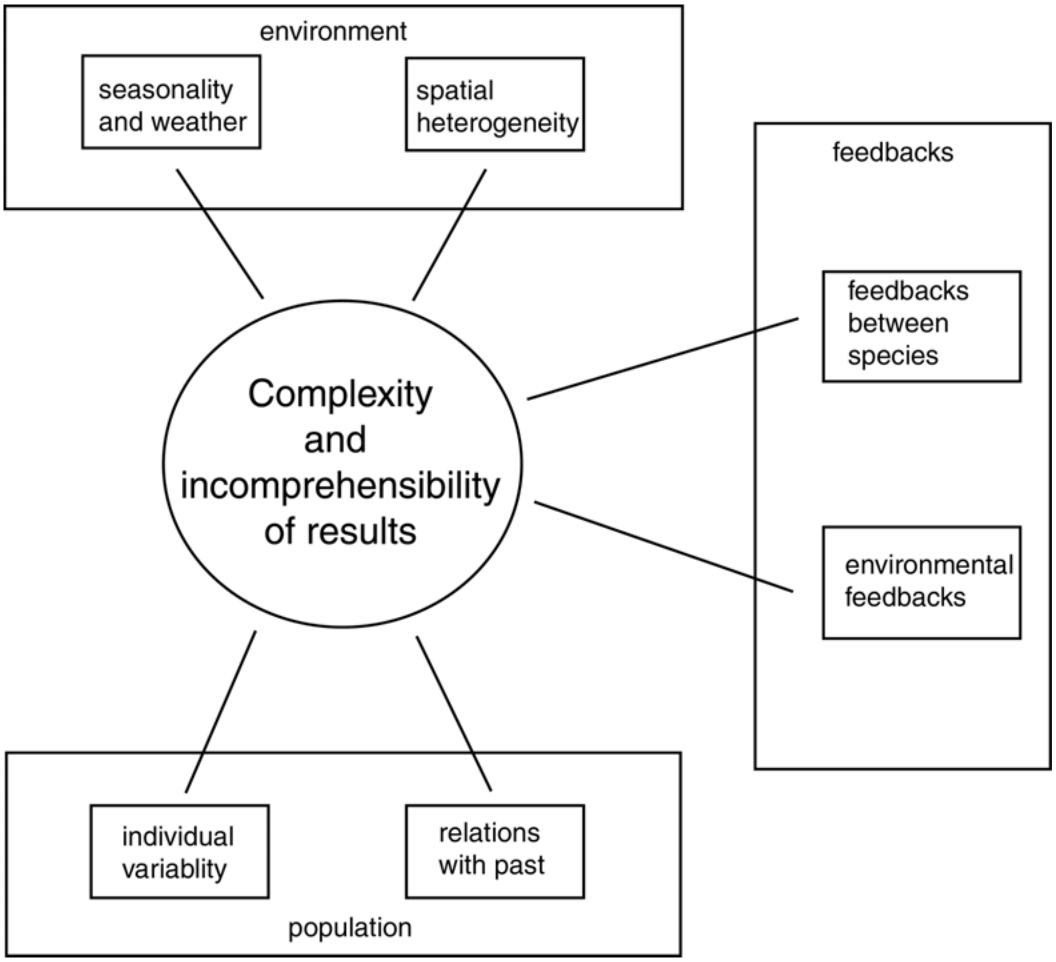

Fig. 1.4 *Some important causes of complexity that may lead to incomprehensible behavior in ecological models.*

Simplifying

The patterns that were generated in the 'scrutinize' phase must be fully understood to substantiate that they are not caused by a model artifact or a bug in the program code.

One reason why complex models are hard to understand is merely the large number of parameters and variables. However, perhaps the most important problem is the number of relations between state variables giving rise to feedbacks. In addition, relations with the history and time lags, can be sources of incomprehensible behavior (May, 1973). Also, if the model includes stochastic processes by drawing from statistical distributions, the behavior is harder to understand (for an overview of important sources of incomprehensible model behavior, see Fig. 1.4).

A powerful way to find out why the model shows its current behavior is to repeat the analyses of the 'scrutinize' phase with simplified versions of the model. The purpose of these simplifications is not primarily to create a simpler and therefore a better model, but to gain understanding about the causes of the patterns in the model. There are several ways to simplify the model. In the next section we will give some examples that we have used in individual-based models.

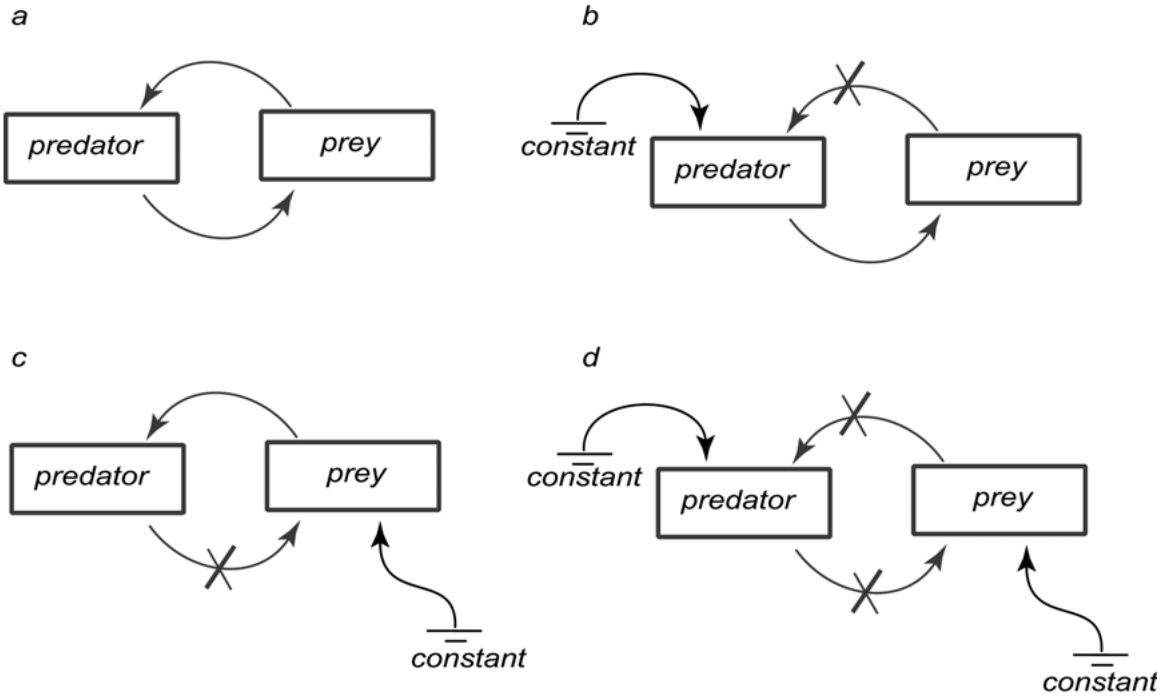

Fig. 1.5 *Three levels of simplification of a predator-prey relationship in a model. (a) The original model with a full feedback loop between predator and prey. (b) The food-dependent consumption of the predator is replaced by a fixed consumption rate. (c) The mortality due to predation is replaced by a fixed mortality rate. (d) The predator is completely independent of the prey biomass and vice versa.*

Firstly, one can remove one or more state variables or species (Chapter 7). Obviously, this kind of simplification will usually have a very large effect. It may even lead to pathological model behavior such as unlimited population growth. Therefore, it can be too rough to isolate the exact mechanism that causes a phenomenon. Nonetheless, it can sometimes generate rough hypotheses like “It must have something to do with competition”. Resource competition (Tilman, 1977), for example, may cause alternative equilibria, which disappear obviously if there is only one species, as was illustrated in simplification study of a multi-species macrophyte model (Chapter 3).

An alternative way of simplifying is more subtle. Instead of removing variables or species completely, the interdependency between the variables is eliminated or simplified. For example in a predator-prey system, predators and preys are related to each other in two ways: the consumption of the predator is limited by the number of preys, whereas the mortality of the prey is determined by the consumption of the predator (Fig. 1.5). This feedback, which may lead to predator-prey cycles, can be simplified in three ways: replacing the consumption of the predator by a fixed rate, replacing the mortality of the prey by a fixed rate, or doing both things (Fig. 1.5 b, c and d).

Another feedback may be due to organisms affecting environmental conditions. Such relation may either lead to competition between species or to facilitation (Holmgren et al., 1997), which both may add to the complexity of the model and may cause alternative equilibria. Replacing the organism effect on the environment by a fixed value reduces the complexity of the model (Chapter 4).

A special kind of relationship is the connection with the past. In temperate regions, aquatic ecosystems may seem to 'reset' seasonally (Knowlton, 1992). If there is no dependence on the population of the previous year, the initial conditions of each year are equal, making it unlikely that phenomena such as multi-year cycles or alternative equilibria will occur. An example of almost complete uncoupling is the recruitment of fish populations, which is often poorly related to the number of mature fishes (Ricker, 1975). However, in most cases (aquatic vegetation (Chapter 3, 4) or plankton (Scheffer et al., 1997)) the relation with the previous year will be strong. In such cases, one can reset (some of) the species or state variables yearly, to check if the 'memory' of the system is essential for the observed dynamics.

Another source of the incomprehensibility of a model is variability and stochasticy. For instance, in individual-based models, the individuals usually have properties drawn from probability distributions. This variability is essential for explaining phenomena such as cannibalism within year classes of predatory fishes (DeAngelis et al., 1979), but can also make the model behavior difficult to understand. An individual-based model can be simplified by making all individuals equal. If the model uses the concept of super-individuals (Chapter 2) this can be relatively easy to accomplish. Analogously, spatial heterogeneity may complicate the analysis of models. In case of grid-based models, it can be useful to simplify it by considering only one grid cell.

Stochastic processes like weather effects can reduce the transparency of the model too, as the patterns become noisy. Using a fitted sinusoid for seasonal variables without any noise superimposed on it, can eliminate this. In individual-based models there can also be stochastic fluctuations if the number of modeled individuals is small and the stochasticity of mortality of single individuals becomes visible. Such effects may be real in certain small populations, but can also be a confusing artifact of considering too few individuals in the model. The effect can be eliminated by increasing the modeled area or replacing stochastic mortality by a fixed mortality rate (again the use of super-individuals (Chapter 2) may help).

The most drastic way to simplify the model is to make an independent minimal model that describes the dominant mechanisms of the full model (e.g., Murray, 2001). If both models produce qualitatively similar results, this approach is very powerful (Chapter 6), as it combines the advantages of both worlds. The simple model can be used to explain and communicate the (possible) causes of the phenomenon clearly, whereas the complex model can help to substantiate that the produced patterns are no artifact of the simplifications of the minimal model.

Synthesizing

The results of a parameter analysis of the simplified models should obviously be compared with the full model. This comparison is necessarily somewhat subjective, because to our knowledge there are no automated ways to compare qualitative patterns. Furthermore, there can be multiple causes for one phenomenon. Therefore, even if the causation in the simplified model is correct, it may capture only part of the mechanisms that cause the phenomenon in the elaborate model. The simplifying approach can fail if all results are simply very different from each other. Then it may help to simplify the model along other lines, often in a more subtle way.

If the mechanism that causes the pattern becomes clear, the next step is to check whether the proposed mechanism is already known and tested in literature or found in other models. If this is not the case, one should discuss whether the created hypotheses are credible and worth to be studied further or whether it is likely to be a model artifact. In the latter case, one may decide to change the model formulation and redo the analysis.

Concluding remarks

The proposed simplifying techniques can be facilitated greatly by a clever software implementation of the model. Object oriented programming (OOP) facilitates a modular design which makes simplification easier and is generally recommended for creating ecosystem models (Silvert, 1993) and individual-based models (Baveco and Lingeman, 1992; Lorek and Sonnenschein, 1999). The scrutinization part requires that the software include tools for finding bifurcations and other important indicators of the model behavior. To our knowledge, none of the published modeling frameworks (reviewed in: Lorek and Sonnenschein, 1999) include tools suitable for such analyses. This is unfortunate, as brute force techniques are still the only option for scrutinizing complex models. Standard techniques for the analysis of simple sets of ordinary differential equations are usually of no use for large simulation models. For instance, construction of zero-growth isoclines is an important classical tool in minimal model analyses. However, such isoclines are of very limited use in complex models because the initial conditions are usually too complex to be described for two or three state variables. Moreover, seasonality and spatial heterogeneity cannot be dealt with using this technique. Also, current techniques for automated continuation of bifurcations which are powerful tools for analyzing simple models (Kuznetsov, 1995), fail in complex simulation models. A practical problem of the brute force techniques that we advocate, is that for some large models, the analyses take days of computation time. Although this will remain a problem, the ever-increasing processor speed of computers makes such analyses certainly more feasible in the future.

Certainly our scrutinize-simplify-synthesize (s^3) approach does not solve all problems with large simulation models. Incomplete documentation, uncertainties in parameter settings and lack of generality remain drawbacks of complex models. However, as argued earlier, minimal models also have their limitations (e.g., testability, focus on one cause and impossibility to address certain mechanisms). Our approach is an attempt to have the best of both worlds. Additionally, the simplifying technique may be used to search for the simplest hypothesis capable of generating an observed pattern (Caswell, 1988). Usually we consider a simple, parsimonious theory to be better than a complex one (Onstad, 1988). Simplifying can also show the robustness of the results to changes in model structure.

Certainly, there is a danger in cycling too long between several versions of models. This process may lead to an increasing faith of the modeler in the model, while the modeled world becomes a world of it own, possibly moving away from reality (Grimm, 1994). Indeed, the synthesis part of the s^3 cycle, in which results are confronted not only between models but also to empirical results, is probably the most important step in advancing towards a real understanding of the studied system.

It is noteworthy that there is a remarkable similarity between our modeling approach and the usual approach in empirical systems ecology. Also in experiments there is a trade-off between realism and understandability. Large ecosystem experiments produce mostly results that are hard to interpret and irreproducible for other scientists and other ecosystems. Controlled small-scale laboratory experiments give much clearer and better reproducible results, but it remains unclear whether observed mechanisms are the dominant mechanisms explaining the behavior of the real system. Studying a phenomenon by combining ecosystem experiments, enclosure studies, mesocosms and small-scale laboratory experiments often gives the best insight in the functioning of the real system.

Certainly, our insight in the functioning of complex ecological systems would benefit most from an integrated approach in which results from small and large scale experiments are confronted in smart ways with results from simple and elaborate models.

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Chapter 2

Super-individuals, a simple solution for modeling large populations on an individual basis

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Abstract

Modeling populations on an individual-by-individual basis has proven to be a fruitful approach. Many complex patterns that are observed on the population level have been shown to arise from simple interactions between individuals. However, a major problem with these models is that the typically large number of individuals needed requires impractically large computation times. The common solution, reduction of the number of individuals in the model, can lead to loss of variation, irregular dynamics, and large sensitivity to the value of random generator seeds. As a solution to these problems, we propose to add an extra variable feature to each model individual, namely the number of real individuals it actually represents. This approach allows zooming from a real individual-by-individual model to a cohort representation or ultimately an all-animals-are-equal view without changing the model formulation. Therefore, the super-individual concept offers easy possibilities to check whether the observed behavior is an artifact of following a limited number of individuals or of lumping individuals, and also to verify whether individual variability is indeed an essential ingredient for the observed behavior. In addition, the approach offers arbitrarily large computational advantages. As an example the super-individual approach is applied to a generic model of the dynamics of a size-distributed consumer cohort, as well as to an elaborate applied simulation model of the recruitment of striped bass.

Introduction

The many advantages of individual-based models in ecology have been pointed out extensively by Huston et al. (1988), by Hogeweg and Hesper (1990), and by various authors in the recently published book on this subject (DeAngelis and Gross, 1992). To mention a few:

- Parameters needed in the models (like speed of movement, amount eaten per day etc.) as well as the predicted variables (like individual numbers, diets and conditions) are typically of the type measured by experimental biologists.
- Model behavior is often rather robust to variations in formulation of the processes.
- Instead of implicitly assuming information processing on the population level, individuals are taken as the natural units, which is more realistic and intuitively straightforward.

Individual-based models seem a promising way to fill the gap between modelers and experimental biologists. They explain often complex population phenomena from common knowledge about individual behavior, rather than mimicking the patterns by means of mathematical constructs that hardly appeal to the average biologist. The obvious disadvantage of modeling populations individual-by-individual, is that it takes impractically much computation time to simulate realistic numbers for most populations, especially if the individual behavior is rather elaborate like in many applied models. There are basically three ways out of this problem: wait until computers are faster; use continuous distributions to represent the population structure rather than separate individuals; or use a smaller number of individuals to represent the population. We will neither attempt to speculate on the development of computer technology, nor mingle in the discussion about the various advantages and disadvantages of distribution models as opposed to individual-by-individual models (Metz and Diekmann, 1986; DeAngelis and Gross, 1992). Instead, we address the common approach to represent the population by a smaller number of individuals. The problems associated with various methods to do this are discussed, and the concept of ‘super-individuals’ is presented as a convenient solution.

Problems of following a subset of the population

Results from simulations with a randomly drawn subset of individuals can differ significantly from full set runs for a number of reasons. Importantly, the represented range of most individual features will be reduced (Fig. 2.1). This can be especially influential when outliers, like large individuals, play a key role in the population (Huston et al., 1988). A bothersome effect of small numbers from the modelers point-of-view, is that simulation outcomes can be quite different depending on the values of seeds of random number generators. A third problem of reduced numbers is that in smaller populations, events like the death of important individuals are increasingly influential to the dynamics of the system. The introduced noise tends to prevent the manifestation of point, cyclic or strange attractors that may be clear in systems with large numbers (Scheffer et al., unpublished).

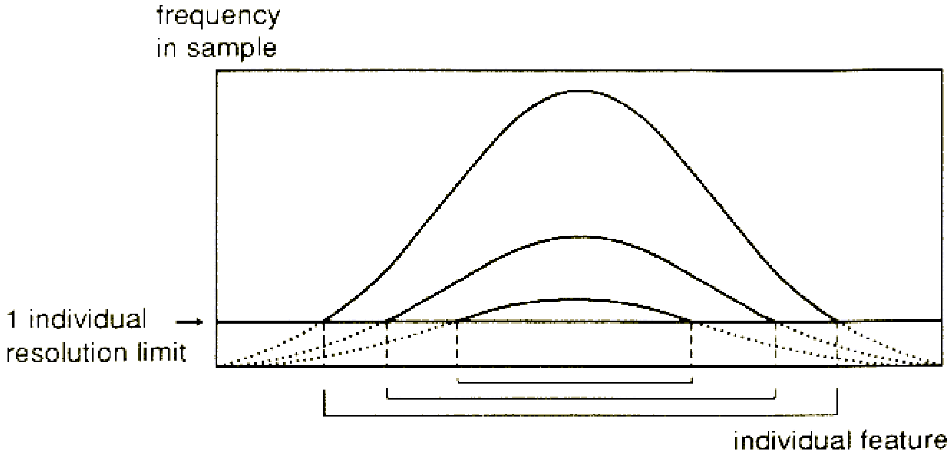

Fig. 2.1 *Loss of variance with decreasing size of a random subset from the population due to the fact that one individual is the smallest unit.*

Obviously, these 'problems' are exactly the reason why individual-by-individual models are a tool par-excellence to study the mechanisms in real small populations. However, when studying large populations, they need to be avoided.

A trivial way to control the side effects of small numbers is to try simulations with different numbers of individuals and select the smallest sample size that does not seem to produce spurious results for further simulation. Obviously, this is a rather arbitrary approach. Furthermore, the required number of individuals will frequently still be very large. Especially in cases where survival is low (e.g. <<1% in early life of many fish, Bailey and Houde, 1989) initial numbers should be huge to allow sufficient survivors, unless scaling is adjusted in some way over time (Rose et al., 1993). Finding a reasonable compromise in scaling is also difficult when different considered groups of animals have very different individual densities, as is often the case with predators and prey. This can be partially solved by following the more abundant groups in smaller hypothetical subspaces (Fig. 2.2a). By choosing the volume ratios correctly, the different groups can then be followed in the same amount of detail. The coupling between the two scales is via the assumption that what happens in the subspace is representative for the rest of the volume. Although tricks like dynamic and multiple scaling reduce the problems associated with following small subsets they cannot eliminate them.

The super-individual concept

The problem of any scaling approach is that there is essentially no free lunch. The effects of reduced numbers can be limited by cutting corners in the smartest way, but they can not be eliminated. We therefore propose to pay for the lunch by adding an extra feature to each model individual, the amount of individuals that it actually represents (Fig. 2.2b). Thus, the resulting 'super-individuals' are in fact nothing else than classes of individuals ('generalized individuals' *sensu* Metz and De Roos, 1992).

A first decision to be made in this approach is which individuals in the population should combined in one super-individual. If simulations start of with a population where the individual properties like weight and length are defined by one or more frequency distributions, an obvious choice is to define super-individuals that combine population individuals within fixed intervals of these properties. This approach is illustrated by the first example given below. Often, however, it may be useful to fuse individuals one or more times during the simulation process. This is typically necessary when reproduction episodes cause large increases in individual numbers. The most pragmatic solution is to select a random subset of the new individuals and turn them into super-individuals by assigning 'internal amounts' (i.e. the number of population individuals each of them represents) computed as the inverse of the sample fraction so as to keep the balance correct. This approach is illustrated by our second example below. A more sophisticated approach is to check the state of each individual first and subsequently fuse clusters of similar individuals into super-individuals with an internal amount set by the cluster size and an individual state set by the cluster centroid. An example of an efficient algorithm to fuse individuals according to their similarity can be found in Stage et al. (1993).

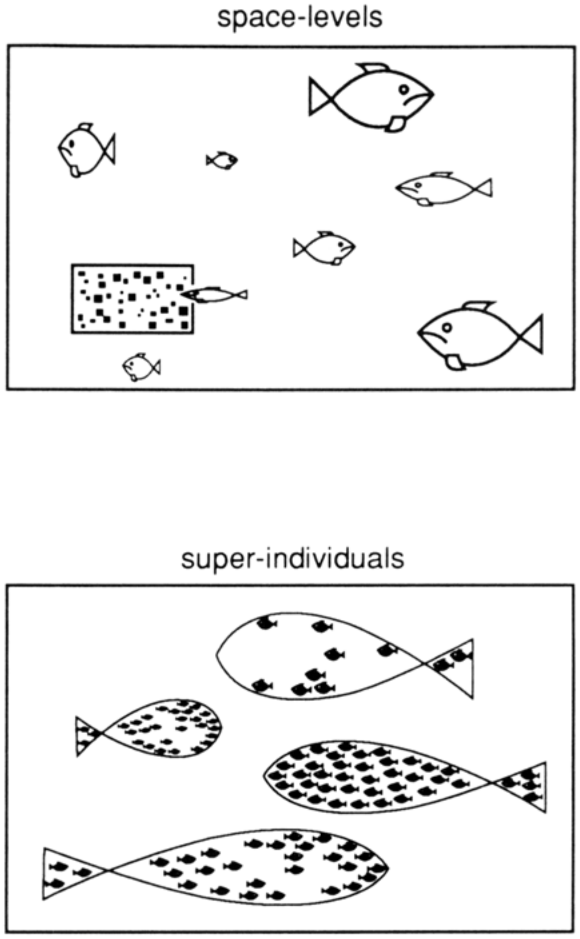

Fig. 2.2 *Two approaches of reducing computational costs in individual-by-individual models.*

In the course of the simulation, the internal amount should of course be affected by loss processes like death and immigration. Often, there will be a fixed background probability of mortality due to causes that are not explicitly modeled, in addition most individual-based models contain conditional mortality, depending on explicitly modeled processes (i.e. individuals die from starvation when they lose more then a critical proportion of their weight). Typically, background mortality is realized in individual-by-individual models by drawing the answer to the to-die-or-not-to-die question for each individual from a Bernoulli distribution. In stead of repeating this procedure n-times (n being the internal amount) for each super-individual, we can draw the number of survivors directly from a binomial probability density distribution with a sample size of n. Handling conditional mortality like the death of individuals from starvation is slightly more complicated. The simplest way of handling it is to let a super-individual die completely when its conditions for mortality are fulfilled (i.e. when it lost half its weight due to starvation). This assumes all population individuals represented by the super-individual to be equal in their sensitivity to the mortality cause. Obviously, individuals being equal in a number of aspects still differ in many others that may not be explicitly modeled or measured, but still influence their fitness and their sensitivity to threats. Even in relatively uniform laboratory populations used to test the toxicity of chemical agents, for instance, some individuals die sooner than others, which is why the results of such tests are usually presented in statistics like the concentration of the substance that, after a standard time, leads to mortality of 50% of the individuals (‘lc-50’). Therefore, it is more realistic to account for such background variance in fitness by letting some individuals die sooner than others within the same super-individual. There are several possible ways of handling this.

A pragmatic solution is to set the mortality probability to a fixed (high) value for as long as the super-individual is in the danger condition. The lower the variance in fitness within a super-individual, the higher this conditional mortality probability should be. The extreme situation is a 100% instantaneous die-off representing a situation again in which all animals represented by the super-individual are equal with respect to their sensitivity to the considered mortality cause.

As argued, mortality can be handled by drawing the number of survivors within each super-individual from a binomial distribution with a sample size equal to the internal amount n. For n=1 this is the same as the traditional drawing of the answer to the to-die-or-not-to-die question from a Bernoulli distribution (which is just a special case of the binomial). This implies that if we start simulations giving each super-individual an initial internal amount of 1, we simply have a full-scale individual-by-individual approach.

Drawing a number A from a binomial distribution sounds easier than it is. A computationally fast way is to use the recursive notation of the binomial frequency distribution. First compute a pseudo-random number *r*. Then compute the probability of zero mortality:

$$p_0 = (1-p)^n \tag{2.1}$$

Proceed through the subsequent classes using the recursive notation:

$$p_x = p_{x-1}\frac{(n-x+1)\,p}{x(1-p)} \tag{2.2}$$

until:

$$\sum_{x=0}^{A} p_x \geq r \tag{2.3}$$

If the product of n and p is larger than 5 the binomial distribution can be approximated by a normal distribution with a mean of p and a standard deviation of $(n\ p\ (1 - p))^{0.5}$, reducing the computational burden further.

It can be useful for some applications (e.g. the reconstruction of complex cycles or strange attractors) to get rid of the stochasticity completely. This can be achieved in the super-individual approach by considering the internal amount as a real instead of an integer and computing the mortality fraction simply by multiplying its value with the probability of mortality. This also speeds up the computations further. For high n the difference between the approaches is small since the stochasticity becomes especially apparent if the remaining number of individuals is small. Therefore, a hybrid approach can be convenient, switching to drawing from probability distributions only below a certain value of n, combining high computational speed with essential stochasticity at low individual numbers. The latter approach is used for the examples given in the final section of this paper.

The possibility of changing from a full-scale individual-by-individual approach to a super-individual one without changing the model formulation, can be very useful. The computational burden imposed by the pure individual-by-individual version can be reduced at any time by decreasing the number of super-individuals while increasing their internal amounts, allowing quick simulations that represent huge numbers of individuals. But perhaps more importantly, the flexibility of switching between the two approaches facilitates the detection of computational artifacts imposed by either of the two. Another useful feature of the super-individual concept is that in the extreme case a whole population or cohort can be represented by just one super-individual. This allows a quick and easy check whether individual differences are indeed essential to produce the observed patterns. Although, in theory, this can also be done by making all individuals initially the same in an individual-by-individual model, it appears difficult to realize that in practice since there will always be an increase of variance over time if there is stochasticity in the events experienced by different individuals.

Related solutions

Among the solutions that have been proposed to reduce the computational problems associated with individual-based modeling, two deserve some special attention here because they appear closely related to the super-individual approach: the resampling algorithm of Rose et al. (1993) and the cohort representation of Metz et al. (1988).

To a certain extent, the resampling algorithm is indeed quite comparable to the super-individual idea presented here. Resampling also uses super-individuals. There is, however, a crucial difference in the way mortality is handled. In the resampling algorithm, mortality always leads to the complete elimination of a ‘super-individual’ rather than reduction of the number of population individuals it represents. To keep the number of super-individuals in the simulated subset of the population constant the perished super-individual is replaced by a copy from a randomly selected surviving super-individual. The number of individuals represented by this survivor is then divided among the original and the cloned version. By definition, this resampling algorithm leads to a decrease of diversity in the simulated set of individuals due to the cloning. When the modeled subset is still large and when cloned individuals quickly diverge because of stochasticity in, for instance, their interaction with the environment, the diversity loss will be minor. Indeed, Rose et al. (1993) show for a model of young striped bass that a version with resampling closely mimics the behavior of the original model. However, in other cases the diversity loss may become more pronounced. While sharing the advantages of the resampling algorithm, the super-individual approach we propose now avoids this side effect.

In the cohort representation (Metz et al., 1988; De Roos et al., 1992) or, more generally, in the *i*-space distribution models (Metz and Diekmann, 1986) with a discrete distribution function, the individuals are grouped in classes and a density function keeps track of the actual number of individuals in each class. Although this suggests a similarity with the super-individual formalism, the approaches differ widely for all practical purposes. The cohort representation belongs in the family of *i*-space distribution models. In these models, partial differential equations are used to follow the frequency distribution of attributes of individuals in the population through time. The various advantages and disadvantages of explicit simulation of individuals relative to the partial differential equation approach are outlined extensively by DeAngelis and Rose (1992). They conclude that, while both approaches have their pros and cons, a key advantage of the actual simulation of individuals is that it allows for much greater flexibility in model formulation. A main caveat of this approach is that computational artifacts tend to arise when a small subset of the population is followed to keep the simulation computationally feasible. As argued in this paper the simple trick of using super-individuals is a practical way to eliminate many of these problems.

Two examples

To illustrate the power of the super-individual approach we give two examples of its application. In the first example the method is applied to a relatively simple generic model of the dynamics of a developing cohort of animals and their food. In the second case, the approach is tested on an elaborate realistic model of the recruitment of a population of striped bass (an American fish species). Although its complexity prohibits an exhaustive description of its formulation within the scope of this paper, we include this example as this model may be considered typical of many applied individual-based models.

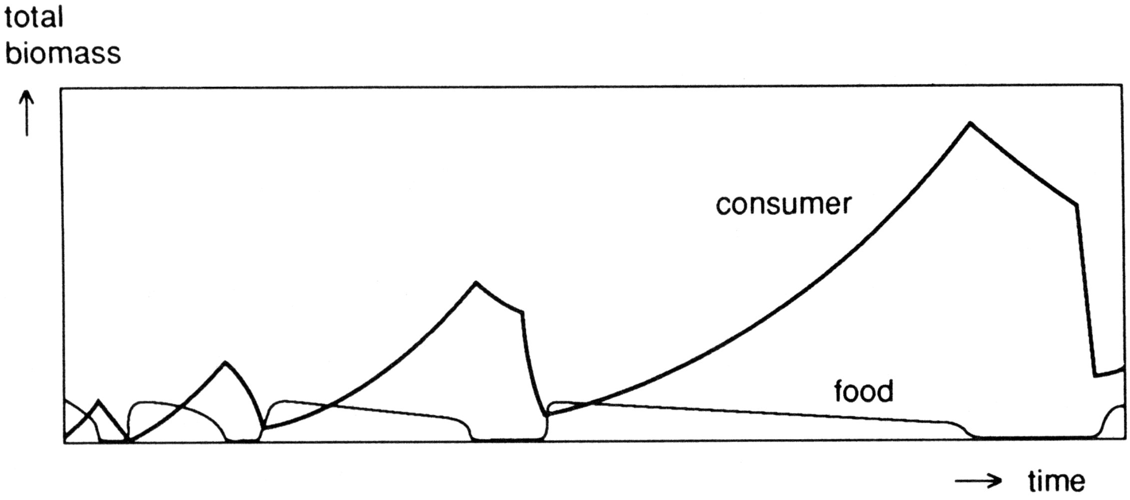

Fig. 2.3 Cycles in the total biomass of a consumer cohort and its food produced by an individual-based model.

Starvation in a size-distributed consumer cohort

As a first example of the application of the super-individual approach we use a model that describes the dynamics of a size-distributed cohort of animals foraging on a logistically growing food population. The model is written in the object oriented language SMALLTALK using a toolkit for ecological modeling called ECOTALK (Baveco and Smeulders, 1994).

The consumer individuals have a weight, W_i (g), which is governed by simple energetic rules accounting for consumption, C_i (g d^{-1}), respiration, R_i (g d^{-1}), and an efficiency for converting food to body weight, e (g g^{-1}):

$$W_{i,t+1} = W_{i,t} + e\ C_i - R_i \tag{2.4}$$

Since small animals have higher weight-specific metabolic rates, the daily ration relative to that of a 1-gram animal, c_{ref} (g d^{-1}), declines with body weight. The actual uptake is also a function of food density, F_t (g m^{-3}), formulated as a Monod function with a half saturation constant, H (g m^{-3}) after subtraction of the lowest exploitable food level, Q (g m^{-3}):

$$C_i = c_{ref}\ W_i^{2/3} \frac{F_t - Q}{F_t - Q + H} \tag{2.5}$$

Respiration, like consumption, is computed relative to that of a 1 gram animal, r_{ref} (g d^{-1}), and is dependent on the body weight of the animal:

$$R_i = r_{ref}\ W_i^{2/3} \tag{2.6}$$

During periods of food shortage, respiration can exceed energy uptake, resulting in weight loss. When animals lose more than 25% of their weight, they are put in a starvation mode. Whether an animal in this mode dies or not is decided by drawing from a Bernoulli distribution with a mean of 0.1 each day.

Growth of the food population is formulated in a logistic fashion as a function of the current density, F_t (g m^{-3}), the maximum growth rate, g_{max} (d^{-1}) a carrying capacity K (g m^{-3}), and the losses due to consumption:

$$F_{t+1} = F_t + g_{\max} F_t \frac{K - F_t}{K} - \sum C_{i,t} \qquad (2.7)$$

If we run the model for a large number of individuals, some interesting patterns emerge. A time plot of food biomass and the total biomass of the consumer cohort shows cycles of increasing period (Fig. 2.3). Each cycle starts with an increase of consumer biomass due to individual growth. At a certain moment food collapses due to the increased consumption and subsequently the consumer individuals begin to lose weight. When the weight loss exceeds 25% starvation mortality speeds up the decline in total consumer biomass. The resulting decrease in grazing pressure allows the food population to recover, saving the survivors from further starvation. Their resumed growth sets off a new cycle. In each new cycle, the maximum biomass of the consumer cohort becomes higher. This is because the cohort consists of increasingly fewer but bigger individuals, and since bigger individuals have a lower weight specific metabolism a higher total biomass of them can be tolerated by the food population before it collapses. A thorough treatment of the phenomenon of periodic die-off in consumer cohorts and its relevance to natural populations is given elsewhere (Scheffer et al., 1995).

If we make snapshots of the size distribution of the consumer cohort after each die-off cycle, it can be seen that with the loss of individuals the shape of the size distribution deteriorates quite fast (Fig. 2.4a). The problem can be postponed by scaling up the system and increasing the number of individuals in the simulation from 500 to 10 000 (Fig. 2.4b), but this also increases the computation time from 6 minutes to more then 2 hours (on a 486 computer). If we think of the consumer cohort as young-of-the-year fish in a lake, the real number of individuals involved will be order of millions rather than thousands. The corresponding computation time in case of this extremely simple model would be a few months and expansion of the model to include a more realistic behavior of the individuals would easily blow up the computation time to a few years.

In order to overcome such computational problems we change the individuals into super-individuals by introducing the extra feature 'internal amount', S_i, being the number of individuals that it actually represents. Instead of drawing the initial size of the animals from a normal distribution, we now shape the size distribution by assigning appropriate internal amounts. If a super-individual enters the starvation mode its internal amount is decreased by 10% each day. When S_i falls below 1, the actual moment of extinction is decided by drawing from a Bernoulli distribution with a mean of 0.1 each day like in the plain individual-by-individual case. The simulation with super-individuals (Fig. 2.4c) takes less than one minute while preserving a smooth pattern in the size distribution throughout the observed period.

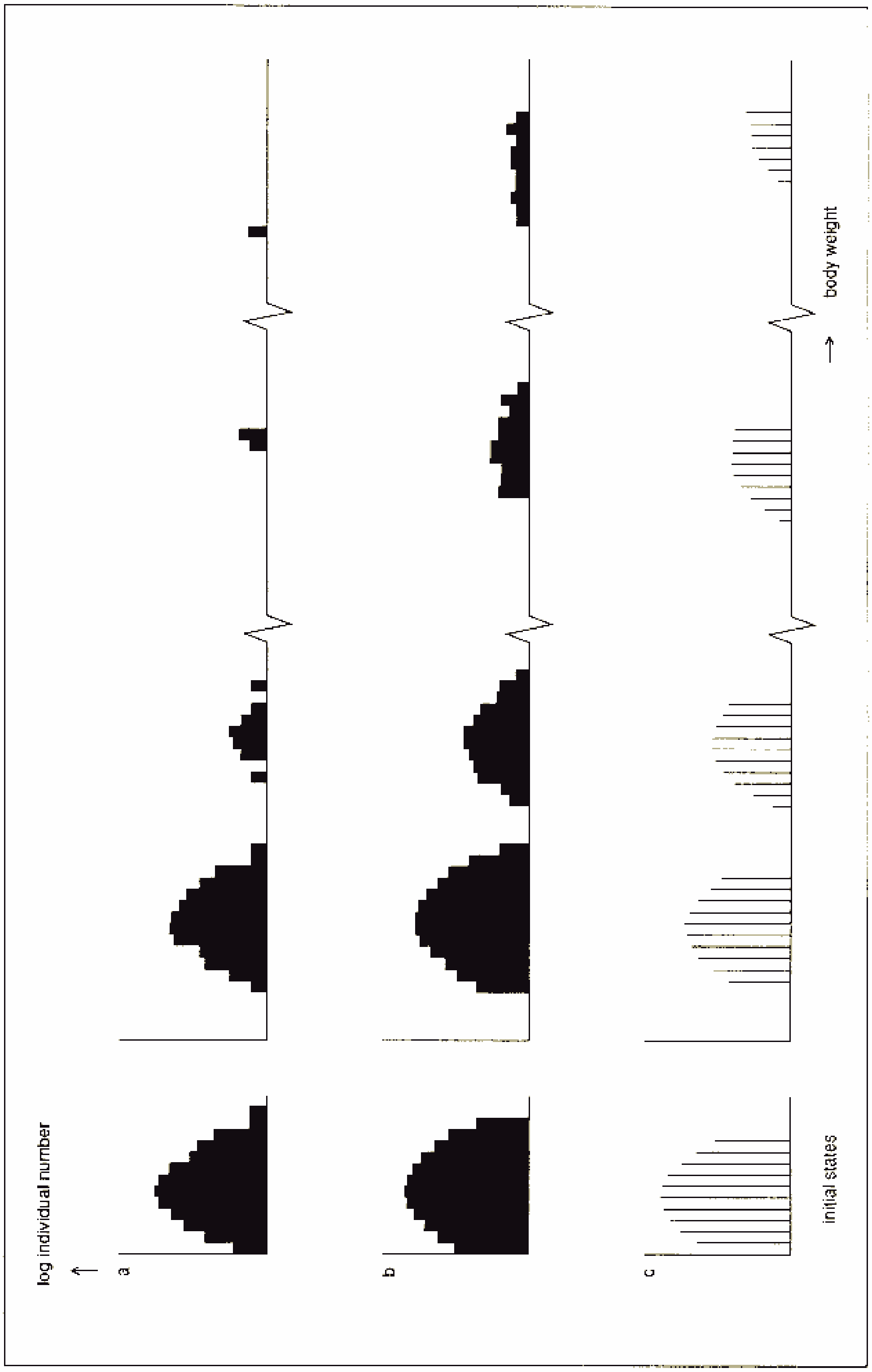

Fig. 2.4 *Snapshots of the size distribution of the consumer cohort after each of the cycles shown in Fig. 2.3. (a) A simulation starting off with 500 individuals. (b) A simulation starting off with 10 000 individuals. (c) A simulation with 10 super-individuals. Note that in the latter case each bar represents one super-individual.*

Recruitment of striped bass

The striped bass model is typical of many of the more elaborate applied individual-based simulation models. A detailed description of the model can be found in Rose and Cowan (1993).

The striped bass model begins with the spawning of individual females and simulates the growth and mortality of the spawned striped bass as they develop through the life stages of egg, yolk-sac larva, larva, and juvenile during their first year of life. The model represents these dynamics on a daily basis in a single, well-mixed compartment (700 m x 700 m x 4 m deep). Model simulations are of one year duration beginning on April 10. The environmental conditions in the compartment consist of daily water temperature, fraction of the day there is daylight, and the daily densities of zooplankton and benthic prey types.

Each female's spawn of eggs is followed as an individual entity (i.e., female's cohort of eggs) with daily temperatures determining hatching into yolk-sac larvae and then, with initiation of exogenous feeding, development into larvae. Upon initiation of first feeding, initial weight (mg dw) and length (mm) of feeding larvae in each female cohort are determined from egg weight which varies with female size. The number of eggs and then yolk-sac larvae in each female egg-cohort are reduced daily according to the fraction dying.

Daily growth of each individual larva beginning with first feeding is represented with a difference form of a bioenergetics equation.

$$W_t = W_{t-1} + p\ C_{\max} A - R_{tot} \tag{2.8}$$

Where W_t = individual weight at day t (mg dw); p = proportion of C_{max} realized; C_{max} = maximum consumption rate (mg dw d^{-1}); A = utilization efficiency; R_{tot} = total metabolic rate (mg dw d^{-1}). The proportion (p) of C_{max} realized by a larva on a given day, is determined based on stochastic prey encounters. Multiple zooplankton prey groups for larvae and benthic prey groups for juveniles are represented in the model. C_{max} and R_{tot} depend on larvae weight and temperature.

Table 2.1 *Average growth and mortality rates of larval striped bass in a full individual-by-individual simulation compared to simulations where the population is represented by increasingly few super-individuals. Results for three different random generator seeds are shown. The number of population individuals (and hence of individuals in the full run) is 209 992, 195 311 and 178 177 for seeds A, B and C respectively.*

Number of model individuals	Growth rate (mm d^{-1}), random generator seed			Mortality rate (d^{-1}), random generator seed		
	A	B	C	A	B	C
Full i-by-i run	0.553	0.564	0.568	0.166	0.162	0.162
10 000	0.552	0.565	0.567	0.165	0.163	0.162
1000	0.554	0.565	0.567	0.165	0.162	0.162
500	0.552	0.566	0.566	0.164	0.163	0.162
100	0.542	0.559	0.567	0.165	0.164	0.163
20	0.553	0.585	0.582	0.162	0.165	0.161

Table 2.2 *Comparison between the loss of accuracy in the super-individual approach and in the resampling procedure of Rose et al. (1993) when the population is represented by an increasingly small number of model individuals. Absolute deviations from the growth and mortality rates produced by a full individual-by-individual run (about 200 000 individuals, see Table 1) are averaged for three simulation runs with different random seeds.*

number of model-individuals	% deviation in growth rate		% deviation in mortality rate	
	super-i	resampling	super-i	resampling
10 000	0.2	0.1	0.4	0.8
1000	0.2	0.8	0.2	0.4
500	0.3	1.7	0.6	2.0
100	0.4	2.6	0.8	2.9
20	2.1	7.4	1.6	4.9

Mortality of individual larvae and juveniles depends on weight and length. Weight-dependent mortality is based on laboratory data at low food levels without predators and therefore can be viewed as starvation-related mortality. The weight of an individual larva or juvenile is evaluated each day, and if its weight is less than some fraction (0.65 for larvae and 0.5 for juveniles) of the average weight for an individual of that length, the individual is assumed to die. Length-dependent mortality is estimated from field data and is therefore representative of predation and other losses. Probability of dying (P_d) is evaluated daily for each individual, based on its length (L); $P_d = (1 - e^{-M})$, where $M = 0.003 + 0.295\ e^{-0.075\ L}$. If a generated random number from a uniform distribution between 0 and 1 is less than P_d, the model individual is assumed to die.

In full individual-by-individual simulations all larvae are followed separately from the moment that they first start feeding (the transition from yolk-sac larvae to larvae). The total number of individual larvae in this stage differs slightly with the randomly drawn sizes of the spawning females but is typically around 200 000. For the super-individual simulation, a sample of individual larvae at first feeding is taken from each female egg-cohort in proportion to the number of surviving first feeding larvae in that cohort. These larvae are converted into super-individuals by assigning them an initial internal amount (S_i), of T/N where T is the total number of surviving first feeding larvae obtained by summing over all female eggs-cohorts and N is the total number of super-individuals to be followed. Mortality in super-individuals is handled as in the former example.

To check how the use of super-individuals affects the model results we performed a simulation with the full individual-by-individual version followed by a series of simulations in which the larval population was represented by an increasingly small number of super-individuals. We focus on the deviations in growth and mortality rates that occur relative to the full-blown simulation (Table 2.1). Those larval rates are important as they greatly influence the overall model predictions of striped bass recruitment. Even if the 200 000 individuals are represented by as few as 20 super-individuals the deviation from the full individual-by-individual simulation is only about 2 percent. The results are more than three times as accurate as the results obtained by the already quite effective resampling procedure (Table 2.2) used in Rose et al. (1993), while taking slightly less computation time.

We conclude that in addition to being conceptually simple and attractive, the super-individual approach is also a powerful tool when it comes to reducing the computational burden of running elaborate individual-based models while retaining a high accuracy.

Acknowledgments

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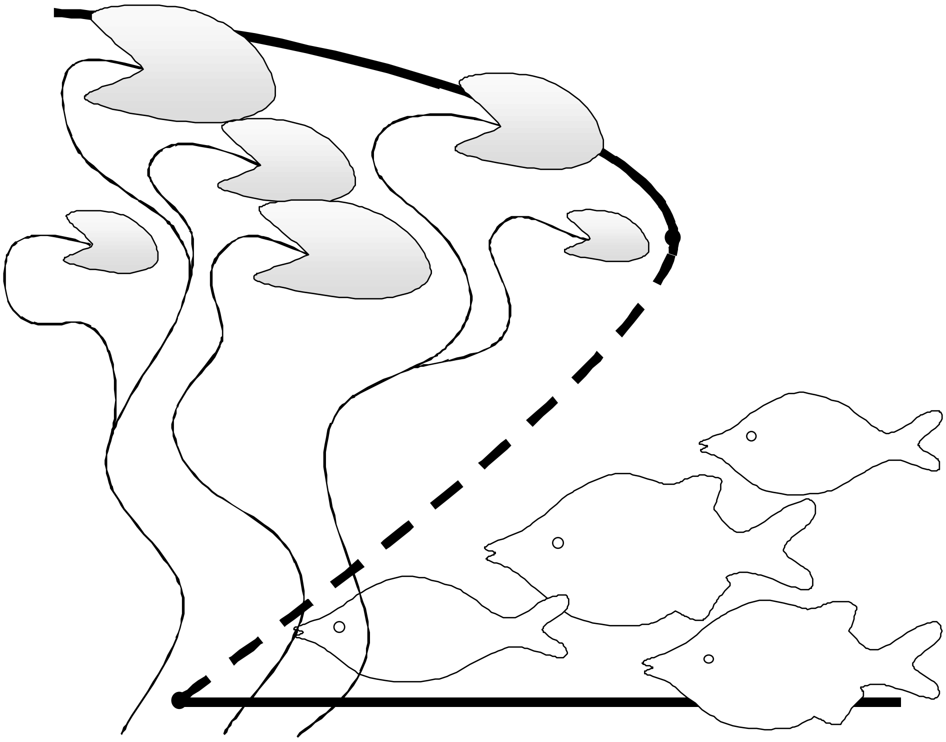
Part II: Modeling Aquatic Vegetation



Chapter 3
Charisma: a spatial explicit simulation model of submerged macrophytes

Egbert H. van Nes, Marten Scheffer, Marcel S. van den Berg & Hugo Coops

Based on:
Charisma: a spatial explicit simulation model of submerged macrophytes, submitted
Alternative attractors may boost uncertainty and sensitivity in ecological models, submitted

Abstract

An important problem in lake management is the replacement of submerged plant species by competing species with undesirable properties. Although dynamics of aquatic macrophytes have been extensively modeled, competition between different species has hardly been addressed so far. We present an individual-based spatially explicit model ('Charisma') designed to simulate the growth of one or more competing species of submerged macrophytes. The model behavior easily becomes rather complex and puzzling if we study more than one species. This probably reflects real complexity in nature, but poses a challenge for calibrating and understanding the model. To control this complexity, we used a flexible design facilitating the elimination of feedback loops and processes to trace the causes of the complex behavior of the model. The resulting 'realistic yet transparent' model appeared useful in many aspects for bridging the existing gap between theory and reality. As an example, we present an analysis of competition between the charophyte *Chara aspera* Deth. ex Willd. and pondweed *Potamogeton pectinatus* L. The model suggests that alternative equilibria may arise as a result of two positive feedbacks: the enhancement of transparency by macrophytes and a feedback caused by bicarbonate competition. Monte-Carlo uncertainty analysis revealed a particular phenomenon related to the existence of such multiple attractors. If the variation of the parameters is large enough to cause a switch between alternative equilibria, a variation of ± 10% in all parameters may lead to a variation of predicted summer biomass as large as ± 90%. Such amplification of sensitivity is restricted to certain regions of the parameter space. Corollaries in terms of real macrophyte dynamics are that under some conditions, small environmental variation may blow up to large changes in vegetation abundance, and that sensitivity to disturbances may vary strongly depending on the conditions.

Introduction

Submerged aquatic plants have significant effects on many abiotic and biotic components of the ecosystem of shallow lakes and streams (Søndergaard and Moss, 1998). One of the most persistently reported effects is that vegetation enhances water clarity, although the mechanisms causing this effect may vary from case to case (see review: Scheffer, 1998). Proposed mechanisms are a reduction of wave resuspension by macrophytes, an allopathic impact on the algal community, and provision of shelter for zooplankton and fish.

Growth of macrophytes is regulated by various environmental factors such as available light, temperature, nutrients including bicarbonate, sediment stability, wave action, changes in water level, and by grazing by several species of birds and fish (Scheffer, 1998). The feedback loops between vegetation growth an environmental factors such as turbidity, can make the response of macrophyte development to environmental change highly non-linear. Since we know still relatively little about many potentially important aspects, such as foraging behavior of grazing birds, deterministic growth models are a rather unreliable tool for quantitative predictions of vegetation dynamics (Scheffer, 1991). Nonetheless, simulation models can be highly valuable to integrate available knowledge in order to obtain a better understanding of the potential causes of observed patterns. Also, such models may generate new hypotheses that can subsequently be tested either in the field or in the laboratory.

Several simulation models of macrophytes have been developed to investigate the effect of macrophytes on their environment and *vice versa*. Such models have been reviewed by Best (1990) and more recently by Carr et al. (1997). Some of these models describe the macrophyte vegetation as a whole, without differentiation of species level (Wright and McDonnell, 1986; Collins and Wlosinski, 1989; Janse, 1998; Muhammetoglu and Soyupak, 2000). More frequently, the simulation models describe the growth of one species, using detailed physiological data on particular species on interest such as *Myriophyllum spicatum* L. (Titus et al., 1975), *Ceratophyllum demersum* L. (Best, 1981), *Hydrilla verticillata* (L.F.) Royle (Chen and Coughenour, 1996), *Potamogeton pectinatus* L. (Scheffer et al., 1993a; Van Dijk and Janse, 1993; Hootsmans, 1994; Asaeda and Van Bon, 1997; Hootsmans, 1999), *Ruppia cirrhosa* Petagna (Grande) (Calado and Duarte, 2000) and *Zostera marina* L. (e.g., Short, 1980; Verhagen and Nienhuis, 1983; Wetzel and Neckles, 1987; Bach, 1993). Other models are mainly focused on spatial processes (Chiarello and Barrat-Segretain, 1997; Wortmann et al., 1997). So far, however, competition between macrophyte species has hardly been addressed in models (Wortelboer, 1990; Davis and McDonnell, 1997).

In this paper, we present the model Charisma, an individual-based macrophyte model, that can be used in a spatially explicit way. The number of interacting species in the model can range from one to many. As an example we use the model to analyze the competition between the charophyte species *Chara aspera* Deth. ex Willd and pondweed *Potamogeton pectinatus* L. The physiological rules of the model are based upon those used in the model MEGAPLANT (Scheffer et al., 1993a) and extended with bicarbonate limitation (Van den Berg, in press) and some spatially explicit processes.

As we will show, the behavior of the model can be rather complex and puzzling if we study more than one species. To control this complexity, the model has a flexible design facilitating analyses of simplified versions. We demonstrate this by shutting off several feedback loops and processes, showing which processes cause the complex behavior of the model. Furthermore, we use Monte Carlo techniques (Klepper et al., 1994) to trace which parameters have the most significant effect on the model output, how effects of different parameters are correlated, and how uncertainty in the model parameters (expressed in posterior probability distributions) is reflected in the model results. We also analyze the phenomenon that alternative equilibria can locally boost the sensitivity of the model.

The model

Much of the formulations are based on an earlier model (Scheffer et al., 1993a), extended along two lines. Firstly, the model is made spatially explicit by associating all plants and overwintering structures (hibernacula) with grid cells, and adding spatial processes, such as seed or oospore dispersal. Secondly, we made it possible to simulate competition for light and nutrients between two or more macrophyte species. The model is also designed in an individual-based way. We use the super-individual concept (Chapter 2) as an efficient and flexible way to simulate a large number of individuals. The essence of this approach is that in addition to features such as individual biomass, length of sprout and the position on the grid, each model individual has one extra property, namely the number of individuals that it actually represents. In the analyses presented in this paper we represent the population by only two super-individuals per grid cell per species. One of these originates from tubers (or bulbils) and one from seeds (or oospores).

The model is implemented in an object oriented modeling framework (Van Nes, unpublished), which provides an extended user-interface, instantaneous visual presentation of results and tools for sensitivity analysis. As programming language Delphi was used (Borland, 1997), which uses an object-oriented Pascal version.

Seasonal cycle

The basis of the model is the seasonal cycle (Fig. 3.1). Plants can survive the winter as shoots and as two possible types of overwintering structures (‘hibernacula’): tubers and seeds. (For simplicity, in the model oospores of *Chara aspera* are considered seeds and the *C. aspera* bulbils are considered tubers.) At a pre-set day, growth is initiated by transforming a certain fraction of the seeds and tubers in a grid cell to young sprouts. The growth of the sprouts is supplemented with a fixed daily percentage (default 10%) of the remaining hibernaculum biomass (cf. Hodgson, 1966). Consequently, plants get an exponentially decreasing input from their seeds and tubers. At the pre-set end of the growing season, part of the plants is transformed into biomass of overwintering structures. Seeds can either be dispersed to neighboring grid cells by a dispersion function or all seeds are added to the grid cell associated with the parent plant.

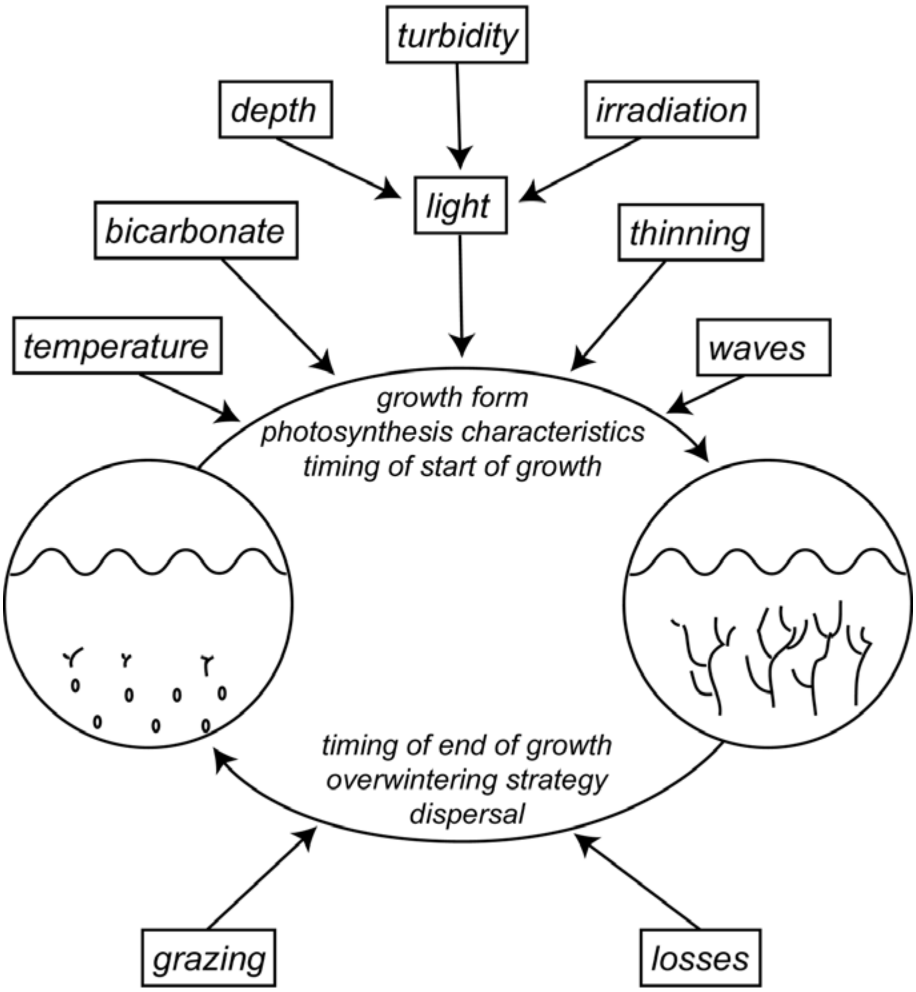


Fig. 3.1 *Seasonal cycle of the vegetation with environmental factors and plant characteristics that can be adjusted in the model (redrawn from: Scheffer et al., 1993a).*

Growth form

The weight of the shoots is defined by a fixed root-shoot ratio (default 0.1). The length of young sprouts increases proportionally with its biomass according to a fixed weight per meter sprout (cf. Ikusima, 1970). If the plants reach their maximum length or the water surface, further growth causes a proportional increase over the whole length of the plants. Optionally, however, plants like pondweeds (*Potamogeton pectinatus*) invest part of their production in shoots spreading just under the water surface. The fraction of the biomass of the sprout that spreads over the water surface is defined by a parameter.

Growth rate

The daily growth of the plants in weight (ΔW) depends on gross photosynthesis (P), respiration (R) and mortality (M).

$$\Delta W = W_s P - W(R + M) \tag{3.1}$$

In which: W_s is the weight of the sprouts (g) and W is the individual plant weight (g). Respiration is formulated as a fixed maintenance respiration, only dependent on temperature by a Q_{10} formulation (default value of Q_{10} is 2). Growth respiration is balanced with maximum photosynthesis rate in the parameter P_{max}.

Photosynthesis of the plants is affected by *in situ* light (I), temperature (T), bicarbonate (C) and distance (D) from the top of the plants following saturation functions:

$$P = P_{\max} \frac{I}{I + H_I} \frac{C}{C + H_C} \frac{1.35\,T^3}{T^3 + 14^3} \frac{H_D}{H_D + D} \tag{3.2}$$

The parameter P_{max} represents the specific daily production of the plant top at 20 °C in the absence of resource limitation. The default values are based on photosynthesis measurements.

The Monod or Michaelis-Menten function is adequate for describing the photosynthetic response to light (Carr et al., 1997). The default half-saturation constants for light (*C. aspera*: H_I = 14 µE m^{-2} s^{-1}; *P. pectinatus*: H_I = 52 µE m^{-2} s^{-1}) are based on growth experiments (Van den Berg, unpublished).

The Hill function describing the temperature dependence of photosynthesis was fitted to literature data by Scheffer et al. (1993a).

Photosynthesis is assumed to decrease with distance to the plant top due to tissue aging or periphyton growth. The half-saturation distance (H_D = 1 m) is set using data from Ikusima (1970).

In the presented analyses we assumed that the plants are not phosphorus or nitrogen limited (Best et al., 1996). In the eutrophic lakes we study, carbon limitation probably occurs frequently (Van Wijk, 1989; Van den Berg, in press). Carbon limitation is described with a Monod function on the bicarbonate concentration (C). Though the plants have a higher affinity for CO_2 over bicarbonate (Vadstrup and Madsen, 1995), the CO_2 concentration is usually below their compensation point during the growth season (Van den Berg, in press). In experiments is shown that *C. aspera* is less sensitive to carbon limitation (H_C = 30 mg l^{-1}) compared to *P. pectinatus* (H_C = 60 mg l^{-1}) (Van den Berg, in press)

Since the *in situ* light intensity follows a daily cycle and varies with depth, photosynthesis should be calculated on several moments of the day at several depths in the vegetation. Gaussian integration (Goudriaan, 1986) of photosynthesis over time and depth was used to calculate total daily photosynthesis efficiently The thickness of the surface layer is neglected, but self-shading in this layer is included by integrating the photosynthesis over an infinitely thin surface layer, using Gaussian integration.

Mortality

Four mortality causes are explicitly included in the model: wave damage, losses due to herbivory, mortality due to competition at high plant densities and seasonal die-off. Optionally, an additional background mortality can be used. Obviously, a negative growth rate leads also loss of biomass. Losses can be effectuated through a decrease in either the number of plants or the average individual weight. Due to the clonal growth of plants, the concept of individual is somewhat obscure for aquatic vegetation. We use pragmatic rules for the allocation of losses: (1) negative growth results in a loss in number of plants; (2) herbivory results in a loss in individual weight only; (3) background mortality and wave mortality result in a loss in numbers if the plants have not yet reached the water surface, otherwise in weight loss. Note that, computationally the individual weight is only relevant for sprouts that have not yet reached the water surface where it determines the sprout length and therefore the light conditions.

At high plant densities mortality occurs in the model, following the thinning law (see review by Westoby (1984)). We assume that the losses in numbers are compensated by a faster growth of the remaining plants. Thus, thinning implies readjusting the individual weight of the remaining plants in such way that there is no loss in overall vegetation biomass.

In very shallow regions (< 0.3 m) of large lakes, aquatic macrophytes are usually absent due to processes such as wave action or desiccation at fluctuating water levels. This is mimicked in the model by means of a depth-related mortality (M_w) which is maximal (M_{max}) at the shoreline and decreases with the water depth (Z) following a Hill-function with a default half-saturation depth (H_w) of 0.15 m (Scheffer et al., 1993a):

$$M_W = M_{\max} \frac{H_W^p}{H_W^p + Z^p} \tag{3.3}$$

The exponent (p) of the Hill function is set to a default value of 4 to obtain a steep reduction in depth-related mortality.

Grazing during the growth season can be simulated by setting a fixed grazing rate in g m^{-2} representing, for instance, the consumption capacity of the local coot population, and a limit in terms of vegetation density below which grazing ceases. In winter, tuber banks can be reduced considerably by bird grazing (Van Eerden et al., 1998), which can be mimicked in the model by setting the threshold density to which hibernacula are reduced in winter. At default there is no grazing.

Seasonal die-off is the most radical mortality. As described earlier, it occurs at a pre-set day of the year and implies transformation of a proportion of the biomass into seeds and tubers. These overwintering structures subsequently also experience a certain mortality rate. This results in propagule bank dynamics where a mortality rate and spring germination are counterbalanced by an input which occurs each autumn.

In situ light

The availability of light is the primary factor controlling photosynthesis in most aquatic systems (Carr et al., 1997), implying that an accurate description of light availability is essential. Irradiance follows a daily cycle and light is attenuated in the water column, resulting in a spatio-temporal pattern. Daily solar irradiance in the model follows a sine wave over the year fitted to data for Dutch shallow lakes. The Photosynthetically Active Radiation (PAR) is assumed to be 50% of the total irradiance. Irradiation at any time of the day is a function of the day length which is calculated from the latitude and the time of the year following equations suggested by Kirk (1983). Reflection of light at the water surface is fixed at 10%, neglecting the impact of variation in solar angle and waves. Light attenuation in the water column follows the Lambert-Beer law. In addition (self-)shading by macrophytes is included in the model using specific light attenuation coefficients of plant material (Ikusima, 1970; Scheffer et al., 1993a), summed over all simulated species.

***Table 3.1** Default parameters for Chara aspera and Potamogeton pectinatus. 'Oospores' are called 'seeds' in the model, and 'bulbils' are named 'tubers'. P. pectinatus only reproduces using tubers. All biomass values are in grams ash-free dry weight. Source - a = calibrated, b = estimated from field observations (Van den Berg, unpublished results), c = unpublished measurements van den Berg, d = Scheffer et al.(1993a), e = assumed to be the same as Potamogeton pectinatus in Scheffer et al. (1993a), f = option.*

Parameter	Description	Unit	*C. aspera*	*P. pectinatus*
SeedsStartAge	Age of the plants where seed formation starts	d	30 [b]	30 [b]
SeedsEndAge	Age of the plants where SeedFraction is reached	d	60 [b]	60 [b]
TuberStartAge	Age of the plants where tuber formation starts	d	30 [b]	30 [b]
TuberEndAge	Age of the plants where TuberFraction is reached	d	60 [b]	60 [b]
hCarbonate	Half-saturation carbonate concentration of growth	mg l^{-1}	30 [b]	60 [b]
hCarboReduction	Half-saturation biomass of carbonate reduction by plants	g m^{-2}	30 [b]	60 [b]
pCarbonate	Power of Hill function of carbonate dependent growth	-	1 [b]	1 [b]
cTuber	Tuber weight lost (d^{-1}) when sprouts starts growing	fraction	0.1 [d]	0.1 [d]
pMax	Maximal gross photosynthesis	hr^{-1}	0.006 [a]	0.008 [a]
Q10	Q10 for maintenance respiration	-	2 [d]	2 [d]
Resp20	Respiration at 20°C	d^{-1}	0.00193 [c]	0.00206 [d]
MaxLength	Maximum length of macrophyte	m	0.35[a]	4[d]
MaxWeightLenRatio	Weight of 1 m young sprout	g m^{-1}	0.03 [c]	0.1 [d]
RootShootRatio	Proportion of plant allocated to the roots	fraction	0.1[a]	0.06[d]
SpreadFrac	Fraction of sprout weight spread under the water surface	fraction	0 [a]	0.5 [d]
FracPeriphyton	Fraction of light reduced by periphyton	fraction	0.2 [d]	0.2 [d]
HExtReduction	Half saturation biomass of extinction reduction	g m^{-2}	40 [a]	70 [a]
hPhotoDist	Distance from plant top at which the photosynthesis is reduced factor 2	m	1 [d]	1 [d]
hPhotoLight	Half-saturation light intensity (PAR) for photosynthesis	μE m^{-2} s^{-1}	14 [b]	52 [b]
hPhotoTemp	Half-saturation temperature for photosynthesis	°C	14 [e]	14 [d]
pExtReduction	Power in Hill function of extinction reduction	-	1[a]	1[a]
PlantK	Extinction coefficient of plant issue	m^2 g^{-1}	0.02 [c]	0.02 [c]
pPhotoTemp	Exponent in temp. effect (Hill function) for photosynthesis	-	3 [e]	3 [d]
sPhotoTemp	Scaling of temperature effect for photosynthesis	-	1.35 [e]	1.35 [d]
BackgroundMort	Background mortality	d^{-1}	0 [f]	0.0006 [f]
HwaveMort	Half-saturation depth for mortality	m	0.1 [a]	0.1 [a]
MaxAge	Maximum age of plants	d	175 [a]	175 [a]
MaxGrazing	Maximum grazing rate	g m^{-2} d^{-1}	0 [f]	0 [f]
MaxWaveMort	Maximum loss of weight in shallow areas	fraction	0.2 [a]	0.2 [a]
pWaveMort	Power of Hill function for wave mortality	-	4 [a]	4 [a]
Thinning	Apply the thinning rule?	-	True [f]	True [f]
GerminationDay	Day of germination of seeds	dayno	114 [b]	-
ReproDay	Day of dispersal of seeds	dayno	250 [b]	-
SeedBiomass	Individual weight of seeds	g	0.00002 [c]	-
SeedFraction	Fraction of plant weight allocated to seeds	yr^{-1}	0.13 [b]	-
SeedGermination	Fraction of seeds that germinate	yr^{-1}	0.2 [a]	-
SeedImport	Import of seeds	No.$m^{-2}yr^{-1}$	0 [f]	-
SeedInitialBiomass	Initial biomass of seeds	g m^{-2}	2 [f]	-
SeedMortality	Mortality of seeds	d^{-1}	0.0019 [a]	-
SeedRadius	Max. dispersal radius for 90% of the seeds	m	0 [e]	-
TuberBiomass	Individual weight of tubers	g	0.00018 [b]	0.05 [d]
TuberFraction	Fraction of plant weight allocated to tubers	yr^{-1}	0.22 [b]	0.2 [d]
TuberGermination	Fraction of tubers that germinate	yr^{-1}	1 [b]	1 [d]
TuberGermDay	The day that tubers germinate	dayno	114 [b]	100 [b]
TuberImport	Import of tubers	No.$m^{-2}yr^{-1}$	0.1 [f]	2 [f]
TuberInitialBiomass	Initial biomass of tubers	g m^{-2}	8 [f]	10 [f]
TuberMortality	Mortality of tubers	d^{-1}	0 [b]	0 [b]

The light attenuation coefficient of plant material is set at 0.02 m^2 g^{-1} (Ikusima, 1970) for both *C. aspera* and *P. pectinatus* for our simulations.

Temperature, turbidity, bicarbonate and water level

Environmental parameters in the model can be either fixed, or modeled as a sinusoidal function of time or supplied as a time series. A reduction of the local turbidity by vegetation (Scheffer, 1998) is modeled assuming an instantaneous effect of vegetation biomass (B, g m^{-2}) on vertical light attenuation coefficient (K, m^{-1}) in each grid cell:

$$K^* = K_{\min} + (K - K_{\min})\frac{H_K}{B + H_K} \tag{3.4}$$

This implies that vegetation can reduce the vertical light attenuation coefficient down to a minimum level (K_{min}, m^{-1}). The half-saturation constant (H_K, g m^{-2}) is estimated from field data from Lake Veluwe (Chapter 4).

We parameterized the model for *C aspera* using results from experiments and data of Lake Veluwe (Table 3.1). Parameters of *P. pectinatus* parameters were taken from Scheffer et al. (1993a), with the exception of the maximum gross production (P_{max}) which has been calibrated using data on vegetation dynamics in Lake Veluwe (Table 3.1).

Methods of analysis

Monte Carlo sensitivity analysis

We used the Monte Carlo sensitivity analysis to investigate which parameters have the strongest impact on model outputs. We generated 5000 sets of parameters, drawing all parameters randomly and independently from uniform probability distributions within ranges of ± 10% around the default values. Five years were simulated with each parameter setting, and the model results (biomass, mean length, numbers, and individual weight) were stored at days 152, 182 and 213 of each year. At the end of each simulation, the model was reset to the starting number of seeds (or oospores) and tubers (or bulbils) (total 10 g m^{-2} for each species). Sensitivity coefficients were defined by linear regression between the parameter values and each model output value, scaled by the ranges used for each parameter (Klepper, 1989). Cluster analysis (average linkage) was used to form groups of parameters that had the same or opposite effect on the qualitative model results. As similarity measure the absolute sine of the angle between the vectors of sensitivity coefficients was used. As measure of the total sensitivity the length of this vector was used (Klepper, 1989).

We also added 100 dummy parameters that have no effect on the model. These dummy parameters were set arbitrarily to 1 and varied in the same way as the model parameters. This allows a test of the hypothesis that the effect of the model parameters is not different from zero. This is done by comparing the total sensitivity of each model parameter with the 99% percentile of the sensitivity coefficients of the 100 dummy parameters. Only parameters that have significantly stronger effect on the model than the dummy variables were included in the cluster analysis.

Monte Carlo uncertainty analysis can be used to show the uncertainty in the model results resulting from the uncertainty in the parameters. A common problem with this approach, however, is that it is difficult to convert vague prior knowledge of parameter uncertainty into the form of exact probability functions (Reichert and Omlin, 1997). Therefore, we choose arbitrarily the same prior distributions for all parameters: normal distributions with coefficients of variation (CV = standard deviation / mean) of 0.1. This way we show how the uncertainty in parameters propagates to the model results. For the first analysis we generated 500 sets of parameters. With each parameter setting, five years were simulated. The distributions of the model outcomes are characterized with percentiles. For further analysis, we also investigate the effect of other distributions and environmental conditions on the equilibrium biomass.

Scanning of asymptotic regimes

'Asymptotic regimes', are defined as the behavior of the model after infinitely long simulations. Simple models in constant environments can converge to an equilibrium. In our case the simplest asymptotic regime is a seasonal cycle. For models with ordinary differential equations (semi-)analytical methods are available to analyze the effect of parameters or environmental factors on the equilibria. We are not aware of such methods for individual-based models. Therefore, we used several 'brute force' numerical procedures, which all include simulation until convergence to a certain seasonal cycle has occurred. Such procedures can be used to scan the effects of different initial conditions or different of environmental factors or parameter settings on the asymptotic regimes.

More precisely, we used the following procedure to scan the asymptotic regime of the model over a range values for a certain parameter or environmental factor. We start with an arbitrary initial biomass of overwintering structures (default 10 g m^{-2}) in a state where vegetation can develop (either in clear or shallow water). The yearly cycle is allowed to stabilize by letting the model run for 200 years. Subsequently, the biomass is plotted at an arbitrarily chosen day in summer (default day 183 (1 or 2 July)) for 5 successive years. Thereafter, one state variable or parameter is changed over a certain range in a number of small steps (default 41), each time using the previous final state as a new starting point for the simulations. In each of these small steps, the model is first run for 100 years to stabilize, and subsequently the new summer biomass is plotted in 5 successive years (to check whether convergence to a one-year cycle occurred).

In order to check for hysteresis due to alternative attractors we subsequently repeat the procedure, moving along the parameter range that we scanned in opposite direction. Thus, we remove all plants, seeds and tubers, let the vegetation colonize the bare location starting from a tiny yearly import of oospores and bulbils of 0.1 m^{-2} yr^{-1}, and do 41 steps backwards along the gradient. If the model has alternative stable states, this can be reflected by a different result on the forward and backward scans. In complex situations (e.g., with several competing species), it is not guaranteed that the alternative equilibria are found with this method. Therefore, we can alternatively use a less efficient method: again by changing a parameter or environmental factor step by step, not using the previous final state as new starting point, but with several very different initial conditions.

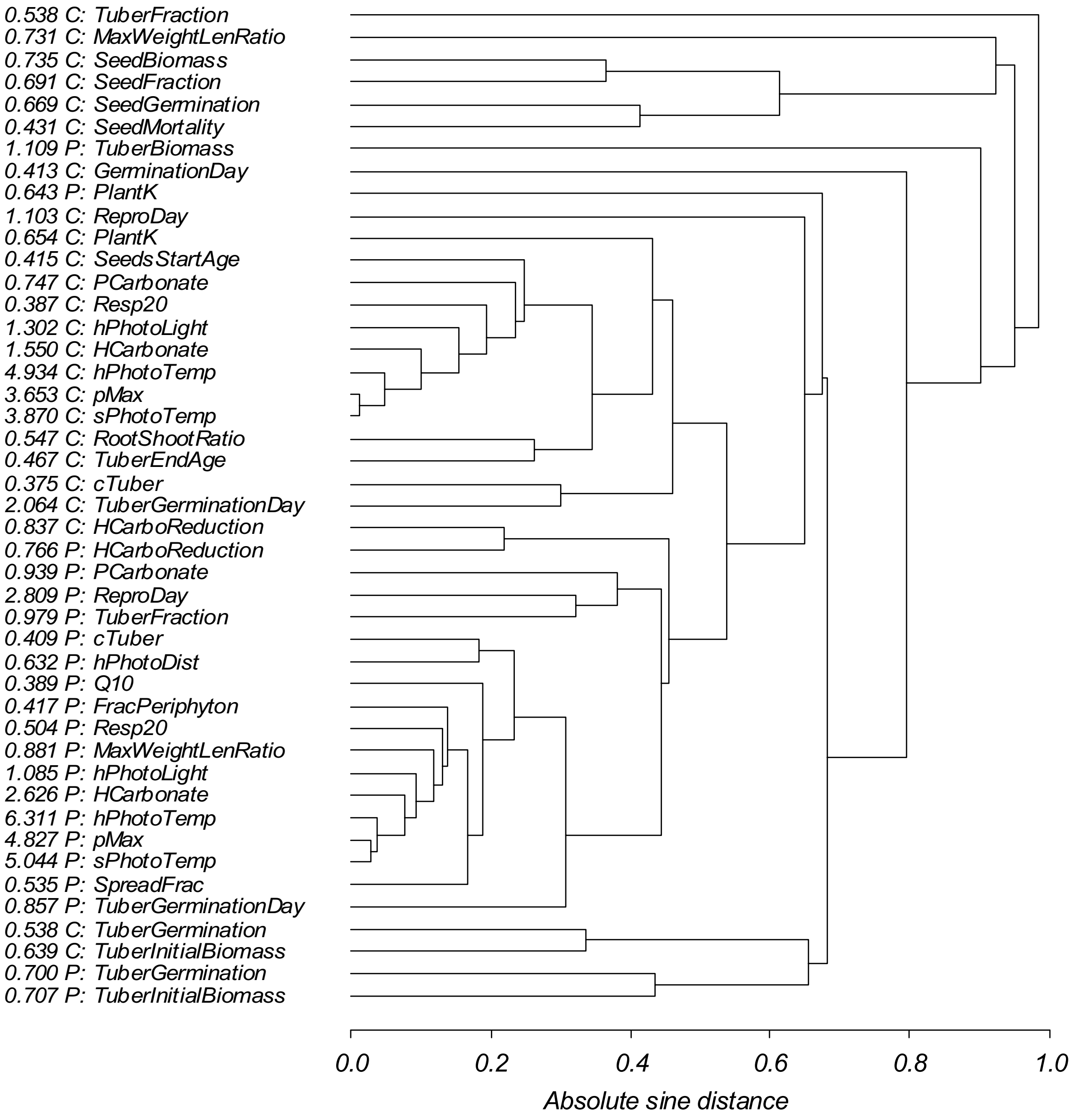


Fig. 3.2 *Cluster analysis of the sensitivity indices of the parameters. Parameters with the same or opposite effect on the model results (biomass, numbers, and mean individual weight) are grouped together. The value before each parameter is the length of the vector of the sensitivity coefficients (Klepper, 1989), which is a measure of the total strength of the effect. The 45 parameters that are shown have a significantly stronger total effect than 99% of 100 dummy variables. C = C. aspera, P = P. pectinatus. The abbreviations of the parameters are explained in Table 3.1.*

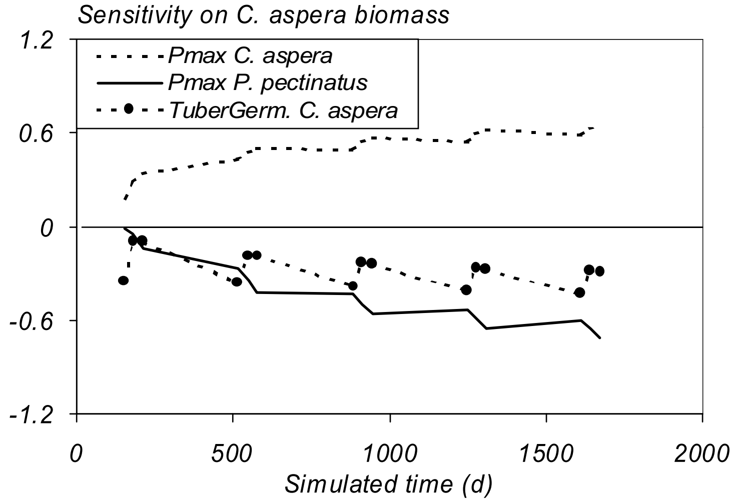


Fig. 3.3 *The sensitivity coefficients of three parameters (P_{max} of C. aspera and P. pectinatus and TuberGerminationDay of C. aspera) on the biomass of C. aspera in time (5 years, 3 points in time per year).*

Results

Monte Carlo sensitivity analysis

For sensitivity analysis we used a version of the model with two competing species (*Chara aspera* and *Potamogeton pectinatus* using a fixed water depth of 1 m and a fixed turbidity (vertical light attenuation coefficient of 2 m^{-1}). Analysis of results from 10 000 randomly selected parameter sets, showed that only 45 of the 90 examined parameters had a 'significant effect', i.e. exceeded the 0.99 percentile of the sensitivity scores of 100 dummy variables included in the analysis. Fig. 3.2 shows the results of this analysis and the accompanying cluster analysis of the parameters with a significant effect. To check whether 'non-significant' parameters really had no effect, a second analysis was done (with 5000 parameter sets) on only those 'non-significant' ones. The result indicated that 17 of these parameters had nonetheless a significantly stronger effect than the dummy variables. This shows that the power of the analysis decreases when there are parameters with a strong effect on the outcomes. A next analysis excluding also the 17 weakly significant parameters confirmed that the remaining 18 parameters really had no significant effect on the model outcome.

The parameters that define the temperature limitation (hPhotoTemp and sPhotoTemp) appeared to have the largest impact on the model results (Fig. 3.2) These parameters are part of clusters of parameters that have a similar effects on the model outcomes. The parameter hPhotoTemp of *C. aspera* is part of a cluster with parameters that mostly related with the primary production of *C. aspera* (P_{max}, hCarbonate). A closer look at the sensitivity matrix (not shown) revealed that this cluster has effect on all model outcomes (biomass, individual biomass, numbers) of *C. aspera*. The effect on *C. aspera* biomass increases with time (Fig. 3.3). The strongest effect appears only after five years of simulation. The same cluster of parameters also has a strong opposite effect on all *P. pectinatus* outcomes, which has reached its maximum already after two years. Probably, in the first years of these standard simulations biomasses are so low that competition is not yet important, and the outcome is dominated by the initial conditions. This is confirmed by the sensitivity of reproduction parameters (for instance the cluster with TuberGerminationDay of *C. aspera*) which increases hardly with time (Fig. 3.3).

Unraveling mechanisms of hysteresis in plant competition

As an example of how specific mechanisms in macrophyte competition can be addressed we show results of the analysis of the effect of variation in the turbidity of the water (K_d) on competition between *Chara aspera* and *Potamogeton pectinatus*. For simplicity we neglect spatial aspects in this analysis, and focus on a single grid cell with a water depth of 1 m. Scanning of asymptotic regimes (Fig. 3.4a) showed that there are two zones with alternative equilibria in this situation. In clear water, with a vertical light attenuation between 1 and 4.5 m^{-1}, there is either a mix of both species or a monoculture of *P. pectinatus*. Another small zone of alternative equilibra occurs around a light attenuation of about 6.5 m^{-1}. In this zone there can either be *P. pectinatus* or no vegetation. The model thus predicts that during eutrophication, the system changes from *C. aspera* to *P. pectinatus* dominance followed by a loss of vegetation in turbid water.

The system shows hysteresis in its response to changing water turbidity. One aspect of this pattern is unexpected: the system does not return to its initial state in clear water. To check whether the positive feedback between plants and water clarity could cause this phenomenon we took out the effect of plants on turbidity in the model. It appears that this eliminates the narrow band of hysteresis in turbid water, but not the irreversible pattern on the left-hand side of the range (Fig. 3.4b). Therefore, there must be another explanation for the occurrence of alternative stable states in clear water.

We therefore checked two other aspects of competition in the model. Firstly, competition for light is asymmetrical, as *P. pectinatus*, forms a canopy above *C. aspera*, which grows as a dense mat covering the sediment. Secondly, both plants compete for bicarbonate, which is a potentially limiting nutrient. We checked the effects of these aspects on the occurrence of alternative equilibria, by repeating the analysis using different versions of the model. First, we made the competition for light symmetrical by setting the maximum length of *P. pectinatus* equal to the value of *C. aspera*. Though the area with alternative equilibria in clear water has become somewhat smaller (between 1 and 3.5 m^{-1}, see Fig. 3.4c), the qualitative behavior of the model is almost the same. The next step is to shut off the feedback in bicarbonate by letting the bicarbonate concentration be unaffected by the macrophytes. Now, the alternative equilibria in clear water disappear (Fig. 3.4d). Charophytes never become abundant, and there is only a small zone with alternative equilibria in turbid water. The latter zone is caused by the turbidity feedback as shown by shutting both feedback loops off (Fig. 3.4e). In conclusion, the model analysis suggests that competition for bicarbonate may be a powerful mechanism causing hysteresis, allowing pondweeds to remain dominant even at low turbidities where charophytes would otherwise take over.

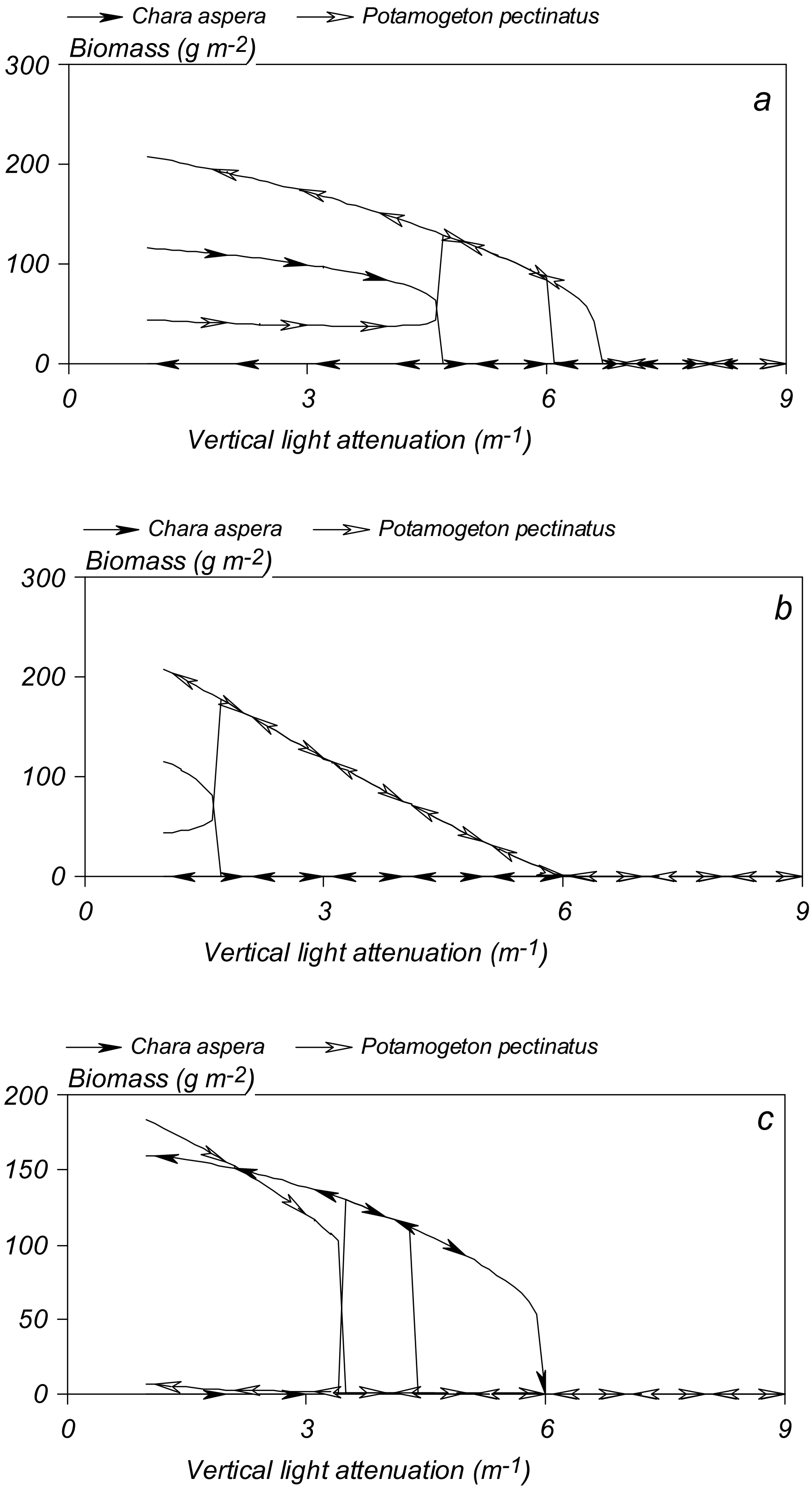


Fig. 3.4 *Continued on next page.*

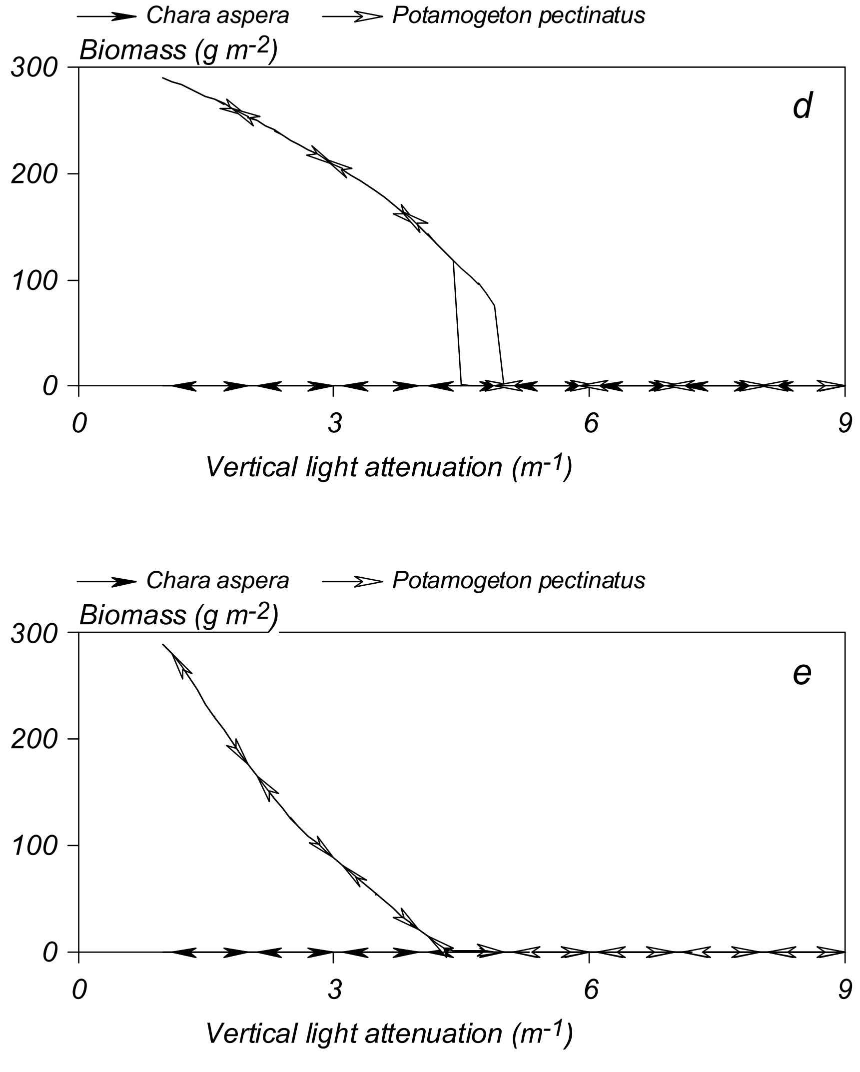


Fig. 3.4 *The effect of a change in the vertical light attenuation on the equilibrium summer biomass (on 2 July) of C. aspera and P. pectinatus on a grid cell of 1 m. The arrows indicate the direction of the change in vertical light attenuation. (a) With default parameter settings. (b) The same analysis, but with the vertical light attenuation feedback closed. This is done by setting the effect of both species on the turbidity to zero. (c) The same analysis as a) but the maximum length of P. pectinatus equals that of C. aspera (0.35 m). (d) The same analysis but the turbidity feedback is closed. This is done by setting the effect of both species on bicarbonate to zero, and setting the bicarbonate concentration to a lower value (60 mg l^{-1}). (e) Both feedbacks closed, see b. and c.*

Uncertainty analysis

We analyzed uncertainty of the model outcomes for the situation with competition between *Chara aspera* and *Potamogeton pectinatus* on one grid cell with a water depth of 1 m and a vertical light attenuation of 2 m^{-1}. Both species were assigned an initial tuber (or bulbil) biomass of 10 g m^{-2}, and all parameters of both species were drawn independently 500 times from normal distributions (CV = standard deviation / mean = 0.1). The biomass of both species was highly sensitive to such parameter changes (Fig. 3.5). Since an uncertainty of 10% is certainly not an exaggeration of real uncertainty, this implies a considerable uncertainty in the model outcome. Moreover, the results diverged during the first five years, indicating that the long-term effects of wrongly estimated parameter values can be even higher than the effect on one-year simulations (Fig. 3.5).

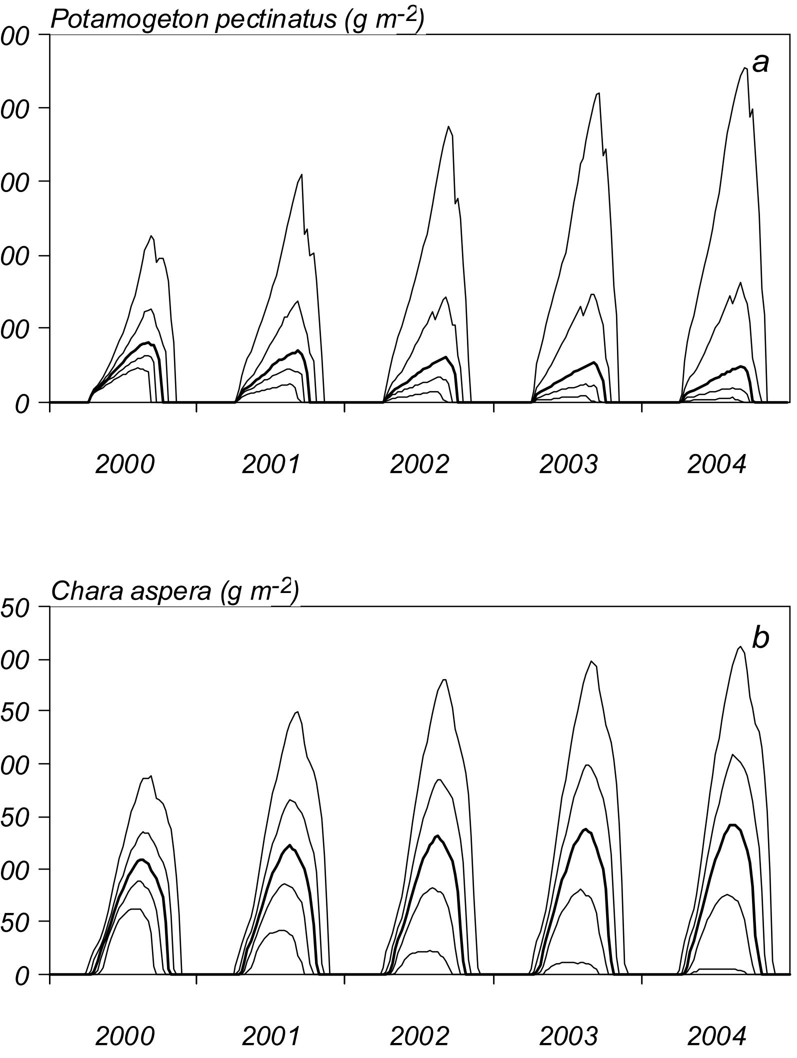


***Fig. 3.5** The effect of drawing all parameters of both species from a normal distribution with a coefficient of variation of 0.1. The figure is based on 500 model runs. Only the 95% (thin line), 75%, 50% (thick line), 25% and 5% (thin line) percentiles of the results are shown. (a) Biomass of P. pectinatus (b) Biomass of C. aspera.*

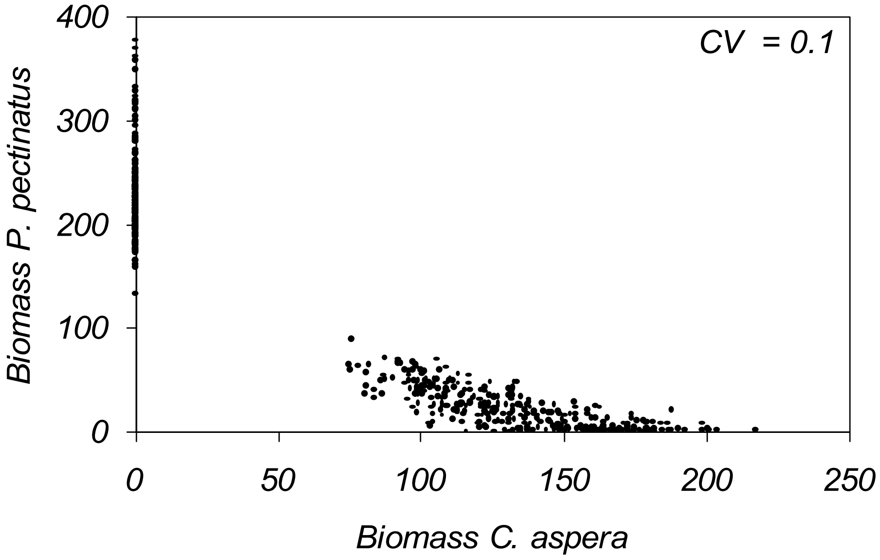


Fig. 3.6 *The long-term effect (after 100 yr) of drawing all parameters of both species from a normal distribution with a coefficient of variation (CV) of 0.1. The figure is based on 500 model runs.*

To show the long-term effect of parameter changes on the asymptotic regime, we performed an uncertainty analysis with longer runs. For each randomly drawn parameter set (500 times from normal distribution with CV = 0.1) we first stabilized the model by running for 100 years and subsequently plotted the summer biomass (Fig. 3.6). It is clear that results can be grouped in two clusters: one cluster with *P. pectinatus* only and one with *C. aspera* dominance and a small *P. pectinatus* biomass. The second cluster had the largest size (*P. pectinatus* 173 and *C. aspera*/*P. pectinatus* 327 times). This shows that the high uncertainty in Fig. 3.5 may be explained from the fact that the system has alternative attractors. The system can switch between asymptotic regimes not only due to changes in the environment (as shown before), but also in response to changes in the parameter settings.

The amplification of sensitivity in the vicinity of catastrophic bifurcation points (i.e. parameter values were the system switches to an alternative attractor), also implies that the sensitivity may vary in a nonlinear way if one gradually increases the CV of parameters (Fig. 3.7 and 3.8). At a low variation of the parameters (CV = 0.01, Fig. 3.7a), the equilibrium state turns out to be always a mix of *P. pectinatus* and *C. aspera* with a relatively low variation. If the coefficient of variation is increased, part of the parameter combinations give rise to the alternative attractor, which is a monoculture of *P. pectinatus*. If the coefficient of variation increases further to 0.1, the proportion of parameter combinations that goes to the other equilibrium increases further. Obviously, variation within the two alternative states also increases with the CV of the parameters. However, the vicinity of an alternative attractor causes the variation in the results to increase sharply around a certain critical CV in the parameters (Fig. 3.8).

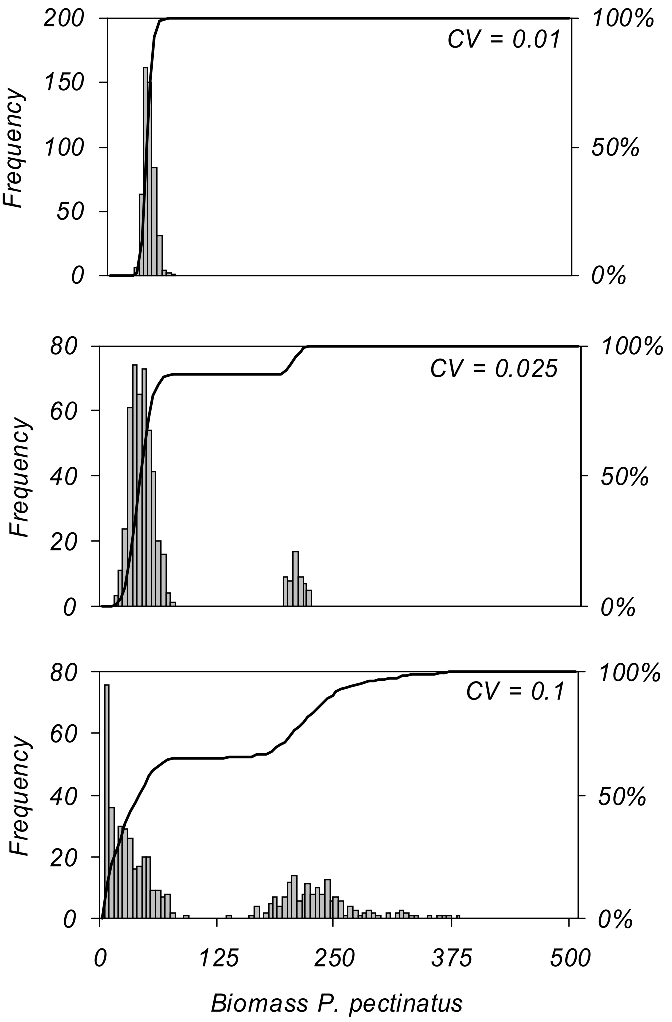


Fig. 3.7 *The long-term effect (after 100 yr) of drawing all parameters of both species from a normal distribution with different coefficients of variation (CV = 0.01, CV = 0.025 and CV = 0.1) on the summer biomass (day 183) of P. pectinatus and C. aspera. The figures are based on 500 model runs.*

The results of the uncertainty analysis also depend on the initial conditions. The *C. aspera-P. pectinatus* equilibrium has a higher probability if you start with a higher biomass of *C. aspera* reproduction organs (Fig. 3.9). Perhaps more importantly, uncertainty in the result of the model depends strongly on environmental conditions. For instance, in shallow water (where *P. pectinatus* dominates) and in deeper water (where *C. aspera* dominates) the range of the model results is relatively small, but there is an intermediate depth at which the outcome becomes highly sensitive to parameter variation (Fig. 3.10a). Close to the catastrophic bifurcation even a tiny change in the parameters (e.g. a CV of 0.001 Fig. 3.10b) may change the dominance of the species, implying a very high sensitivity. Of course, this is a rather theoretical and extreme example of the uncertainty caused by alternative equilibria. In reality, variations in the environment will mask this effect and make it unlikely that the system stays in an equilibrium that is so vulnerable to disturbance.

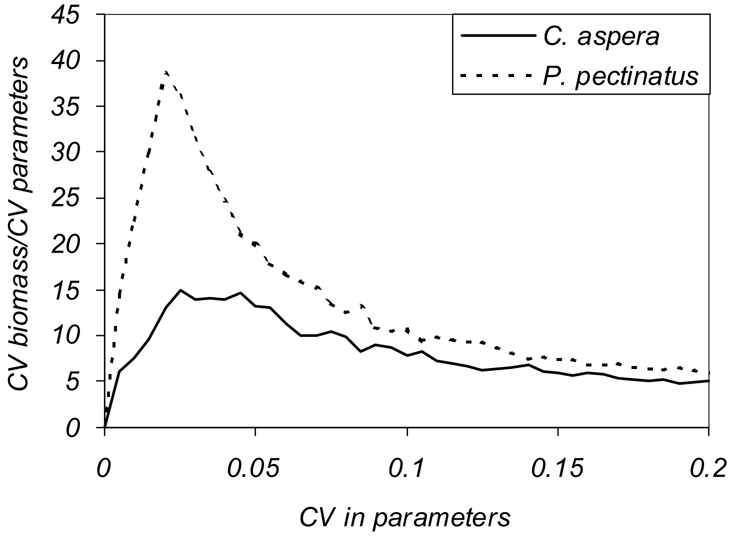


Fig. 3.8 *The relative uncertainty in the equilibrium biomass as a function of the used variation in the parameters. The uncertainty is expressed as the ratio between the coefficients of variation of the parameters and the coefficients of variation of the resulting equilibrium biomass of both species in summer (on day 183 after 100 years of simulation). Each point in the figure is based on 500 model runs.*

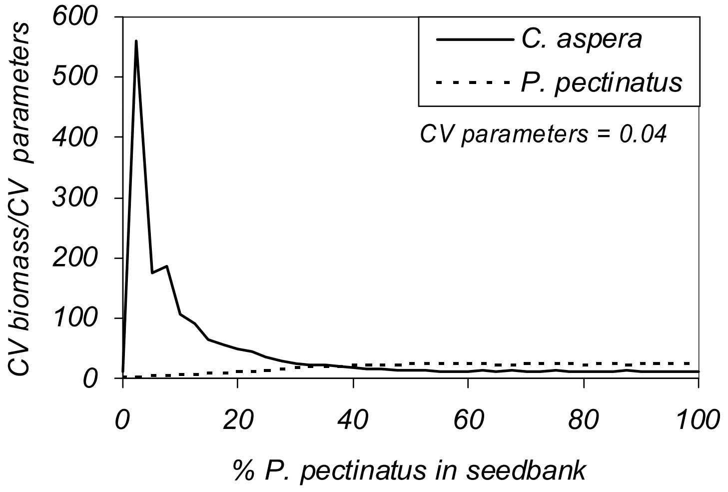


Fig. 3.9 *The effect of the distribution of the initial biomass between both species (the total initial biomass was always 10 g m^{-2}) on the relative uncertainty in the biomass of C. aspera and P. pectinatus. Each point in the figure is based on 500 model runs of 100 years.*

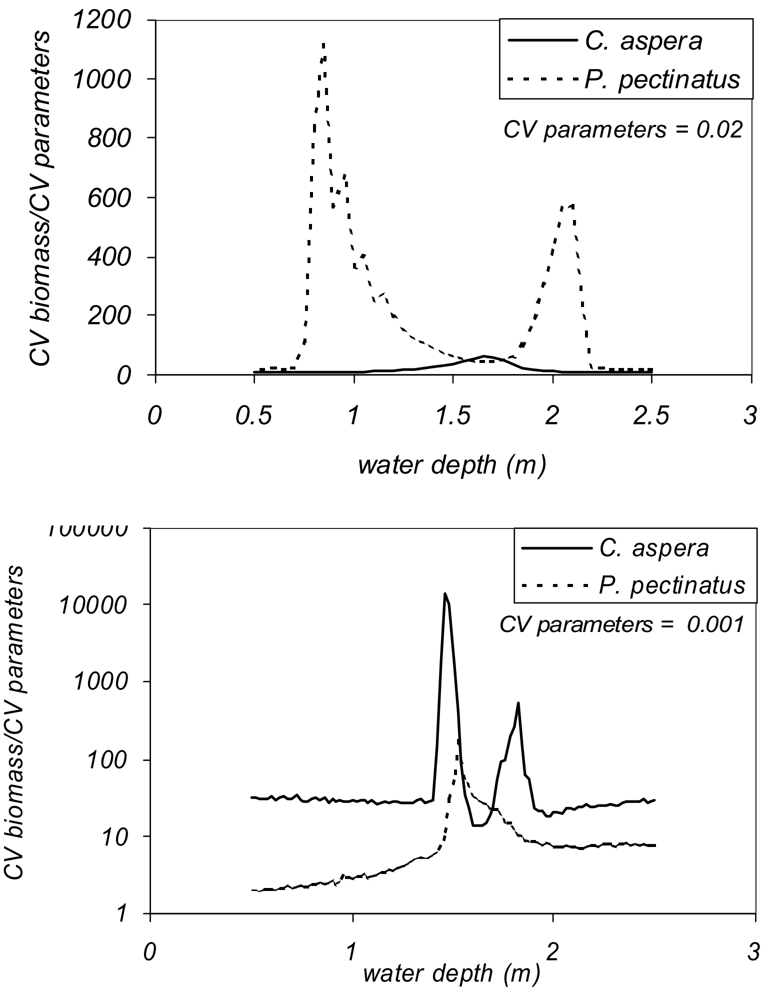


Fig. 3.10 *The effect of the water depth on the relative uncertainty (ratio of CV in biomass and CV in paramters) in the summer biomass of both species at two different coefficients of variation (CV=0.02 and CV=0.001) of the distributions of the parameters. Each point in the figure is based on 500 model runs of 100 years.*

Discussion

The model Charisma is not meant as a predictive tool, but rather for the purpose of gaining insight and generating hypotheses. This is also the general aim of much simpler so-called 'minimal models'. However, these models usually ignore or highly oversimplify aspects such as seasonality, space and numerous quantitatively important processes. The niche of models such as Charisma is to explore questions with more realism, while allowing thorough scrutinization of causality of generated patterns. Our results demonstrate how this type of models can help to fill the gap between reality and theory.

An often discussed problem of complex ecological simulation models is the fact that a good fit of the generated results to field data does not guarantee that the model is correct (Scheffer and Beets, 1994; Rykiel, 1996). Therefore, perhaps the most rewarding result is a persistent discrepancy between model predictions and field patterns. As an example consider the prediction of Charisma that once *P. pectinatus* has gained dominance it will not be replaced by *C. aspera* even if water quality is greatly improved. This contrasts with the recovery pattern in Lake Veluwe where Charophytes eventually replace *P. pectinatus* and became completely dominant (Meijer, 2000). This suggests that other mechanisms than the modeled ones may be important in the field. A possible explanation is that winter grazing by Bewick's swans on *P. pectinatus* tubers creates bare spots that *C. aspera* can colonize, and that the resulting ‘hot spots’ produce enough oospores to expand into the neighboring areas, thus displacing *P. pectinatus* from other parts. Indeed, in Lake Veluwe, *C. aspera* recolonized the lake very slowly, expanding from a few initial spots gradually in about 10 years. Thus, the model is realistic and transparent enough to suggest interesting research questions.

The model is also useful to explore the consequences of complex systems properties such as multiplicity of attractors. It is often stressed that the presence of alternative equilibria has profound implications for ecosystem management as it may imply unexpected collapse of the system and large resistance to restoration efforts (Scheffer, 1998). Our analysis stresses that alternative attractors have also important consequences from the technical modelers' point-of-view. It is well known that for all non-linear models, the parameter sensitivity may depend strongly on the selected environmental conditions, which makes it hard to perform a ‘global’ sensitivity analysis over the parameter space, even with Monte-Carlo methods. Although this remains a difficult problem, it can be handled for instance by performing a sensitivity analysis of a sensitivity analysis (Drechsler, 1998). However, performing a sensitivity analysis of models with alternative attractors is particularly tricky. The size of the ranges used in the sensitivity analysis can determine the sensitivity of the parameters. Moreover, the differences in sensitivity of parameters are expected to be discontinuous if the model reaches the alternative basin of attraction For example, if the sensitivity of a parameter that is changed 10% is relatively low, it can still be that changes higher than 12% may have a much higher impact on the result if this change causes a switch to the other equilibrium. Furthermore, the results of a sensitivity analysis will also depend on the initial values of the state variables.

The corollary of the magnification of sensitivity in the vicinity of catastrophic bifurcations in terms of real macrophyte dynamics is that under some conditions, small environmental variation may blow up to large changes in vegetation abundance. A perhaps even more important consequence is that results from experiments designed to analyze the sensitivity of an ecosystem to micropollutants (e.g., Van Wijngaarden and Brock, 1999) may have only limited value if the ecosystems can have multiple stable states. Low sensitivity under conditions far from a bifurcation, does not guarantee low sensitivity under other conditions.

Although it is difficult to characterize sensitivity or uncertainty in an absolute sense, relative ranking of the sensitivity to different parameters can give a clue to which aspects are most important in driving dynamics of the real system. Our sensitivity analysis indicated that macrophyte growth is particularly sensitive to temperature which is in line with earlier model analyses (Scheffer et al., 1993a) and with empirical results from lab experiments (Barko and Smart, 1981; Spencer, 1986) and field studies (Best and Visser, 1987; Scheffer et al., 1992). In view of the key role of submerged plants in many lakes, the temperature sensitivity suggests that this aspect could be an important focus of future research on effects of climate change on lake ecosystems.

A good example of the way in which models such as Charisma can fill the niche between reality and minimal models is the analysis of causes and consequences of alternative stable states described in this paper. In previous work, the prediction of alternative equilibria has been based largely on results from extremely simple (1 or 2 differential equations) models without seasons (e.g. Scheffer, 1998). It is not at all obvious that persistent alternative equilibria would also be possible in situations with seasons, as the ecosystem is often thought to be ‘reset’ in winter (Knowlton, 1992). Our results demonstrate that for submerged macrophytes the dependency on the previous-years' population known from field studies (Kautsky, 1990) is likely to be strong enough to make alternative equilibria possible.

Also, our analysis of causes of alternative stable states goes well beyond the highly simplified plant-turbidity feedback mechanism described in minimal model studies (Scheffer, 1998). Charisma can have alternative equilibria for at least three reasons: the turbidity feedback, competition for bicarbonate, and harvesting or grazing (described in detail in Chapter 6). The positive feedback on the turbidity is an intuitively straightforward reason to expect alternative equilibria in macrophyte stands. However, the models employed so-far do not allow an estimate of the conditions under which hysteresis should really be expected. Using Charisma, a more realistic picture has been produced showing the dependence of this phenomenon on the strength of the clearing effect and on the depth gradient and mixing processes in a lake (Chapter 4). Competition for bicarbonate, as analyzed here, has not been described earlier as a mechanism causing alternative attractors. The underlying positive feedback is due to the higher consumption of bicarbonate by *C. aspera*, which can also tolerate lower bicarbonate concentrations than *P. pectinatus*. Therefore, if the biomass of *C. aspera* increases, the biomass of *P. pectinatus* is more strongly suppressed, which causes better light conditions for *C. aspera*. Our results are also more or less analogous to that obtained from Tilman's resource-ratio theory describing competition for two resources (Taylor and Williams, 1975; Tilman, 1977).

In nature environmental variability, the turbidity feedback, competition for bicarbonate, and harvesting or grazing will often interact to produce shifts in vegetation dynamics. Models such as Charisma allow one to explore the complex potential consequences of such simultaneously acting mechanisms, while retaining the possibility to scrutinize causality in a systematic way. Obviously, they are only one type of tool in the toolbox needed to unravel the forces that drive ecological systems in the real world. However, we feel that this type of transparent, moderately realistic models are essential to fill the notorious gap between minimal models, field pattern analyses and controlled experiments.

Chapter 4

Dominance of charophytes in eutrophic shallow lakes - when should we expect it to be an alternative stable state?

Egbert H. van Nes, Marten Scheffer, Marcel S. van den Berg & Hugo Coops

Aquatic Botany, in press.

Abstract

Submerged plant dominance and a turbid state with few submerged plants have been hypothesized to represent alternative stable states in eutrophic shallow lakes. Here, we analyze the conditions for occurrence of alternative stable states in shallow lakes further, using Charisma, a simulation model describing the growth of *Chara aspera*. The model includes seasonality and spatial structure, aspects which were absent in earlier models predicting alternative equilibria. The parameterization of the model is largely based on experimental results and field observations. Over a range of conditions, the model does indeed predict alternative stable states. The range of conditions over which alternative stable states exist, appeared most sensitive to the assumed reduction of local turbidity by plants and the maximum growth rate of the plants. Aboveground biomass disappears during winter in most lakes in temperate regions. Our analysis indicates that from an evolutionary perspective there is an optimum biomass allocation strategy with respect to investment in overwintering structures. Too little investment reduces chances to regain dominance in the subsequent year, whereas too much investment in dormant overwintering structures such as seeds and tubers reduces photosynthesis. Interestingly, the optimal investment is lower for obtaining maximal summer biomass than for realizing the maximum stability of the vegetated state.

The model also suggests that a short clear-water phase enhances the probability of vegetation survival. The optimal timing for a clear-water phase is at the end of May or in June, as is indeed the case in many lakes.

In line with earlier theory, shallow lakes with a ‘flat’ depth profile are predicted to have the strongest hysteresis. In lakes with a depth gradient, the response to changes in turbidity is predicted to depend strongly on horizontal mixing of the water between vegetation stands and the open water. Hysteresis disappears predominantly due to a strong horizontal mixing of water. In case of little mixing, on the other hand, local alternative stable states are predicted to occur.

Introduction

There have been many observations indicating that eutrophic shallow lakes under certain conditions can be in either of two states: a vegetated state with clear water and a turbid state dominated by phytoplankton (e.g., Timms and Moss, 1984; Moss et al., 1986; Schelske and Brezonik, 1992; Hargeby et al., 1994; Van Donk and Gulati, 1995). This phenomenon has been explained by the theory that the two states represent alternative equilibria that exist over a certain range of nutrient conditions (Scheffer, 1989). The theory has important implications for lake management, because it predicts that shallow lakes will show hysteresis in response to changing conditions. The vegetated state of clear lakes is robust during eutrophication, but once the lake has switched to a turbid state to restore the vegetated clear state, the nutrient level must be reduced to a much lower level than the level at which vegetation collapsed. Field evidence supporting the theory is increasing (Scheffer et al., 1993b). However, the theoretical background remains rather basic. Simple and abstract models (Scheffer, 1998) as well as complex ecosystem models have produced the hysteresis (Janse, 1997). However, all of these models lack important processes in vegetation such as seasonal die-off, the role of the seed bank and the description of dynamic spatial structure implied by seasonal growth of plants over a depth gradient.

In this paper, we show that hysteresis can also occur in a simulation model with a more realistic description of the vegetation, and we analyze which aspects should be expected to be most influential to stability of aquatic vegetation. Several other realistic plant models have been constructed (reviewed by Carr et al., (1997)). To our knowledge, none of these models shows alternative equilibria.

The model

Overview

A technical and detailed description of the model is presented elsewhere (Chapter 3). Here, we merely give an outline of the properties of the model. Charisma is designed as a general model of submerged plants, but is applied here for the species *Chara aspera* Deth. ex Willd. Some spatial processes can optionally be included in the model. Then, a representative part of a lake is modeled as a rectangular grid of $n \times n$ cells of a fixed size, on which the plants grow. Each cell has its own environmental features (altitude, vertical light attenuation coefficient) and a seed (or oospore) and tuber (or bulbil) bank. The integration step of Charisma is one day, but for each day the photosynthetical rate over the depth profile is computed as a function of the daily light variation by a three-point Gaussian integration (Goudriaan, 1986). The model describes the seasonal cycle of macrophytes. Vegetation can survive the winter as shoots and two types of overwintering structures: tubers (or bulbils) and seeds (or oospores). At a pre-set day, growth is initiated by transforming part of the seeds and tubers in each grid cell into young sprouts.

Growth and mortality of plants

The physiological rules of the model are based largely upon those used in the model MEGAPLANT (Scheffer et al., 1993a). Growth of the plants depends on photosynthesis and respiration. Respiration is formulated as a fixed maintenance respiration, only dependent on temperature by a Q_{10} formulation (the default value of Q_{10} is 2). The extra respiration needed for the plants to grow, is accounted for in the maximum gross photosynthesis rate (P_{max}). The gross photosynthesis (P in g AFDW sprout d^{-1}) on a certain spot on the sprout of the plants is affected by *in situ* light (I), temperature (T), bicarbonate (C) and distance (D) between the top of the plant and the considered location.

$$P = P_{max} f(I, T, C, D) \tag{4.1}$$

The effect of each factor is formulated as a simple Monod saturation function with the exception of the saturation function of temperature, for which a sigmoidal saturating function is used (see: Scheffer et al., 1993a). A fixed part of the daily production is invested in roots, bulbils and oospores. These structures have no primary production. In reality, the formation of reproduction organs could start somewhat later in the season (though oospores can be seen on very young plants), but we don't have enough data for *Chara aspera* to describe that effect in more detail. The length of growing young sprouts increases proportionally with their biomass keeping a fixed weight per meter sprout. If the plants reach either their maximum length or the water surface, further growth causes a proportional increase over the whole length of the plants.

Three mortality causes are explicitly included in the model: wave damage, mortality due to competition at high plant densities and seasonal die off. Optionally, an additional background mortality can be used. Obviously, respiration exceeding production also leads also to a loss of biomass. This will probably lead to an extra loss of biomass (Hootsmans, 1994), which was not included in the model because we lack data for *C. aspera*.

Wave damage is included in the model as a sigmoidal decreasing mortality with water depth. This depth-related mortality (M_w) is maximal (M_{max}) at the shoreline and decreases with rooting depth (Z) following a sigmoidal Hill-function:

$$M_W = M_{\max} \frac{H_W^p}{H_W^p + Z^p} \tag{4.2}$$

The exponent (p) of the Hill function is set to a default value of 4 to obtain a steep reduction in depth-related mortality.

Mortality due to competition at high plant densities is modeled using the thinning law, which relates spatial density of plants to their individual weight (see review by: Westoby, 1984). We assume that the losses in numbers are compensated by a faster growth of the remaining plants. This is done in the model by adjusting the individual weight of the remaining plants in such way that there is no loss in overall vegetation biomass.

At the pre-set end of the growing season, the above ground parts of the plants die in the model. The part of the plant biomass that was allocated to overwintering structures is added to the sediment seed bank a few days before, as the production of overwintering structures, essential for long-term survival, is assumed to be negligible in autumn.

The bulbils and oospores that are formed can either be stored in the grid cell associated with the parent plant or be dispersed to neighboring grid cells. To compute the spatial redistribution of propagules in case of dispersal, we used a modified normal distribution, which relates the number of seeds (or oospores) at a location on the grid ($p_{i,j}$) to the distance D (m) to the parent plant:

$$p_{i,j} = \frac{1}{2\pi D_{i,j}} \frac{2}{\sigma\sqrt{2\pi}} \mathrm{e}^{\frac{D_{i,j}^2}{2\sigma^2}} \qquad (4.3)$$

The standard deviation σ (m) defines the distance of dispersal.

Environmental variables

The availability of light is the primary factor controlling photosynthesis in aquatic systems (Carr et al., 1997), making an accurate description of light availability necessary. The irradiance follows a daily cycle and varies with depth. Daily solar irradiance is used as basic information. It follows a sine wave over the year fitted to data for Dutch conditions. The fraction Photosynthetically Active Radiation (PAR) is assumed 50% of the total irradiance. The irradiation at any time of the day is a function of the day length (Kirk, 1983). The day length on its turn is calculated from the latitude and the time of the year using equations of Kirk (1983). Reflection of light at the water surface is fixed at 10%, neglecting the impact of solar angle and wind speed. Light attenuation in the water column follows the Lambert-Beer law. In addition (self) shading by macrophytes is included in the model by the specific vertical light attenuation coefficient of plant material (Ikusima, 1970).

All other environmental parameters incorporated in the model (vertical light attenuation, temperature, bicarbonate concentration and water level) can either be set to a constant value or follow a yearly sine wave function. Alternatively, they may be read from a time series included as input file. In our current analyses, temperature is entered as a sine wave calibrated on data from Lake Veluwe.

The vertical light attenuation coefficient can be affected by the presence of vegetation. Vegetation can decrease the vertical light attenuation coefficient through a number of mechanisms (Scheffer, 1998). We simply use the following empirical relationship between vegetation biomass (B, g m^{-2}) and vertical light attenuation coefficient (K, m^{-1}):

$$K^* = K_{\min} + (K - K_{\min}) \frac{H_K}{B + H_K} \qquad (4.4)$$

This implies that vegetation can reduce the vertical light attenuation coefficient down to a minimum level (K_{min}, g m^{-2}). The half-saturation constant (H_K, g m^{-2}) is estimated from field data from Lake Veluwe.

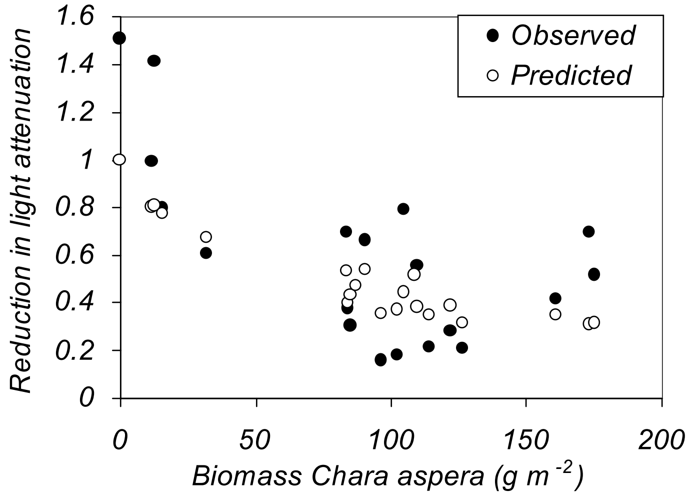


Fig. 4.1 *Fitted relationship between vegetation biomass and the ratio between the vertical attenuation coefficient of the open water and in vegetation stands. Data of Lake Veluwe of 1995 (Van den Berg et al., 1998). Eq. 4.4 is used and the background turbidity (K_{min}) and the half-saturation constant (H_k), were fitted by hand. The explained variance (R^2) of observed vs. predicted was 0.72.*

Parameter values

The default values of parameters and their dimensions and sources are shown in Table 4.1. As indicated, most parameters are derived from literature sources or from our own observations and measurements of growth of charophytes in Lake Veluwe. A few are obtained through calibration of the model to dynamics observed in Lake Veluwe. The effect of plants on turbidity deserves special mention, as it implies an important feedback in the model. We used the difference between the vertical light attenuation coefficient in dense *C. aspera* stands and adjacent open water areas without vegetation (data: Van den Berg et al., 1998) to fit Eq. 4.3. K, B and K^* are known, K_{min} and H_k were fitted by hand. This way, H_K is estimated to a value of 40 g AFDW m^{-2} and the background turbidity K_{min} to 0.5 m^{-1}. The resulting model rather accurately predicts ($R^2 = 0.72$) the ratio between light attenuation in vegetation stands and of the open water given the measured open water turbidity and vegetation biomass in Lake Veluwe (Fig. 4.1).

Methods of analysis

To analyze alternative stable states in the model, we used a special simulation procedure. We start with an arbitrary substantial initial biomass of oospores and bulbils (default 10 g m^{-2}) in a state where vegetation can develop (clear or shallow water).

For any simulation, the model was run for a certain number of years. A period of 40 years proved to be sufficient for the analyses in this paper to let the modeled vegetation reach an equilibrium. Note that we use the term equilibrium if the same pattern is repeated each year, although the more neutral term ‘asymptotic regime’ would be more appropriate.

***Table 4.1** Default parameters for Chara aspera without grazing. 'Oospores' are called 'seeds' in the model, and 'bulbils' are named 'tubers'. All biomass values are in g ash-free dry weight. Source - cal. = calibrated, obs. = estimated from field observations (Van den Berg, unpublished results), meas. = unpublished measurements Van den Berg, 1 = Scheffer et al.(1993a), 2 = assumed to be the same as Potamogeton pectinatus in Scheffer et al. (1993a)*

Parameter	Description	Unit	Value	Source
hCarbonate	Half-saturation carbonate concentration of growth	mg l^{-1}	30	obs.
hCarboReduction	Half-saturation biomass of carbonate reduction by plants	g m^{-2}	30	obs.
pCarbonate	Power of Hill function of carbonate dependent growth	-	1	obs.
cTuber	Tuber weight lost (d^{-1}) when sprouts starts growing	fraction	0.1	1
P_{max}	Maximal gross photosynthesis	hr^{-1}	0.006	cal.
Q_{10}	Q10 for maintenance respiration	-	2	1
Resp20	Respiration at 20°C	d^{-1}	0.0019	meas.
MaxLength	Maximum length of macrophyte	m	0.35	obs.
MaxWeightLenRatio	Weight of 1 m young sprout	g m^{-1}	0.03	meas.
RootShootRatio	Proportion of plant allocated to the roots	fraction	0.1	obs.
SpreadFrac	Fraction of sprout weight spread under water surface	fraction	0	obs.
FracPeriphyton	Fraction of light reduced by periphyton	fraction	0.2	1
H_K	Half saturation biomass of light attenuation reduction	g m^{-2}	40	obs.
hPhotoDist	Half-saturation distance from plant top for photosynthesis	m	1	1
hPhotoLight	Half-saturation light intensity (PAR) for photosynthesis	μE m^{-2} s^{-1}	14	meas.
hPhotoTemp	Half-saturation temperature for photosynthesis	°C	14	2
pExtReduction	Power in Hill function of light attenuation reduction	-	1	obs.
PlantK	Vertical light attenuation coefficient of plant issue	m^2 g^{-1}	0.02	meas.
pPhotoTemp	Exponent in temperature effect for photosynthesis	-	3	2
sPhotoTemp	Scaling of temperature effect for photosynthesis	-	1.35	2
BackgroundMort	Background mortality	d^{-1}	0	option
HwaveMort	Half-saturation depth for mortality	m	0.1	cal.
MaxAge	Maximum age of plants	d	175	obs.
MaxGrazing	Maximum grazing rate	g m^{-2} d^{-1}	0	option
MaxWaveMort	Maximum loss of weight in shallow areas	fraction	0.2	cal.
pWaveMort	Power of Hill function for wave mortality	-	4	cal.
Thinning	Apply the thinning rule?	-	True	option
GerminationDay	Day of germination of seeds	dayno	114	obs.
ReproDay	Day of dispersal of seeds	dayno	250	obs.
SeedBiomass	Individual weight of seeds	g	$2\ 10^{-5}$	meas.
SeedFraction	Fraction of plant weight allocated to seeds	yr^{-1}	0.13	obs.
SeedGermination	Fraction of seeds that germinate	yr^{-1}	0.2	cal.
SeedImport	Import of seeds	No.$m^{-2}yr^{-1}$	0	option
SeedInitialBiomass	Initial biomass of seeds	g m^{-2}	2	option
SeedMortality	Mortality of seeds	d^{-1}	0.0019	cal.
SeedRadius	Max. dispersal radius for 90% of the seeds	m	0	option
TuberBiomass	Individual weight of tubers	g	$1.8\ 10^{-4}$	obs.
TuberFraction	Fraction of plant weight allocated to tubers	yr^{-1}	0.22	obs.
TuberGermination	Fraction of tubers that germinate	yr^{-1}	1	obs.
TuberGermDay	The day that tubers germinate	dayno.	114	obs.
TuberImport	Import of tubers	No.$m^{-2}yr^{-1}$	0	option
TuberInitialBiomass	Initial biomass of tubers	g m^{-2}	8	option
TuberMortality	Mortality of tubers	d^{-1}	0	obs.

Subsequently, the biomass is plotted at an arbitrarily chosen day in summer (day 183 (1 or 2 July)) for 5 successive years. Thereafter, we start a procedure in which one parameter of interest (e.g. the water depth) is changed in an arbitrary number of small steps. The final state of the modeled vegetation after each step is used as a new starting point for the simulation of the next step. For each step the modeled vegetation is allowed to stabilize during 40 years, after which the new summer biomass is plotted during 5 years.

After the last step, we remove all plants, seeds and tubers from each grid cell. Then we take the same number of small steps in the reverse direction, letting the vegetation colonize the bare location. A tiny yearly import of oospores and bulbils is needed to give the plants a starting biomass and to prevent total extinction of the vegetation (we used an import as small as 0.1 oospores m^{-2} yr^{-1}). Again, 40 simulation years of stabilizing and 5 years of plotting results follow each step. If the model has alternative stable states, the biomass during this reverse analysis will be different from that of the forward version over a range of values of the parameter for which we scanned (e.g. the water depth). This tendency of the model to stay in the same state (vegetated or unvegetated) is called ‘hysteresis’.

Between two alternative equilibria, there is always an unstable equilibrium, just like there must always be a top of a hill between two valleys. We could find an estimate of the unstable equilibrium using a rather complex numerical method. We varied the initial concentrations of oospores and bulbills, and simulated with each combination till an equilibrium was reached. This way we could find the critical initial biomass where vegetation can just recover. This value could be transformed to the critical summer biomass by plotting the biomass of the first year of the simulation.

To analyze the effect of parameter changes on the hysteresis, we repeated the above procedure with a range of different settings of a second parameter of interest. Then, the zones of parameter values where the model has alternative equilibria can be plotted. Such diagram is called a ‘bifurcation diagram’. These diagrams allow a quick overview of the conditions for which we find alternative stable states. The lines that enclose zones with alternative stable states are called bifurcation lines. These lines show in general the parameter combinations where equilibria (or asymptotic regimes) change their nature. Zones with alternative stable states are enclosed by two catastrophic bifurcations, which means that a small change in parameters can have a large effect on the simulation results. The bifurcation where the macrophytes collapse is analogous to the ‘fold bifurcation’ of nonlinear dynamical systems theory (e.g. Strogatz, 1994), the point where the macrophytes reappear is called a ‘transcritical bifurcation’.

We also used the simulation model to investigate which parameters are most influential to the location of the catastrophical bifurcations in relation to the vertical light attenuation coefficient. To do so, we use a simple sensitivity analysis. The default parameter setting of *Chara aspera* at 1 m water depth, is used as a basis. Each parameter of *C. aspera* is changed twice (plus and minus 20%). We use the equilibrium scanning technique that is described above, to find out what the mean effect of these changes is on the difference between both bifurcations.

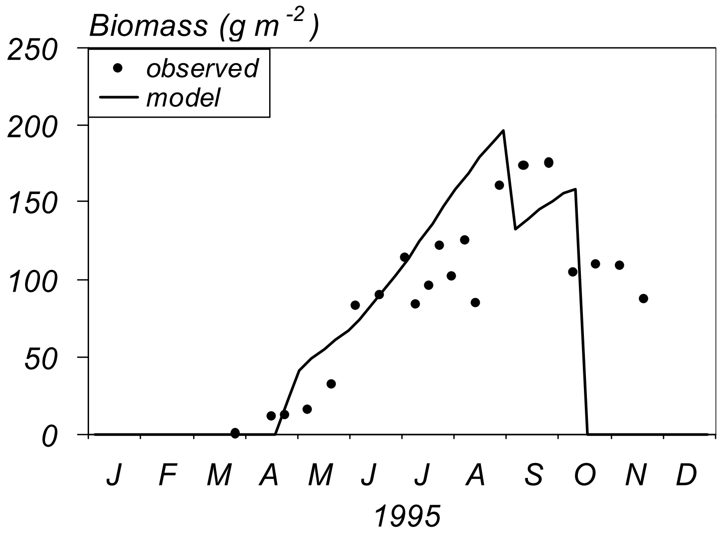


***Fig. 4.2** Predicted and observed Chara aspera biomass in Lake Veluwe through 1995 (data of: Van den Berg et al., 1998), excluding the last 3 points in autumn, $R^2 = 0.73$.*

Results

The design of Charisma allows us to analyze the model both as a traditional age structured model and as a more complicated model with competition between species and a spatially explicit environment. In order to keep track of mechanisms behind patterns, we first analyzed the most simple case and gradually increased complexity. We started with one grid cell, with a water level of 1 m, with one species (*Chara aspera*) and the default parameter settings (Table 4.1). The seasonal pattern of biomass observed in Lake Veluwe at 1 m (Van den Berg et al., 1998) could be reproduced reasonably well for this case (Fig. 4.2).

Alternative stable states and hysteresis

We analyzed the effect of changing turbidity on the equilibrium biomass of vegetation using the equilibrium scanning technique described in the previous section. Increasing the vertical light attenuation coefficient ('turbidity') of open water leads to a gradually decreasing equilibrium biomass of *C. aspera* from 140 to 70 g AFDW m^{-2} in summer (Fig. 4.3). The vegetation collapses at a vertical light attenuation coefficient of 6.4 m^{-1}. In the reverse scenario, vegetation reappears at a much lower vertical light attenuation coefficient of 3.9 m^{-1}. Between both critical vertical light attenuation coefficients ('bifurcations') the model has two alternative stable states: one with vegetation (70-115 g AFDW m^{-2}) and one without vegetation. This phenomenon is caused by the fact that vegetation reduces turbidity, which obviously results in better light conditions and enhanced growth of the vegetation. Thus, by clearing the water locally, established vegetation promotes its own persistence, even if the turbidities in open water are too high to allow colonization by plants.

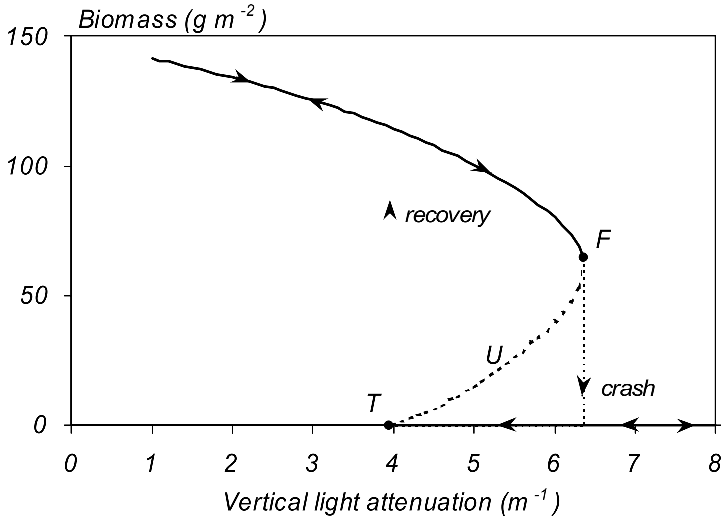


Fig. 4.3 *The effect of changing the vertical light attenuation coefficient of the open water on the calculated equilibrium biomass at day 183 of a Chara aspera vegetation. F is the point where vegetation collapses ('fold bifurcation'); T is the point where vegetation recovers ('transcritical bifurcation'). U is an estimate of the unstable equilibrium, which is between both alternative equilibria.*

In the range of vertical light attenuation coefficients where there are alternative equilibria, the initial state of the model determines whether vegetation can recover or not. Vegetation can recover only if the initial summer biomass of the model is above the unstable equilibrium, indicated by the dashed line in Fig. 4.3. This implies that in conditions where both equilibria exist, the size of the seed bank (biomass of the bank of oospores and bulbils) is critical for vegetation regeneration in summer. For instance, at a vertical light attenuation level of 5 m^{-1} the initial size of the bank of oospores and bulbills should be above 10 g m^{-2} to let a stable vegetation develop which will eventually reach a fixed equilibrium biomass in summer. At exceptionally high initial biomasses the summer biomass will decrease till the equilibrium value during the first years, because the seed bank can not be maintained.

Obviously, the critical biomass bank of overwintering structures is dependent on the vertical light attenuation of the lake. In clear shallow water (below bifurcation point *T* in Fig. 4.3), an infinitesimally small input of overwintering structures is sufficient to trigger establishment of vegetation, which will reach an equilibrium after several years. Above the higher threshold vertical light attenuation (*F*), a stable vegetation cover can never develop. In the area with alternative stable states (between *T* and *F*) there is a critical biomass of overwintering structures needed for vegetation establishment. This critical biomass is higher in turbid water.

Since overwintering structures are essential for vegetation regrowth in the next year in the temperate lake that we model, allocation of biomass to oospores and bulbils should enhance the chances of remaining vegetation dominance over the years. On the other hand, this investment also has costs in terms of photosynthetic production, since reproductive organs do not photosynthesize. Indeed, a bifurcation plot (Fig. 4.4a) confirms that chances for maintaining vegetation dominance in a lake with increasing turbidity are highest at an

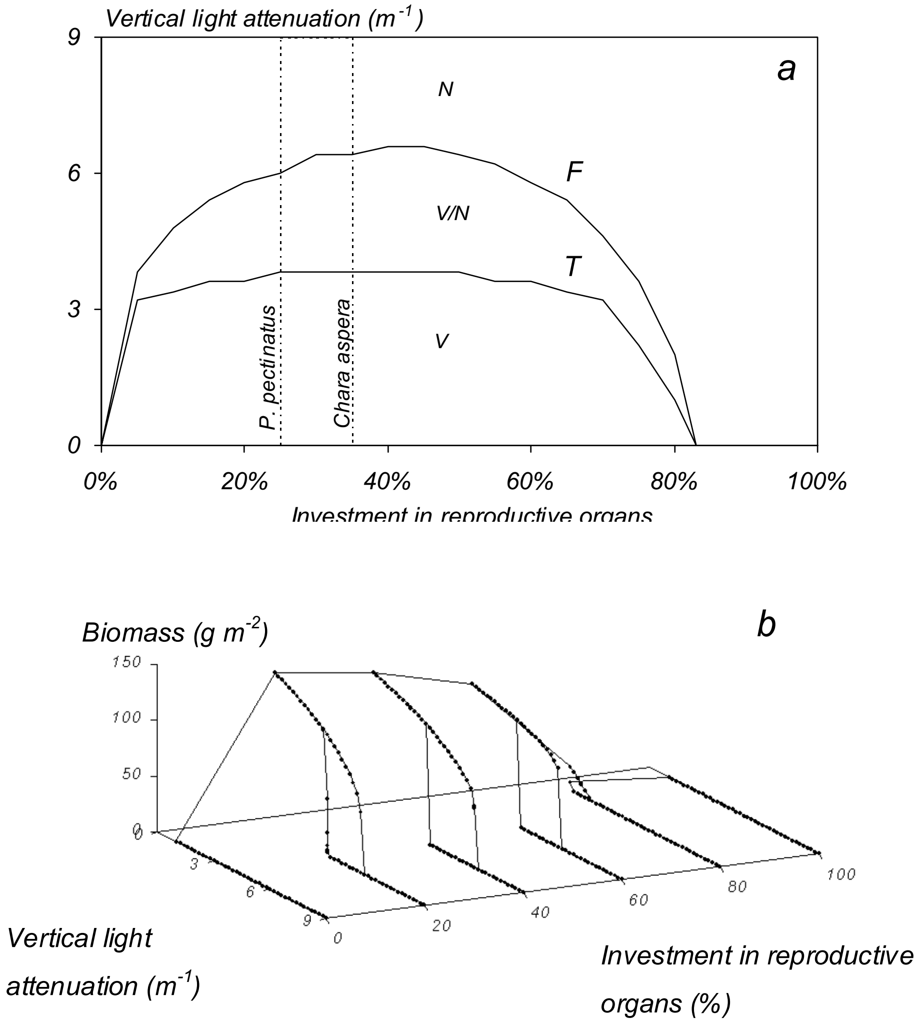


Fig. 4.4 *(a) Bifurcation plot as a function of the vertical light attenuation coefficient of unvegetated water and the investment of the plants in reproductive organs as a percentage of the biomass. V = only vegetated state; N = no vegetation; V/N alternative stable states. To vary the investment in reproduction, both the fraction invested in oospores and the fraction invested in bulbils is changed simultaneously, while keeping the balance between both fractions constant at 0.13/0.22. The default values of Chara aspera and Potamogeton pectinatus are indicated. (b) The effect of investment in reproduction on the equilibrium C. aspera biomass (day 183) at different levels of the vertical light attenuation coefficient of unvegetated water.*

intermediate investment in reproduction. The lower curve in this figure representing the critical turbidity for re-colonization has a less defined optimum between 20 and 60%. The optimum in realized summer biomass (in relatively clear water) occurs at a somewhat lower investment of reproduction organs (ca. 20%, Fig. 4.4b) than the maximum size of the hysteresis (ca. 40%, Fig. 4.4a). Interestingly, *C. aspera* in Lake Veluwe invests about 35% in overwintering structures (Van den Berg, unpublished results), which is close to what the model predicts to be optimal for maintaining vegetation dominance in a lake that becomes increasingly turbid (upper curve in Fig. 4.4a).

Table 4.2 *The effects of a +20% and -20% change in parameters on the width of range of vertical light attenuations where there is hysteresis and the mean sensitivity coefficient. The sensitivity coefficient is calculated as the mean relative change. The sign of the sensitivity coefficient indicates the direction of the change. All other parameters of Table 4.1 had a minor effect (< 2.1%) on hysteresis.*

	hysteresis with +20% change (%)	hysteresis with -20% change (%)	mean sensitivity coefficient (%)
H_K	75	150	-37.5
P_{max}	125	75	25.0
hPhotoTemp	75	121	-22.9
hCarbonate	83	117	-16.7
PlantK	88	117	-14.6
hPhotoLight	92	117	-12.5
TuberGerminationDay	83	104	-10.4
hCarboReduction	108	92	8.3
RootShootRatio	92	108	-8.3
TuberFraction	104	92	6.2
Resp20	92	100	-4.2
FracPeriphyton	92	100	-4.2
pPhotoTemp	104	96	4.2
SeedFraction	96	104	-4.2
SeedGermination	104	96	4.2
SeedMortality	96	104	-4.2
SeedBiomass	100	104	-2.1

The sensitivity of hysteresis to parameter change

Sensitivity analyses (Table 4.2) show that the difference between both critical turbidity levels is most sensitive to changes in H_K, the parameter determining the clearing effect of vegetation. The cluster of parameters P_{max}, hPhotoTemp, hCarbonate, PlantK, hPhotoLight, TuberGerminationDay, hCarboReduction and RootShootRatio also has a large impact on the size of the hysteresis. These parameters all have a large effect on growth and on the average summer biomass (Chapter 3). The clearing effect of vegetation is dependent on vegetation biomass, which explains the impact of this cluster of parameters on hysteresis. The remaining parameters that affect hysteresis (Table 4.2), have either a small effect on summer biomass or an effect on the investment in reproduction.

The effect of the changing H_K is analyzed more detailed by constructing a bifurcation plot (Fig. 4.5). If the clearing effect is large (H_K is small), a low biomass is sufficient to keep the water clear, and the area of hysteresis is large. With increasing H_K (= small effect), the size of the hysteresis reduces asymptotically. Note that H_K has no effect on the critical vertical light attenuation level (bifurcation *T*) at which vegetation reappears (3.8 m^{-1}), as the clearing effect only helps established vegetation to persist. Estimates from field data suggest that a value of 40 g m^{-2} is realistic for *C. aspera.* The model predicts a pronounced hysteresis in this situation. The open-water turbidity tolerated until vegetation collapses (*F*) is almost twice as high as the turbidity needed for initial colonization (*T*).

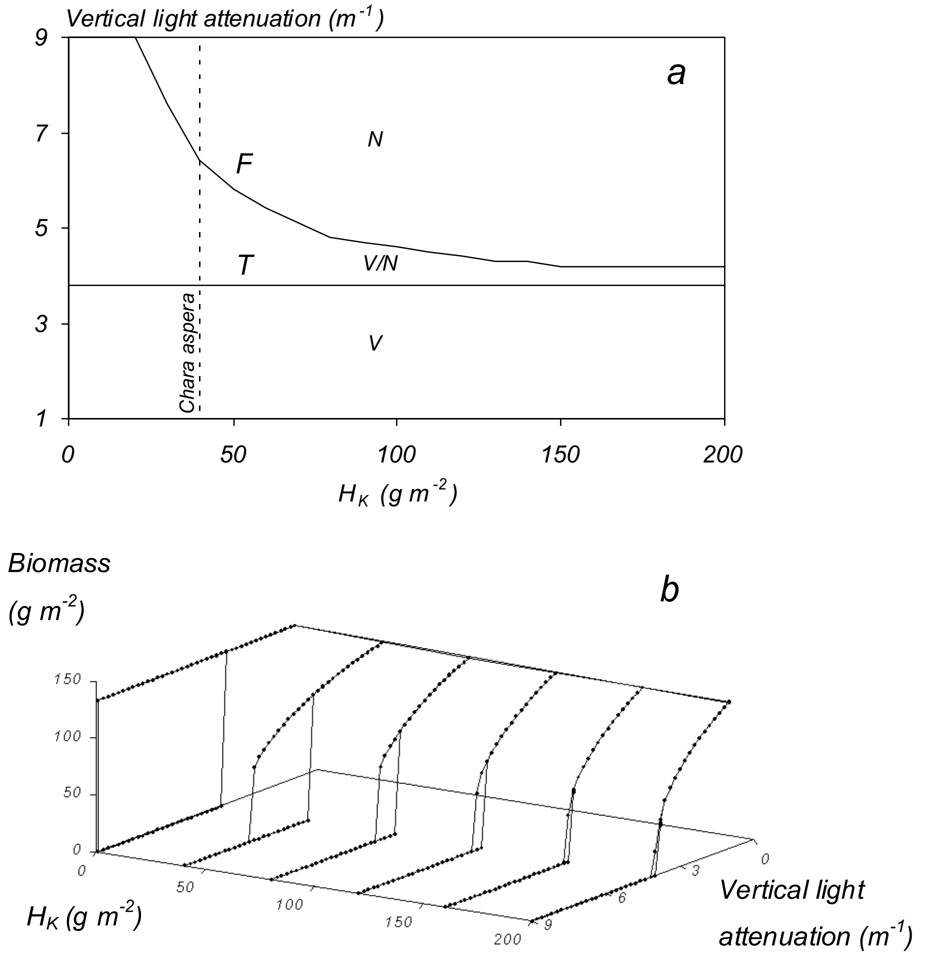


Fig. 4.5 *(a) Bifurcation plot with respect to the vertical light attenuation coefficient of unvegetated water and the half-saturation coefficient of the reduction of vertical light attenuation by vegetation (H_K). The default value of H_K of Chara aspera in Lake Veluwe is indicated. V = only vegetated state; N = no vegetation; V/N alternative stable states. F = fold bifurcation. T = Transcritical bifurcation (b) The effect of changing H_K on equilibrium C. aspera biomass (day 183) at different levels of the vertical light attenuation coefficient of unvegetated water.*

As shown by the sensitivity analysis (Table 4.2), the maximal photosynthetical rate (P_{max}) also has a strong impact on the occurrence of alternative stable states (Fig. 4.6). At a P_{max} lower than *c.* 0.0022 hr^{-1}, no vegetation can persist, not even in crystal clear water. Increasing P_{max}, the critical turbidity for colonization (*T*) becomes higher. Even stronger, however, is the increase of open-water turbidity tolerated until vegetation collapses (*F*). This may be explained by the fact that the effect of vegetation on water clarity is a function of macrophyte biomass. As a result the total range of hysteresis increases with ‘vigor of growth’ represented by P_{max}. Similar effects are caused by change in other parameters (hPhotoTemp, hCarbonate and others), that have a strong effect on the photosynthesis (not shown).

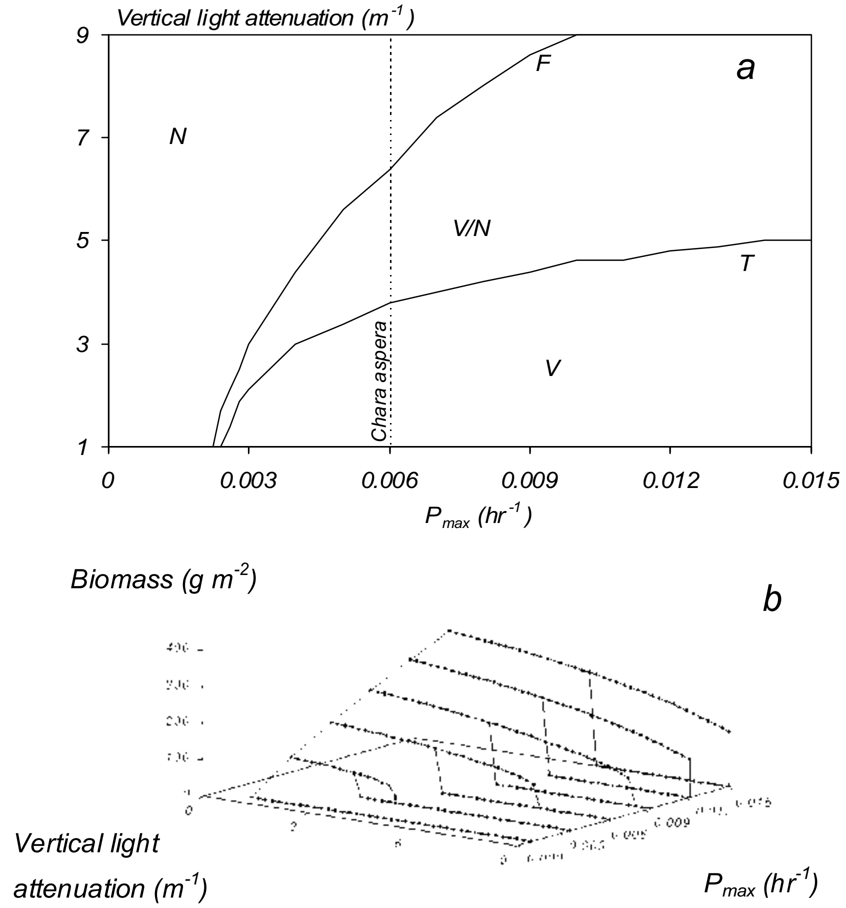


Fig. 4.6 *(a) Bifurcation plot of the vertical light attenuation coefficient of unvegetated water and the maximal photosynthetical rate (P_{max}). The default value of P_{max} of Chara aspera in Lake Veluwe is indicated. (symbols: see Fig. 4.5) (b) The effect of changing P_{max} on the equilibrium C. aspera biomass (day 183) at different levels of the vertical light attenuation coefficient of unvegetated water.*

The interplay of water level and turbidity

If a system has the potential to have alternative stable states, as our model, the response to all changes in conditions may be characterized by hysteresis. An important environmental variable for submerged plants is the water depth. In conjunction with turbidity, it affects the light reaching the plants. Indeed, analysis of the model (Fig. 4.7b) confirms that with increasing water depth the vegetation disappears at a (turbidity dependent) critical water level (*F*), which is higher than the critical water level needed for colonization (*T*). From the bifurcation diagram (Fig. 4.7a) we can see the hysteresis with respect to both water level and turbidity: horizontal cross sections show the size of hysteresis after change in water level, vertical cross sections indicate the hysteresis in response to changing external vertical light attenuation. Note that the size of the hysteresis is quite constant and relatively small with respect to water depth, whereas the area with alternative equilibria with respect to vertical light attenuation is rapidly increasing in shallower water, reaching maximal values at a water depth of between 0.5 and 1 m.

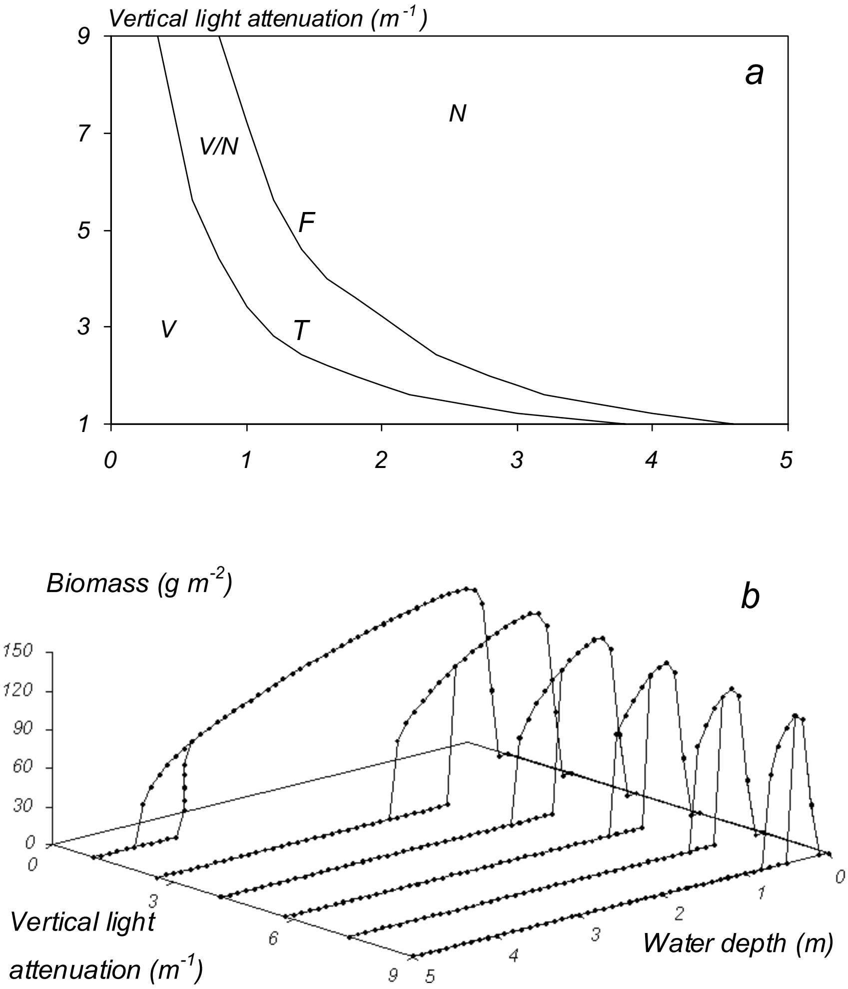


Fig. 4.7 *(a) Bifurcation plot showing the area of hysteresis depending on the vertical light attenuation coefficient of unvegetated water and the water depth. (symbols: see Fig. 4.5) (b) The effect of changing water depth on the equilibrium C. aspera biomass (day 183) at different levels of the vertical light attenuation coefficient of unvegetated water.*

The effect of a spring clear water phase

All previous simulations were done with a constant open water turbidity. In reality there is a seasonal pattern with often high chlorophyll concentrations and turbid water in summer but a clear water phase in spring. It has been hypothesized that a spring clear water phase is of particular importance for promoting vegetation colonization, because the plants are still small in this period and therefore more sensitive to turbidity of the water layer than full grown individuals that reach the water surface (Meijer and Hosper, 1997; Perrow et al., 1997b). The spring clear water phase is usually in May and the minimum chlorophyll content is typically about 10% of mean summer chlorophyll concentration (Scheffer et al., 1997). To test the effect of a clear water phase, we lowered the vertical light attenuation coefficient (K, m^{-1}) of unvegetated water during three weeks using the following equation:

$$K^* = K_{min} + 0.1\ (K - K_{min}) \tag{4.5}$$

In which K_{min} is the background vertical light attenuation coefficient (m^{-1}). The effect of the timing of this clear water phase on vegetation colonization and collapse is shown in Fig. 4.8. Our simulations indicate that the occurrence of a short period of clear water in spring can have a pronounced effect on vegetation (Fig. 4.8). June is the period in which a clear water phase has the strongest effect in our model. It may be surprising that clear water in the period directly after germination, from late April to early May has less effect. Apparently, clear water in the period of maximal production is more important for a long-term effect on plants. Note that this timing is more important for the persistence of existing vegetation (line *F* in Fig. 4.8) than for colonization (line *T* in Fig. 4.8). In Dutch and Danish lakes clear water periods occur most frequently in May or early June (Jeppesen et al., 1997; Scheffer et al., 1997), coinciding with a period in which according to our model they are indeed quite effective in promoting vegetation dominance.

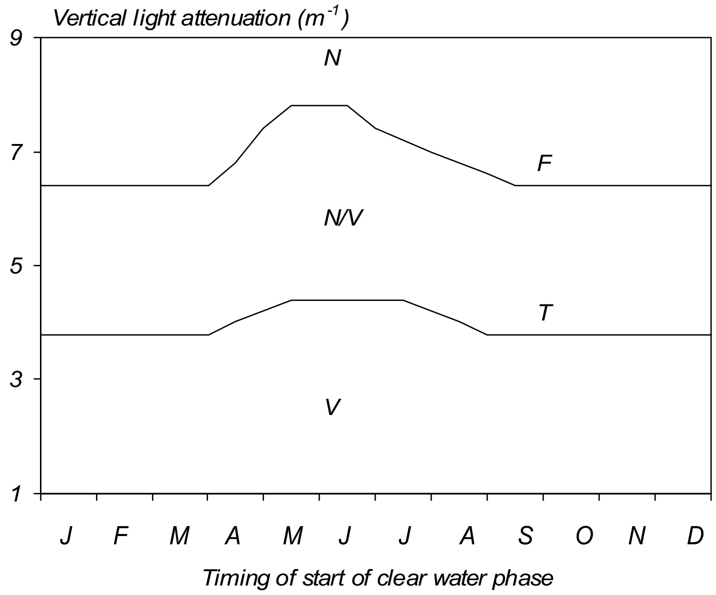


Fig. 4.8 *Bifurcation plot of the vertical light attenuation of unvegetated water and the timing of the start of a clear water phase (lasting 28 days in which the external vertical light attenuation is reduced for 90%). Symbols are explained in Fig. 4.5.*

Consequences of spatial heterogeneity

It has been hypothesized that the depth profile of a lake and the horizontal redistribution of water and organisms could be crucially important for the occurrence of alternative stable states in vegetation dominance (Scheffer, 1998). We analyzed this by simulating spatially explicit dynamics over depth gradients. For simplicity we focussed on a simple linear gradient of a hypothetical lake bank (Fig. 4.9). While keeping the average depth equal at 1.5 m, the effect of different depth profiles is explored by varying the linear slope of the bank between two extremes: (1) slope of 0%: all grid cells have a water depth of 1.5 m; (2) slope of 2%, the lake has a linear depth gradient between 0 and 3 m (mean water depth remains 1.5 m).

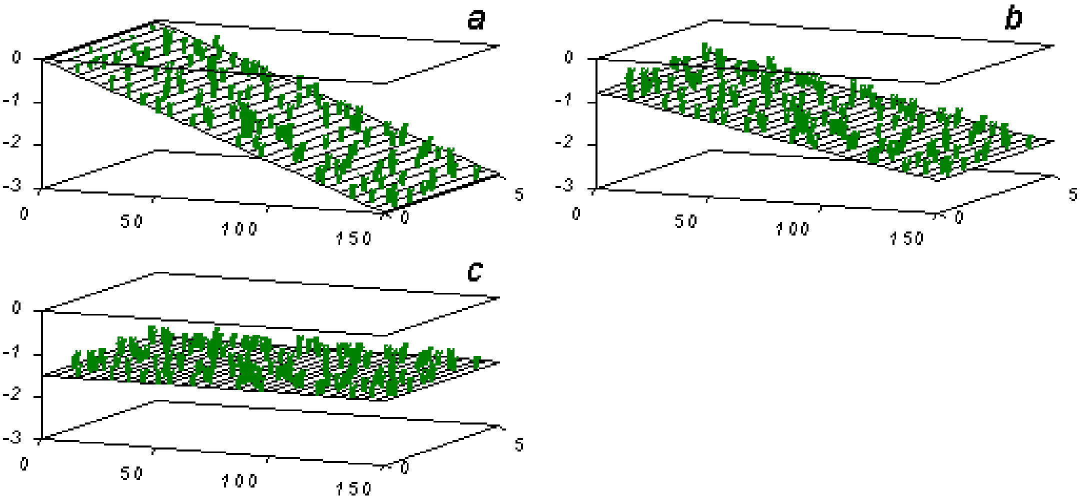


Fig. 4.9 *The effect of different depth profiles is explored by changing the minimum and maximum water depth of a grid of 30 cells of 5x5 m, while keeping the mean water depth constant at 1.5 m. (a) Maximum gradient (slope = 2%); (b) intermediate gradient (slope = 1%); (c) flat lake (slope = 0%).*

Our first analysis is without propagule dispersal and without horizontal water mixing, so that there are no interactions between the cells (Fig. 4.10a). In case of a zero slope, all cells are equal. As a result, they all switch between the alternative stable states at the same critical turbidity values, and the response averaged over the entire spatial grid is the same as in simple non-spatial simulations. In contrast, if there is some slope the response to increasing turbidity becomes more smooth, as vegetation disappears first from the deep cells and then from the shallower parts. Conversely, recovery from a turbid state without vegetation occurs first at the shallowest cells and gradually proceeds to the deeper parts. The resulting overall response of the hypothetical lake still shows hysteresis in the sense that the equilibrium follows a different path in response to increasing turbidity than to decreasing turbidity. However, rather than switching entirely at a critical turbidity, we now have a situation with a gradually expanding or retreating front of plant cover. Note that if the depth gradient is strong (0-3 m, slope 0.02), there is very shallow (and deep) water in our simulations. In the shallowest zones, vegetation can then persist even at very high turbidities, causing the persistence of some vegetation even in turbid water (Fig. 4.10a).

Although sharply delineated local areas with clear water and vegetation are sometimes observed (Scheffer et al., 1994), it seems realistic to assume at least some horizontal mixing of water. We mimicked the effect of such mixing on turbidity simply by averaging the vertical light attenuation coefficient of adjacent grid cells within a certain radius (‘mixing distance’). To get an indication of the effect of mixing, the analysis of the changing steepness of the slope (Fig. 4.10a) is repeated using a mixing distance of 100 m (Fig. 4.10b).

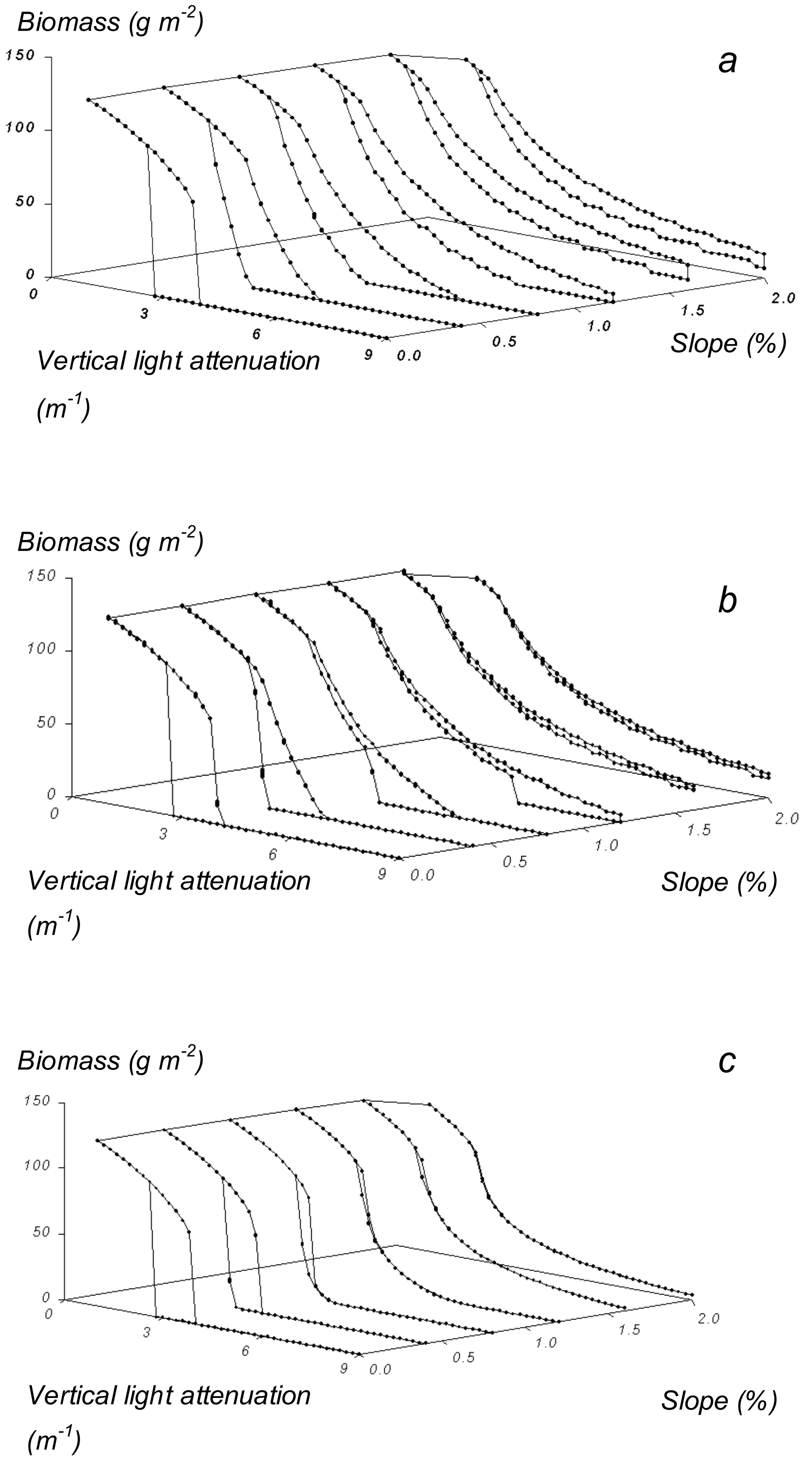


Fig. 4.10 *The effect of changing slope of the depth profile (see also: Fig. 4.9) of 30 grid cells of 5x5 m on the hysteresis: (a) without mixing and propagule dispersal; (b) with 'mixing' by averaging the vertical light attenuation over a radius of 100 m; (c) with propagule dispersal over a radius of 20 m.*

Obviously, mixing has no effect again in ‘flat-bottom lakes’ (with one depth), because mixing between identical cells does not make any difference. However, with increasing slope, the response of vegetation in mixed lakes becomes quite different from the previously simulated situation with entirely isolated grid-cells. Hysteresis becomes much smaller with mixing and the averaged response over the gradient becomes sigmoidal (Fig. 4.10b). The phenomenon that dense vegetation can survive in locally clear shallow water even at very high open water turbidity, disappears as a result of mixing.

We also checked the effect of simulated propagule dispersal to neighboring grid cells (Fig. 4.10c). As with horizontal mixing of water, horizontal oospore dispersal causes the difference between the two branches of the hysteresis (‘collapsing’ and ‘recovering’) to shrink. Note also that the vegetation persisting at very shallow areas (resulting from strong experimental slopes) provides ‘hot spots’ of oospore dispersal that trigger recovery of neighboring zones. This prevents sustained absence of plants with decreasing turbidity found in the ‘low slope’ simulations.

Discussion

Our analysis indicates that alternative stable states may be expected to arise from the interaction between water clarity and aquatic plant growth in shallow lakes. Previous results using minimal models (Scheffer, 1998), thus, probably are not an artifact of simplifications such as neglecting seasonality and the vertical gradient of light in the water column. Our results also show that the possibility of multiple stability depends on various factors. In the current model, the effect of plants on water clarity is essential for obtaining alternative stable states and thus for obtaining hysteresis in the response on various factors. If we consider a shallow lake of homogeneous depth, the model predicts that even a slight clearing effect leads to alternative stable states, although hysteresis becomes more pronounced if the effect of plants on turbidity is stronger. Several studies have reported a distinct effect of vegetation on water clarity either of the whole lake (Timms and Moss, 1984; Jeppesen et al., 1997) or on a local scale (Pokorný et al., 1984; Van den Berg et al., 1998). Our estimate of the clearing effect is based on field observations in Lake Veluwe, comparing turbidity within vegetation and outside vegetation. Using data of a review of the clearing effect of vegetation (Scheffer, 1998), we estimate that the H_k may range between about 18 and 105 g AFDW m^{-2} in different situations. Note that all of these estimates may be conservative as mixing might obscure field estimations of the clearing effect of vegetation. The precise shape of the relationship between vegetation biomass and turbidity is yet unclear. Although there is some evidence that the relation between vegetation biomass and turbidity is concave, indications for a discontinuous drop in turbidity beyond a critical plant biomass have also been found (Scheffer, 1998). In any case, it seems reasonable to assume that a higher biomass of vegetation results in a lower vertical light attenuation coefficient of the water. The model prediction that vegetation with a high growth rate will have a wider range of hysteresis, is unlikely to depend on details of the clearing effect.

Our analysis also indicates that in temperate lakes, where plants disappear in winter, the formation of a substantial bank of overwintering propagules is a key factor for maintaining vegetation dominance in eutrophic shallow lakes. In fact, the model suggests that there should be an optimum with respect to investment in reproductive organs due to a trade-off between investment in non-photosynthesizing reproductive organs and primary production. More precisely, there are probably two optimal values: (a) a certain investment in bulbils and oospores yields an optimal biomass in summer; (b) a somewhat higher investment produces a maximal stability of the vegetated state (range of hysteresis). A similar effect has been predicted by another model (FLORA), which includes a more detailed description of the formation of reproductive organs (Van Dijk and Janse, 1993). Interestingly, the dominant species in Lake Veluwe *Potamogeton pectinatus* L. and *Chara aspera* both invest roughly the predicted optimum percentage (respectively 25% and 35%) to overwintering structures (van den Berg unpublished results). However, for *P. pectinatus* the investment in overwintering structures is known to be highly variable and much lower percentages (ca. 12%) have been reported as well (Van Dijk and Van Vierssen, 1991).

Importantly, the model shows that spatial processes can have a very large impact on hysteresis. Vegetation in lakes that have slopes in the underwater landscape, respond more gradually to changes in turbidity than vegetation in ‘flat-bottom’ lakes. Horizontal mixing of water and propagules reduces hysteresis in ‘sloped’ lakes. It is important to note that the effect of plants does not only propagate to open water through horizontal mixing of water and propagules. In reality, vegetation may also reduce turbidity of the whole lake, by changing the food web (e.g., Timms and Moss, 1984; Schriver et al., 1995; Jeppesen et al., 1997).

Although Charisma is more realistic than simple vegetation models as presented in Scheffer (1998), there are still many processes not included in the model or modeled in a simplistic minimal way, such as nutrient limitation, periphyton, bird grazing and sediment erosion. The latter two deserve special mention as they could well cause hysteresis even in the absence of any clearing effect of vegetation. Bird grazing is highest in late summer and autumn when territories break up and large flocks of migratory birds visit lakes foraging on shoots and overwintering structures (Perrow et al., 1997b). Although the impact of birds is thought to be limited in general, grazing may delay colonization of previously unvegetated lakes (Lauridsen et al., 1993; 1994). Indeed, model analyses suggest that this mechanism may cause hysteresis even if no clearing effect is involved (Scheffer et al., 1993a). Also, the initial plant settlement can be difficult in wind exposed lakes if the sediment is soft and unstable. Once the vegetation is established, the mortality by erosion is reduced due to stabilization of the sediment and reduction of wave action. Such a feedback mechanism may in itself lead to alternative stable states (Scheffer, 1998). Obviously, including bird grazing and erosion in the model would enlarge the range of hysteresis. More specifically, these mechanisms will tend to increase the range of conditions over which the poorly vegetated state is stable.

We also like to stress that in the current analysis we only studied the effect of different factors on the equilibria of the system under constant environmental conditions. It takes the model about 5-10 years to approach an equilibrium, and real vegetations may therefore spend most of the time in ‘transient states’ if conditions vary. An earlier simulation study

(Scheffer et al., 1993a), showed that this ‘slowness’ leads vegetation biomass to be rather constant, although under certain critical conditions even a small variation in environmental conditions may cause large and erratic fluctuations in vegetation biomass. In practice, the relatively slow dynamics of the vegetation may delay recovery and disappearance of vegetation for years.

Conclusions

Our model analysis shows that alternative stable states may be expected on the basis of relatively realistic assumptions about macrophyte growth and their effect on transparency of the water. Furthermore, the following specific hypotheses were generated:

1. In lakes with relatively poor conditions for plant growth, macrophytes may recover only if the initial biomass of the seed bank exceeds a critical threshold level. In contrast, under poor (turbid) conditions no recovery at all is possible, whereas under good (clear) conditions the slightest initial seed bank is sufficient to trigger recovery.
2. Clear-water phases are important for ensuring vegetation persistence, and are most effective in promoting seasonal return of plants if they occur in end May and June.
3. In lakes with a flat depth profile alternative stable states occur over a larger range of conditions than in lakes that have a more varied depth distribution.
4. In case of poor horizontal mixing of water, local alternative states can occur. With increasing water quality vegetation may then expand gradually, clearing the water locally.
5. Strong horizontal mixing of water can reduce the chance of colonization of vegetation in very shallow zones of large lakes, as it hampers local clearing effects.

Besides these hypotheses that are testable in field situations or experiments, we generated hypotheses that would be harder to test. However, it would be useful to test whether these results also can be generated with other models using different formulations, to show the robustness of the results.

1. Investment in reproductive organs is important to ensure long term stability of vegetation in temperate regions. However, there is a trade-off as more investment in reproduction means less photosynthesis. The optimum value for obtaining maximal summer biomass in clear water is predicted to be lower than the optimum investment for realizing a maximum stability of the vegetated state (ca. 40%).
2. Propagule dispersal has little effect on stability of the vegetated and unvegetated state.

Acknowledgements

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Chapter 5
A simple model for evaluating the costs and benefits of aquatic macrophytes

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Abstract

Dense beds of aquatic macrophytes often cause nuisance to boaters and swimmers, and may obstruct water flow. Management of aquatic vegetation is, therefore, often aimed at reducing the biomass of the plants. If the nuisance is caused by exotic invasive species, there usually is no controversy with nature conservation aims. In shallow lakes, however, the interests of recreational users may conflict with nature conservation because the promotion of indigenous submerged vegetation is considered an important tool for lake restoration. Aiming at intermediate vegetation biomass seems a good solution for this controversy at first sight. However, we argue that such a compromise is often not the best policy from a welfare economic point-of-view. We present preliminary results of a graphical model, showing that the overall benefit for all ecosystem users may be minimal at the intermediate vegetation biomass. Furthermore, even if there is an optimal benefit at an intermediate macrophyte biomass, we argue that it may not always be feasible to force the vegetation biomass to the desired level. Due to ecological feedback mechanisms, the system can have two alternative stable states: one with high vegetation biomass and one with little or no vegetation. It is concluded that it will often be better to realize a management strategy aimed at keeping some lakes (or parts of lakes) free of aquatic plants, whereas allowing others to be densely vegetated.

Introduction

Dense beds of macrophytes can be a nuisance for boating, fishing, swimming in lakes, and may obstruct the water flow in irrigation channels. Therefore, aquatic weed control is the topic of much research (e.g. Caffrey and Wade, 1996) and management of aquatic vegetation is often aimed at reducing the biomass of vegetation. If the nuisance is caused by exotic invasive species, there usually will be no controversy with nature conservation aims, as these species are a threat for native species (De Winton and Clayton, 1996). In many shallow lakes, however, lake managers are trying to restore the vegetation that vanished as a result of eutrophication, which has led to turbid water and cyanobacterial blooms. Establishing a stable aquatic vegetation is considered as a very important tool to restore eutrophic lakes (Crawford, 1979; Perrow et al., 1997a; Scheffer, 1998). The main benefit of an abundant vegetation is that vegetation reduces turbidity in shallow lakes (e.g., Hasler and Jones, 1949; Timms and Moss, 1984; Van den Berg et al., 1998). Also bird abundance and biodiversity of many groups of animals is usually higher in vegetated lakes (Scheffer, 1998).

Aiming at an intermediate biomass of macrophytes seems the obvious solution to restore lakes without causing nuisance, as shown by the graphical model of Clayton (1999). In this paper we present an extension of this model, which shows that such compromise is not always the optimal policy (i.e. the policy that maximizes the mean benefit for all ecosystem users).

A graphical model of the costs and benefits of aquatic vegetation

Aquatic macrophytes are of importance to several different groups of ecosystem users, for example people interested in nature conservation, recreational users, farmers and boaters. The interests of these groups often conflict, but it is hard to compare the interests of these different groups. We use the approach of environmental economists to account for all interests in a common unit, namely ‘welfare’ or ‘benefit’ (Hanley and Spash, 1993; Perman et al., 1996; Varian, 1996). Environmental economists have ways to quantify the welfare of different groups including the value of environmental services (e.g., Carson and Mitchell, 1993; Dixon et al., 1994). Determining detailed quantitative welfare functions is beyond the scope of this paper; we will only discuss qualitatively different possibilities.

In our simple model we included the welfare functions of two groups of users:

- Nature conservationists aiming at the restoration of eutrophic waters. In general, this group promotes indigenous macrophytes, possibly up to an optimum level, above which dense macrophyte beds could have a negative impact on biodiversity, water quality and conservation values. This group includes recreationists that are interested in nature: ‘eco-recreation’.
- Recreational users that are hindered by dense vegetation. This group includes boaters, wind surfers and swimmers.

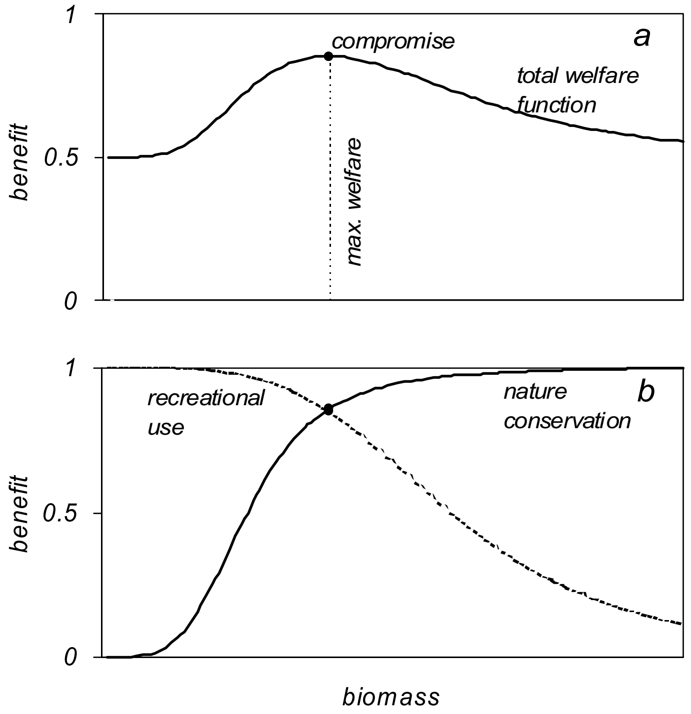

***Fig. 5.1** Vegetation with a low growth form. (a) the total welfare function (mean of functions in lower panel). The point with a compromise between both groups (closed circle) coincides with the maximum total welfare. (b) functions of benefit for recreational use and nature conservation.*

Of course there may be more groups of stake holders involved in many lakes. For simplicity, we ignore these groups in the current analysis, but our approach may be extended to include any group whose welfare depends in a known way on vegetation abundance in the lake. For simplicity, we also ignore in the welfare function of biomass harvesting costs and other costs to maintain biomass at a desired level.

In our model, the welfare functions of both groups link the biomass of vegetation to the benefit or cost of these two ecosystem users. The welfare functions are defined as functions ranging from 0 (minimal benefit or maximal nuisance) to 1 (maximal benefit or minimal nuisance). The overall welfare of the society is composed of the contribution from welfare by users in each group, weighted by the number of individuals in that group.

The optimal strategy from a 'rational social planner's' point-of-view is to aim at the biomass where the total welfare function is optimal.

For restoration of eutrophic lakes, the benefit of aquatic vegetation is strongly connected to the effect of macrophytes on turbidity and vice versa. Although the exact shape of especially the clearing effect of vegetation is yet unclear, the positive feedback of macrophytes on their own growth is known to cause alternative stable states (Scheffer, 1998). If a lake has alternative stable states, the benefit of vegetation is typically a threshold function. Below a certain biomass, the vegetation is not able to cause a shift from the turbid state to the clear water phase. The exact value of the critical biomass is not only dependent on the trophic state of the ecosystem, but also on the growth form of the macrophytes. Most beneficial are probably low growing species like charophytes (Crawford, 1979; Clayton and Tanner, 1988; Coops and Doef, 1996). Besides the clearing effect of macrophytes, there are also other benefits associated to macrophytes, such as an increase of habitats for invertebrates (e.g., Hargeby et al., 1994) and food sources for birds (e.g., Perrow et al., 1997b) and fish (e.g., Van Donk et al., 1994). These effects are probably more gradual. The total nature benefit of most types of indigenous macrophytes is probably most appropriately characterized by an increasing sigmoidal curve (Fig. 5.1b solid line).

The nuisance caused by aquatic plants for recreational users increases with macrophyte biomass. To our knowledge, the shape of this nuisance function has not yet been assessed. It seems reasonable, however, to assume a sigmoidal curve for this function also. Below a certain biomass level, boating and swimming is not hindered. If the vegetation stands exceed a certain density, and especially if the plants cover the water surface, vegetation becomes a nuisance (Fig. 5.1b dotted line). The growth form of the macrophytes is important for this group too. The tolerance of recreational users for low growing species will be higher than for floating or canopy forming species.

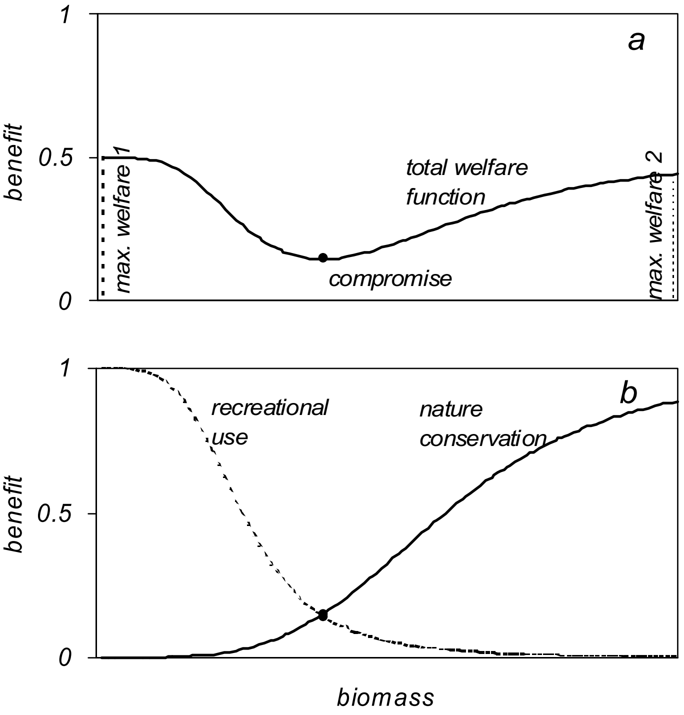

Fig. 5.2 Canopy forming or floating vegetation. (a) the total welfare function (mean of functions in lower panel). The point with a compromise between both groups (closed circle) coincides with the maximum total welfare. (b) functions of benefit for recreational use and nature conservation.

Hill functions offer a convenient way to model such welfare functions. The Hill function has two parameters: the half saturation H which defines, in our case, the biomass (B) of plants where the welfare (w) is 0.5 and the exponent p which defines the steepness of the function:

$$w = \frac{B^p}{H^p + B^p} \tag{5.1}$$

This increasing function can be mirrored to become a decreasing function by changing it the following way:

$$w = \frac{H^p}{H^p + B^p} \tag{5.2}$$

We explored the effect of different combinations of welfare functions on the resulting total welfare. For simplicity we give both user groups an equal weight. Several different situations may arise, of which we highlight three examples in our analysis:

1. Vegetation with a low growth form (Fig. 5.1). The benefit of low growing plants for water quality is relatively large, whereas the nuisance is relatively low. Therefore, the half saturation of nature benefit is assumed to be lower than the half saturation of recreational nuisance. This large overlap in welfare functions causes an optimum in total welfare at intermediate vegetation densities. Thus, the compromise between both types of ecosystem users coincides with an optimum overall welfare and aiming at intermediate biomass seems the optimal policy in such a case.

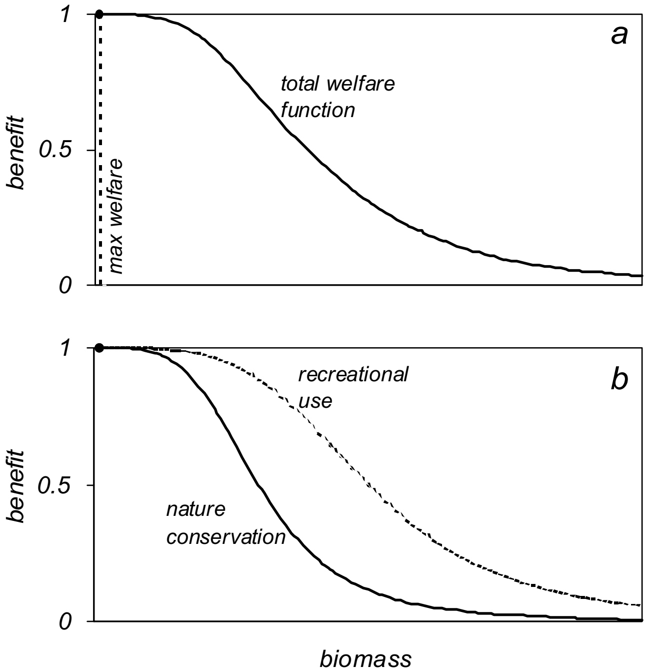

Fig. 5.3 *Exotic invasive species. (a) the total welfare function (mean of functions in lower panel). The point with a compromise between both groups (closed circle) coincides with the maximum total welfare. (b) functions of benefit for recreational use and nature conservation. Both groups have the same interests, the target of the management should be control (or eradication) of the plants.*

2. Canopy forming or floating vegetation (Fig. 5.2). This type of vegetation causes more nuisance for boating and swimming and is less beneficial for lake restoration. As a result a moderate amount of such plants may be too much from a recreational point-of-view and insufficient from a nature conservation point-of-view. In the model we represent this by setting the half saturation of nature benefit higher than the half saturation of recreational nuisance. This causes the total welfare to be at minimum at an intermediate biomass. Compromising between both groups is obviously a bad policy in this case, provided that the same strategy is applied to the entire water body. Designing separate areas for recreation and nature conservation can a better policy in such situations, if free-floating species are not dominant.
3. Vegetation dominated by exotic invasive species (Fig. 5.3). As mentioned before, the interests of nature conservationists and recreationists do not usually conflict in this case. We have mirrored the Hill function of nature conservation to represent this. The exact shape of the curves and the value of the half saturation coefficients is not essential in such a situation. The optimum policy is always to eradicate the species.

In conclusion, aiming at an intermediate vegetation biomass is only a good strategy for maximizing overall welfare in a limited class of cases (Fig. 5.1).

Discussion

Whether or not aiming at an intermediate vegetation biomass is a good policy from an environmental economist's point-of-view, depends on the way in which welfare of different groups of lake users varies with vegetation biomass and the cost of harvesting biomass or other management costs. For a thorough analysis, one would need to assess the actual shape of these curves to analyze any field situation in practice and the management characteristics. However, our analysis shows that, at least, the qualitative point can be made that a compromise with intermediate vegetation biomass will only lead to a high average welfare for all users of the lake in a limited subset of cases.

Obviously, the benefit curves will not always have the shape as presented in our model. The Hill curves that we used in our model are not appropriate to describe all complex relations that exist in reality. We disregarded the fact that very high biomass levels of canopy forming and floating vegetation can have a detrimentally impact on water quality, biodiversity and conservation values. The benefit curve of nature conservation will have an optimum then. Furthermore, the nature value of a water body that is dominated with exotic species can still have a substantial value for nature conservation. Again, there will be situations where an optimum curve would be a better description. For clarity and because we lack detailed information on the real shape of the benefit curves, we presented these simplified relationships.

Another aspect that we did not consider in the current benefit analysis is that loss of vegetation usually invokes algal blooms in shallow eutrophic lakes. For swimmers and other recreational users that often complain about high vegetation biomass, such algal blooms would also cause nuisance (Boggess et al., 1997; Herath, 1997). This implies that recreational users may wish for a situation (a clear lake with little vegetation) that is ecological impossible under the high nutrient conditions. With our model, it would mean that recreational users really have a more complex welfare function: aiming at the lowest biomass that is sufficient for preventing algal blooms would yield the highest welfare for recreational users in this case. Also, in reality, recreational users are a diverse group with often conflicting interests. For instance, power boating is incompatible with many other recreational activities (Nuttall and Richardson, 1989).

An interesting feedback could result from damage to aquatic vegetation by recreational users, which is observed frequently (Murphy and Eaton, 1983; Best, 1987; Mumma et al., 1996). Murphy & Eaton (1983) showed that heavy pleasure-boat traffic can even be a principal factor in suppressing macrophyte abundance in British canals. If such cases, it is likely that recreational users have a positive effect on the suitability of the water for recreation, implying a potential positive feedback in recreational use, which could lead to alternative stable states. Moreover, Murphy & Eaton (1983) found a critical level of boat traffic above which the macrophyte community was affected. This is a further indication that there could be alternative stable states (Scheffer, 1998). This phenomenon would be a much like the maintenance of ‘grazing lawns’ in which invasion by large unpalatable (hindering) plants is prevented by intense use by terrestrial and aquatic grazers (McNaughton, 1984).

From the environmental economic analyses, we concluded that, in certain situations (with low growing macrophyte species), the optimal management strategy could be to aim at intermediate biomass. However, if the system has alternative stable states (Scheffer, 1990; Scheffer, 1998), it will be impossible to set vegetation to any desired level. The vegetation biomass could suddenly drop to zero after a certain critical biomass is exceeded. One should therefore keep in mind that the economical best policy might not be feasible due to ecological constraints.

In conclusion, environmental economic aspects suggest that aiming at intermediate vegetation biomass is only a good policy for maximizing overall welfare of different types of lake users in a limited number of situations. An example of such a situation is for vegetation with a low growth form as illustrated in Fig. 5.1. In situations where recreation and nature conservation are competing, a compromise can be better achieved by assigning lakes or parts of lakes to recreational use and other areas for nature conservation. Alternatively, a selective control of submerged macrophytes aimed at a shift in the species composition towards low growing species, could be a good solution for the controversy.

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We want to thank the organization of the 10th EWRS International Symposium on Aquatic Weeds for bringing together researchers working on the control of aquatic weeds with people studying the functional ecology of macrophytes. Discussions during the symposium led to the model described in this paper. An anonymous referee made useful suggestions to improve the manuscript.

Chapter 6
Aquatic macrophytes: restore, eradicate or is there a compromise?

Egbert H. van Nes, Marten Scheffer, Marcel. S. van den Berg & Hugo Coops

Aquatic Botany, in press.

Abstract

Promoting indigenous submerged macrophytes is considered an important measure to restore shallow lakes. On the other hand, dense stands of aquatic vegetation often cause nuisance for boating, swimming and by obstruction of water flow. Consequently, the interests of recreational users may conflict with nature conservation. At first sight, aiming lake management at intermediate vegetation biomass seems a good solution for this controversy. However, as can be shown with a simple economical model, such a compromise may not always be an optimal solution in terms of total welfare across all users of a lake. Here, we show that a management strategy aimed at moderate plant biomass can also be unfeasible for ecological reasons. This is shown by applying two very different models: a minimal logistic model of plant growth which is easy to understand, and the relatively complex and realistic simulation model Charisma which, among other things, includes the seasonal cycle and a detailed description of the dynamics of light availability for macrophytes. The qualitative results of both models were remarkably similar. If the ecosystem has no alternative stable states it is possible to set vegetation to any desired sustainable level using an appropriate harvesting strategy. However, if an intermediate vegetation biomass is to be realized the costs of harvesting are high, because the yield is predicted to be maximal in that case. If the ecosystem has alternative stable states, harvesting becomes risky because the vegetation may collapse entirely below a certain, in practice unknown, biomass. Also, even moderate harvesting may reduce the resilience of the vegetated state, making the ecosystem more vulnerable to adverse conditions such as unfavorable weather conditions or bird grazing.

Introduction

The interests of different groups of lake users often conflict. This is especially true with respect to the proliferation of aquatic macrophytes, for which nature conservationists and recreationists often have opposing interests (Clayton and Tanner, 1988; Chapter 5).

In general, a dense macrophyte vegetation is desirable from a conservationist's point-of-view. Both bird abundance and biodiversity are higher in vegetated lakes than in lakes without vegetation (Scheffer, 1998). Furthermore, vegetation reduces the turbidity of shallow lakes (e.g. Hasler and Jones, 1949; Timms and Moss, 1984; Van den Berg et al., 1998). Therefore, promotion of vegetation should be an important tool for lake restoration (Moss, 1990). Van Nes et al. (Chapter 5) argue that the conservation benefits of most types of indigenous macrophytes can probably be represented by a sigmoidally increasing function of vegetation biomass. Possibly, the function has an optimum, above which dense macrophyte beds have a negative effect on biodiversity. The critical biomass at which macrophytes become beneficial for nature conservation, will vary considerably for different lakes and depends on the growth forms of the predominant plant species.

In contrast, recreational users (including boaters, surfers and swimmers) are often hindered by dense vegetation (Clayton and Tanner, 1988). Nuisance to recreational users may generally increase with macrophyte biomass (Chapter 5). Although the exact nature of the nuisance is unknown, it may be reasonable to assume a similar sigmoidal curve with vegetation biomass. Below a certain biomass level, boating and swimming are not hindered at all. If the vegetation stands exceed a critical density, in particular when the plants cover the water surface, vegetation becomes a nuisance. As for conservation, the growth form of the vegetation is highly relevant for recreation.

Although it is hard to compare the interests of the two very different groups, a possible way to deal with this is to use the approach of environmental economists to account for all interests in the common currency of ‘welfare’ or ‘benefit’ (Hanley and Spash, 1993; Perman et al., 1996; Varian, 1996). The overall welfare of the society is composed by the contribution of each group weighed with the political impact of the group. The optimal strategy from a ‘rational social planner's’ point-of-view is to aim at the biomass where the total welfare function is at an optimum.

Van Nes et al. (Chapter 5) explored welfare functions for some distinct groups of macrophytes. They showed that the shape of the overall welfare function, describing vegetation of different growth forms, would be very different. For vegetation with a low growth form that does not reach the water surface, such as many *Chara* species, the conservation benefit is relatively high (Crawford, 1979; Clayton and Tanner, 1988; Coops and Doef, 1996), whereas the nuisance obviously is relatively low (Fig. 6.1). The result is a situation where a simple compromise between the two interest groups coincides with an optimum in overall welfare obtained from the lake. Aiming at an intermediate biomass seems the optimal policy in such case.

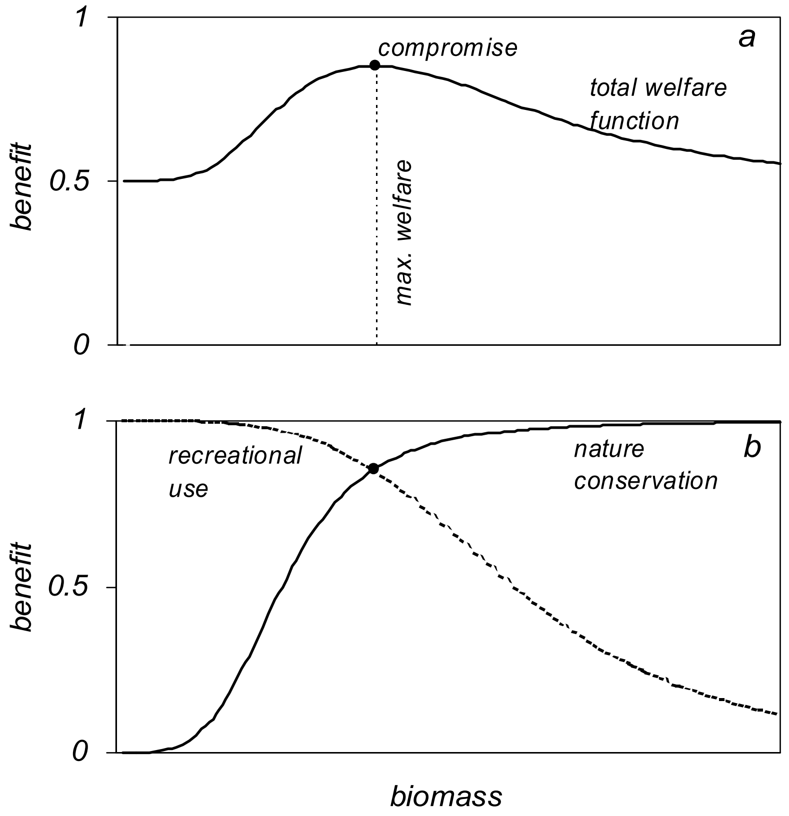


Fig. 6.1 *Benefit obtained from a lake by recreational users and nature conservationists assuming aquatic vegetation with a low growth form such as charophytes (see text). The total benefit (panel a) is the mean of the benefit functions of the separate user groups (panel b) The point with a compromise between both groups (closed circle) coincides with the maximum total benefit (Chapter 5).*

Canopy-forming or floating vegetation causes nuisance for boating and swimming at relatively low densities and such vegetation is of low benefit in lake restoration (Fig. 6.2). As a result, the total welfare may often be minimal at an intermediate biomass. Seeking a compromise between both groups by realizing an intermediate plant biomass is obviously the worst policy in this case (Chapter 5).

In this paper we analyze the response of an aquatic plant population, subject to harvesting by means of a simple generic model and a more complex and realistic model describing the growth of *Chara aspera* Deth. ex Willd. The results indicate that even if the intermediate biomass is desirable from an economic point-of-view, it would in some cases be impossible or at least very costly to keep the vegetation biomass at such level.

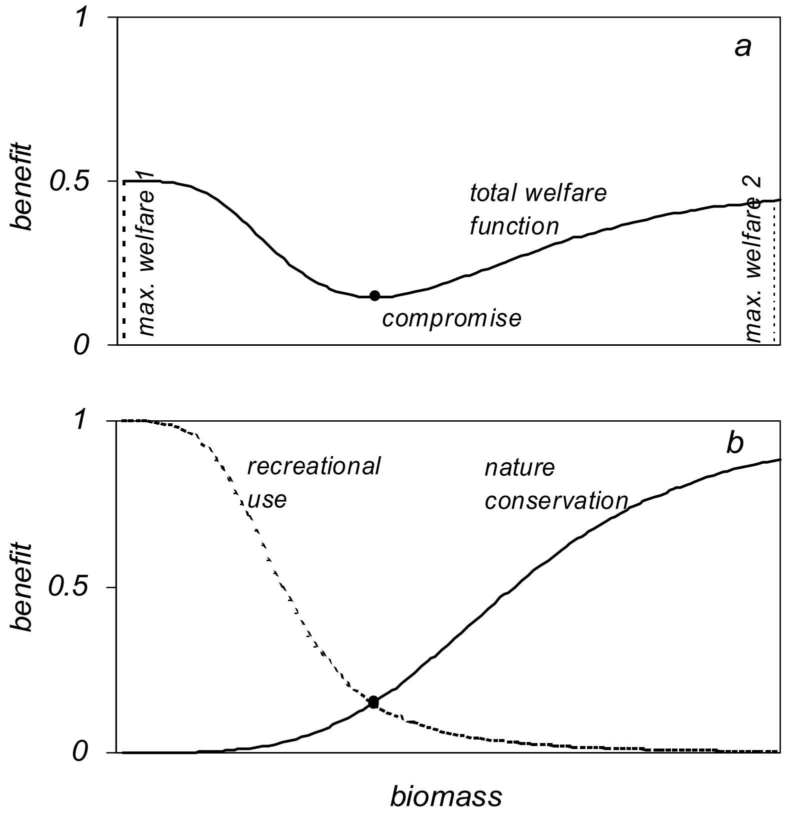


Fig. 6.2 *As in Fig. 6.1, but for canopy-forming or floating vegetation that causes nuisance to recreationists even at low biomass while having relatively little benefit from a nature conservationist point-of-view. The point with a compromise between both groups (closed circle) coincides with the minimum total benefit (Chapter 5).*

A minimal model of harvesting vegetation

The simple model is similar to those used to analyze the dynamics of grazing systems in terrestrial ecology (Noy-Meir, 1975; Van de Koppel et al., 1997). The main difference here is that the vegetation is not grazed by herbivorous animals, but instead harvested by humans.

We describe the change of vegetation biomass (V) by a logistic equation with a carrying capacity K:

$$\frac{dV}{dt} = r\,V\,(1 - \frac{V}{K}) \qquad (6.1)$$

This classical model assumes that intraspecific competition causes a linear decrease of the relative growth rate ($dV/dt/V$) with increasing vegetation biomass. At carrying capacity (K), the net relative growth rate is zero. At a very low biomass, the maximum relative growth rate (r) is approached.

We describe harvesting (H) as a Holling type I functional response, viz. a harvesting rate increasing linearly with vegetation biomass (Holling, 1959):

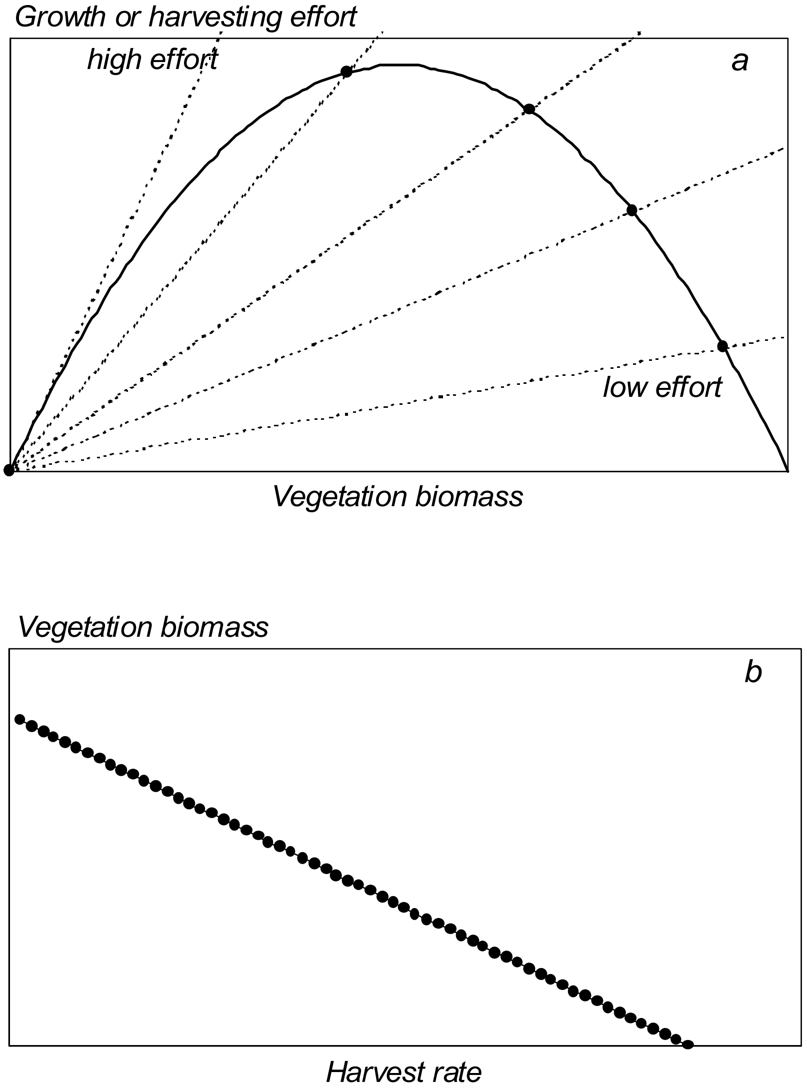


Fig. 6.3 *(a) The growth (g m^{-2} d^{-1}) (solid lines) and harvest yield (g m^{-2} d^{-1}) (hatched lines) of logistically growing vegetation at different harvesting rates as function of vegetation biomass. Harvesting is implemented as a type I functional response. The closed circles at the intersections of the growth lines and the harvest lines show the equilibrium biomass with harvesting. (b) The relation between daily harvesting effort and biomass of the vegetation.*

$$\frac{dH}{dt} = hV \tag{6.2}$$

This type of functional response implies there is no limitation of the harvest due to handling time. This functional response implies that at each time step a fixed proportion (*h*) of the vegetation is removed, independent on standing crop (for example, a mowing boat cuts the vegetation in 10% of the lake area daily). Fig. 6.3a shows the production of the vegetation and the losses due to such type I harvesting with several harvesting rates (h). At the intersections of the production and the harvesting lines, consumption equals production and the vegetation is in equilibrium. With increasing harvesting effort (steeper lines), the equilibrium vegetation biomass decreases. The resulting relationship between the harvesting rate and the equilibrium vegetation biomass (obtained by equaling Eq. 6.1 and Eq. 6.2) is linear (Fig. 6.3b). This means that in this case it is easy to set the vegetation biomass to any desired level by manipulating the harvest effort. Note that the realized harvest is maximal at the intermediate vegetation biomass, because for the logistic growth model, population growth is highest when biomass is half the carrying capacity (Fig. 6.3a).

There is strong evidence of a positive feedback for vegetation growth in shallow lakes (Scheffer, 1998), which is ignored in the above analysis. Vegetation enhances its own growth conditions by clearing the water and by reducing erosion. Due to this effect, growth of plants within a dense bed may occur under conditions where growth of few isolated plants would be impossible (negative) due to, for instance, inadequate under water light conditions. To represent such a situation in a very simple way, we add a term to Eq. 6.1 allowing growth to become negative at low vegetation biomasses, while raising it to positive values once vegetation biomass is larger than a critical value (H_g):

$$\frac{dV}{dt} = \left(\frac{2V^P}{V^p + H_g^p} - 1\right) r\,V(1 - \frac{V}{K}) \tag{6.3}$$

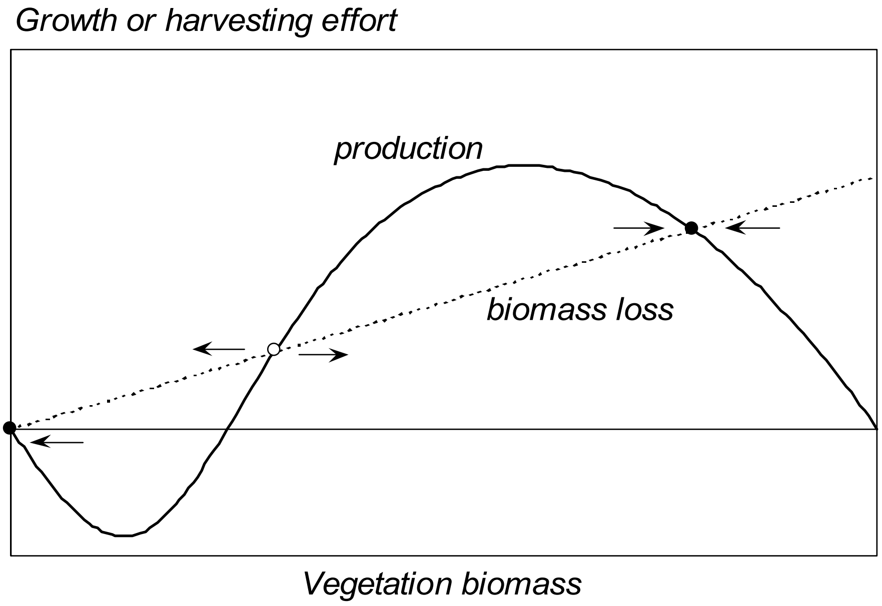


Fig. 6.4 *The growth rate of the vegetation in a situation with a positive feedback of vegetation on its own growth and a Holling type I harvest line. The harvest line can intersect at three points. These intersection points are equilibria. If the production curve exceeds the biomass loss, there is a net increase of the biomass (indicated with arrows). From these arrows can be concluded that two of the equilibria are stable (closed circles), and the other equilibrium is unstable (open circle).*

The added term $\left(\frac{2V^{P}}{V^{p}+H_{g}^{p}}-1\right)$ is a Hill function that rises from -1 to 1 with increasing vegetation biomass V. The power (p) determines the steepness of this sigmoidal 'clearing effect'.

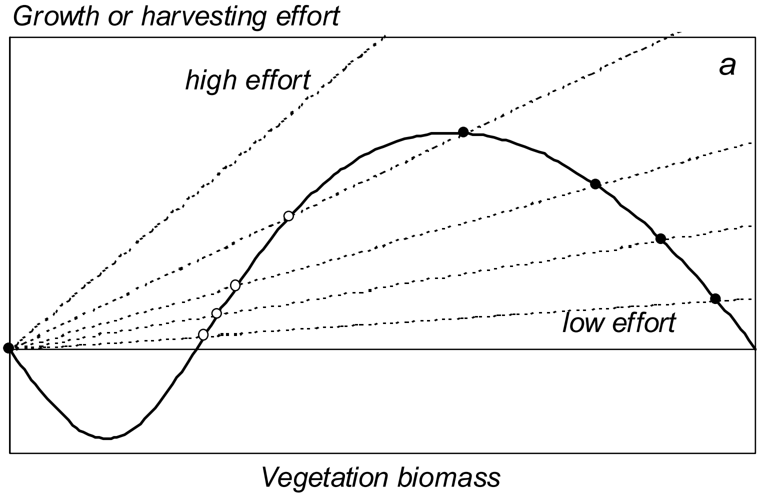
The consequence of this extension is that even with a linear functional response the harvest line can now intersect at two points (plus the origin) with the production curve, hence there can be three equilibrium biomass values (Fig. 6.4). It can be seen easily that the middle intersection point (open dot) represents an unstable equilibrium. At the left-hand side of this unstable equilibrium the biomass loss is higher than the plant production, therefore the vegetation biomass will decrease. At the right-hand side, the production is higher than the losses, so the biomass will increase, moving away from the equilibrium. If the system is in such an unstable situation, only a tiny disturbance is needed to invoke the system to move away towards one of the stable equilibria. In practice, the system will never stay in an unstable equilibrium. Thus, the origin and the right-hand intersection point represent the two alternative stable states of the model.

An important consequence of this situation is that the relationship between the harvesting rate and the equilibrium vegetation biomass is not linear anymore (Fig. 6.5). As in Fig. 6.3, the response to increasing harvesting rates can be shown by plotting equilibrium vegetation biomass (the intersection points in panel 6.5a) as a function of harvesting rate (panel 6.5b). The resulting graph has a stable and an unstable (dashed) branch, which meet in a point generally referred to as a 'fold' or 'saddle-node' bifurcation (Strogatz, 1994). If the harvesting rate in a vegetated lake is increased, vegetation biomass decreases until the bifurcation point is reached. Beyond this point, the vegetation biomass collapses, and settles to a stable state with zero biomass. This implies that it is not possible to set the vegetation biomass to any desired level, since only relatively high biomass or no biomass at all can be achieved. Note that the maximum realized harvest occurs just before the collapse of the vegetation (Fig. 6.5a).

Other harvesting strategies

The condition that there is no limitation in the daily harvest is probably not realistic, especially when mechanically harvesting large areas with removing of the plant material from the water body. In those cases, the removing of the biomass is time consuming and often the limiting factor (Wade, 1990). Then, at higher vegetation biomasses, the efficiency of the harvesters will become relatively lower. In such situations, the functional response should level off at high vegetation biomass rather than increase linearly. The consequences can be illustrated using the Holling type II functional response (Holling, 1959), which is a commonly used relationship to describe predation and grazing:

$$\frac{dH}{dt}=h_{max}\frac{V}{V+H_{V}} \qquad (6.4)$$



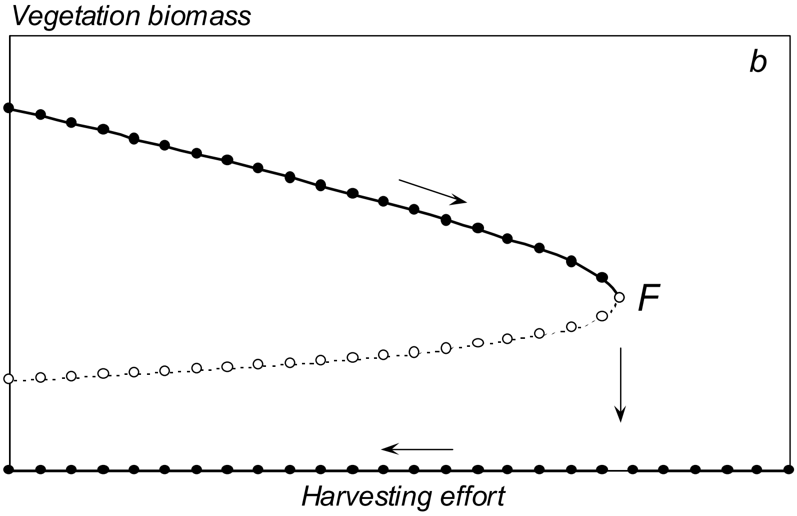


Fig. 6.5 *(a) Growth rate of vegetation in a situation with alternative equilibria and harvesting with several intensities. Harvesting is represented by a type I functional response. Closed circles show the equilibrium biomass with harvesting; open circles are unstable equilibria. (b) Relationship between harvesting effort and biomass of the vegetation. F is a fold bifurcation. If the harvesting rate exceeds this critical value, the alternative equilibria disappear and the vegetation is lost.*

The half saturation H_V (g m^{-2}) is the vegetation biomass where the harvest is half the maximum harvesting rate h_{max} (g m^{-2} d^{-1}) which is achieved at very high vegetation biomass. For certain values of H_V and h_{max}, Eq. 6.4 intersects with the logistic production curve at two points (plus the origin), hence three equilibria exist (Fig. 6.6a). Analogous to the analysis of the model with alternative stable states (Fig. 6.4), it can easily be seen that two of these equilibria are stable whereas the middle one is unstable (open dot).

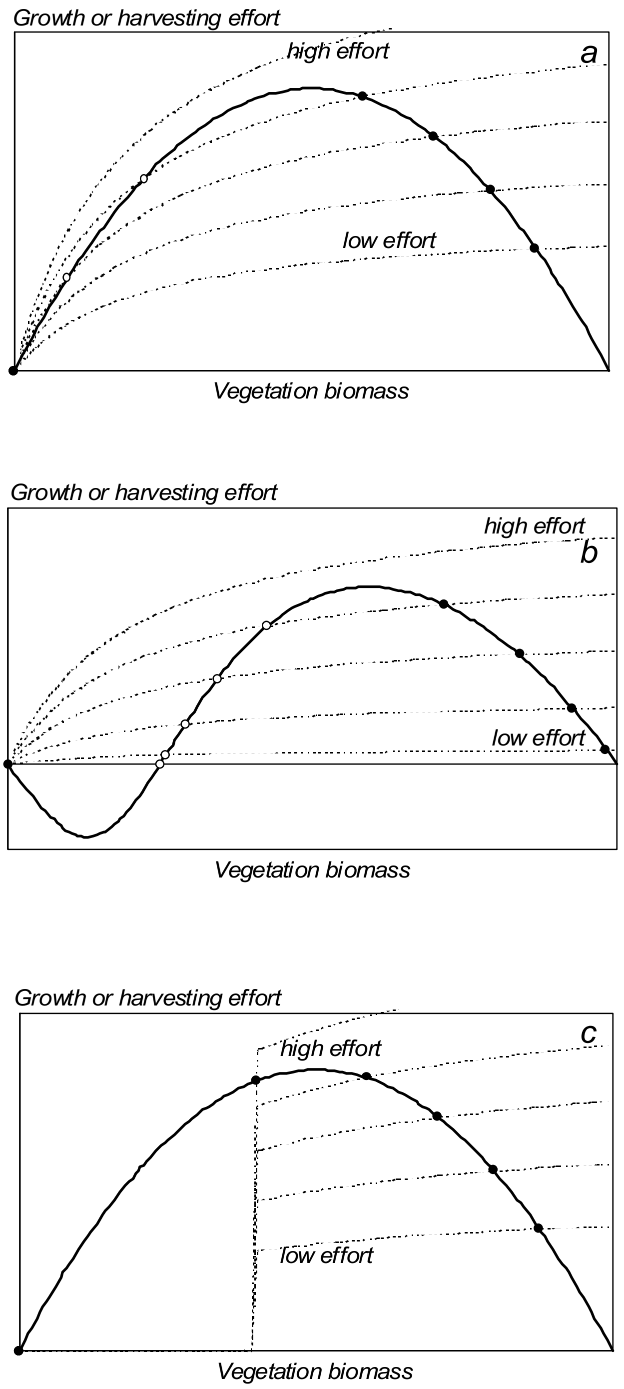
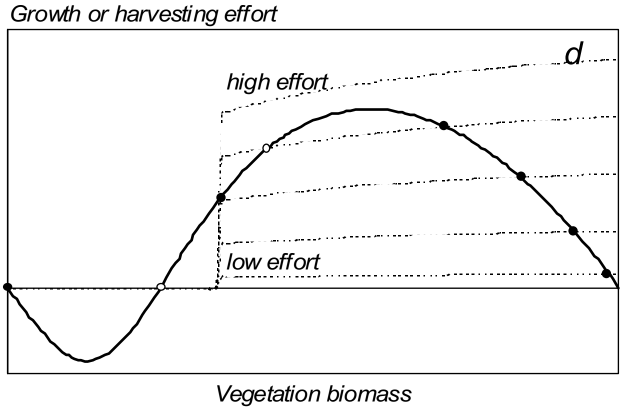


Fig. 6.6 *The effect of harvesting with a type II functional response with several intensities on the logistic growth model with or without positive feedback. The intersections between the harvesting lines (hatched) and the production line (solid) are equilibria that can either be stable (closed circles) or unstable (open circles). (a) Type II functional response with logistic growth model; (b) Type II functional response when there are alternative equilibria due to positive feedbacks; (c) and (d) The stabilizing effect of a stopping rule added to the type II functional response. (e) As (d) but with a slightly different positive feedback.*



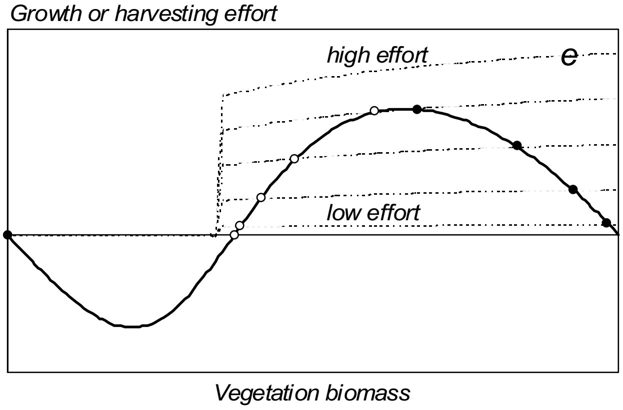


***Fig. 6.6** (continued).*

The origin represents the over-exploited state, which means that all produced biomass is removed repeatedly by harvesting. In this state, the number of reproducing individuals is limiting the biomass. The right-hand intersection point represents the under-exploited state, at which the interspecific competition limits the population growth. In case that the model has also a positive feedback without a harvester (Fig. 6.6b), the situation is similar to that with a Holling type I harvest strategy (Fig. 6.5). Over a wide range of parameters the model then has alternative stable states, only at very high harvesting rates there is only an overexploited state without vegetation.

Like the strategies discussed earlier, this harvesting strategy is probably unrealistic for lake managers, because they may anticipate on the vegetation biomass and do not keep the vegetation in an overexploited state if the target biomass is intermediate. Adding a stopping rule to the harvest function, by harvesting only if the biomass exceeds a critical level, does achieve this (Fig. 6.6c, d, e). If the biomass exceeds the critical level, the manager will start harvesting with a type II functional response (Eq. 6.4). This harvesting strategy is stabilizing if an appropriate critical biomass is chosen. Without positive feedback

(Fig. 6.6c), there is mostly only one under-exploited equilibrium (unless a very small critical level is chosen). If the model has alternative equilibria, the situation is more complicated (Fig.6.6d, e). If the critical level is chosen at the right-hand side of the intersection of the production line with the origin (Fig. 6.6d), harvesting is quite safe. If the harvesting rate is low, harvesting will lead to the under-exploited equilibrium (right-most solid dots). At moderate harvesting rates, the critical vegetation biomass becomes a stable equilibrium. In this case, the system has three alternative equilibria: one at the origin, when there is not enough plants to keep the water clear, one at the critical vegetation biomass and one under-exploited state (right-hand solid dot). If the harvesting rate is even higher, the under-exploited state is not possible anymore. Thus, if the capacity of harvesting is large enough it is easy to set the vegetation to a certain biomass. However, the exact shape of the production curve is usually unknown. If the production curve has a slightly different shape (Fig. 6e), harvesting with a large capacity (upper lines) will always result in a collapse of the vegetation.

A more elaborate model of harvesting macrophytes

The above minimal models use an extremely simple description of vegetation growth. To investigate whether the results are not an artifact of simplifications, we did the same analysis with the macrophyte model Charisma (Chapter 3, 4), an elaborate simulation model based on the model MEGAPLANT (Scheffer et al., 1993a). The base of this model is the seasonal cycle of individual plants. In autumn the vegetation dies off to survive the winter as underground structures. In spring, growth is initiated and the overwintering structures are transformed into vegetation. Photosynthesis depends on the biomass distribution of the growing plant over the vertical gradient of light in the water column. Population regulation results from self-shading and competition for inorganic carbon. A positive feedback of plants on their own growth is included by allowing vegetation to reduce turbidity of the water. Due to this effect, the model has alternative stable states over a certain range of vertical light attenuation coefficients (Chapter 4). We used parameter settings that were calibrated for *C. aspera* in Lake Veluwe (Chapter 4). While the model may run on a spatially explicit basis, we used a single grid cell with a water depth of 1 m for simplicity. A small import of overwintering structures (0.1 m^{-2} yr^{-1}) was used to prevent the vegetation from becoming completely extinct in the studied grid cell. For the current purpose we added a 'harvester' that can have different functional responses. For simplicity, the harvester was programmed to remove vegetation continuously during the whole growing season using the same strategy, though this is usually not a realistic harvesting regime.

To analyze the effect of different harvesting intensities on the equilibrium vegetation biomass we used the following numerical procedure. We started with a fixed initial biomass of overwintering structures (default 10 g m^{-2}) in a state where vegetation can develop (low harvesting rate). During the simulations, the harvesting intensity was increased in small steps until disappearance of the vegetation. To check for hysteresis, we then took the same number of steps backwards (decreasing harvest intensity) to allow the vegetation to re-establish itself.

At each step in this procedure, a 200-year vegetation development was simulated to allow the biomass to reach a stable level; subsequently, the biomass at day 183 (1 July) for 5 successive years was plotted. Thereafter, in the next step, the final state of the previous step was used as a starting point.

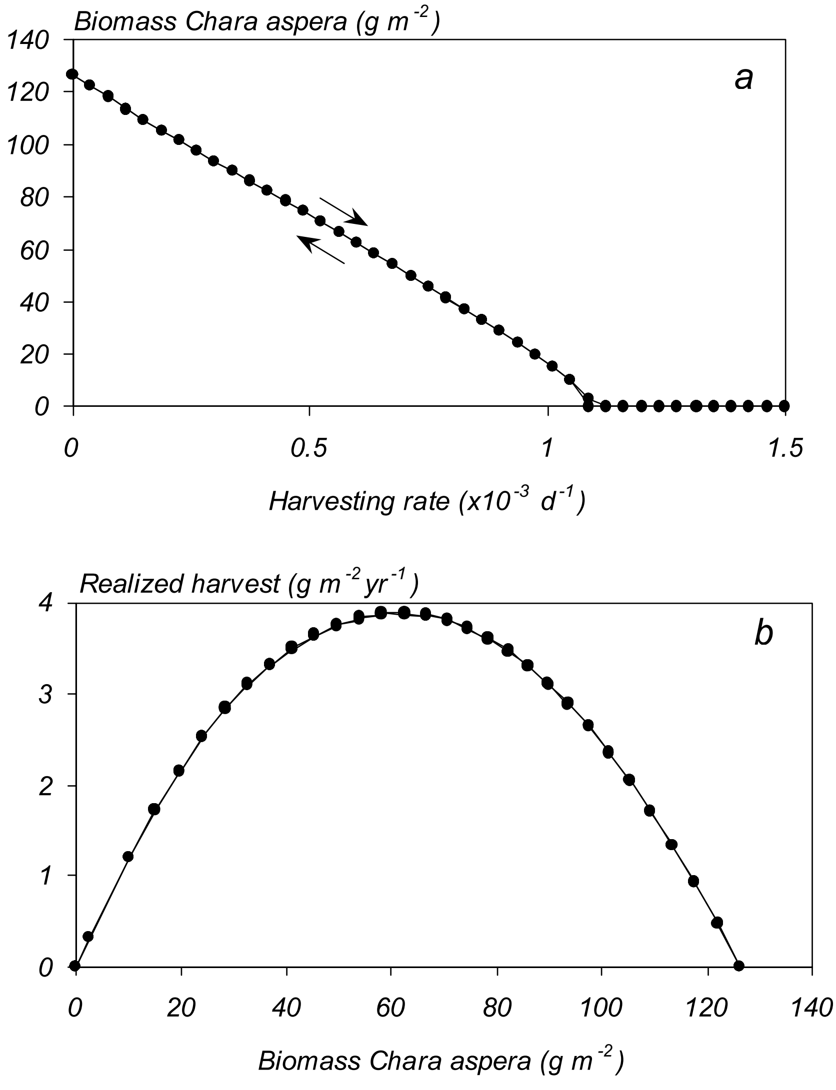


Fig. 6.7 *Effect of harvesting on Chara vegetation evaluated with the more realistic model Charisma, using a Holling type I functional response of harvesting at a vertical light attenuation of 2 m^{-1}. (a) The effect of different harvesting rates on the equilibrium summer biomass of Chara (day 183). The arrows indicate the direction of changing the harvesting rate, showing that there are no alternative equilibria. (b) The realized harvest per year and the realized equilibrium summer biomass. These combinations were generated by varying the harvesting rate.*

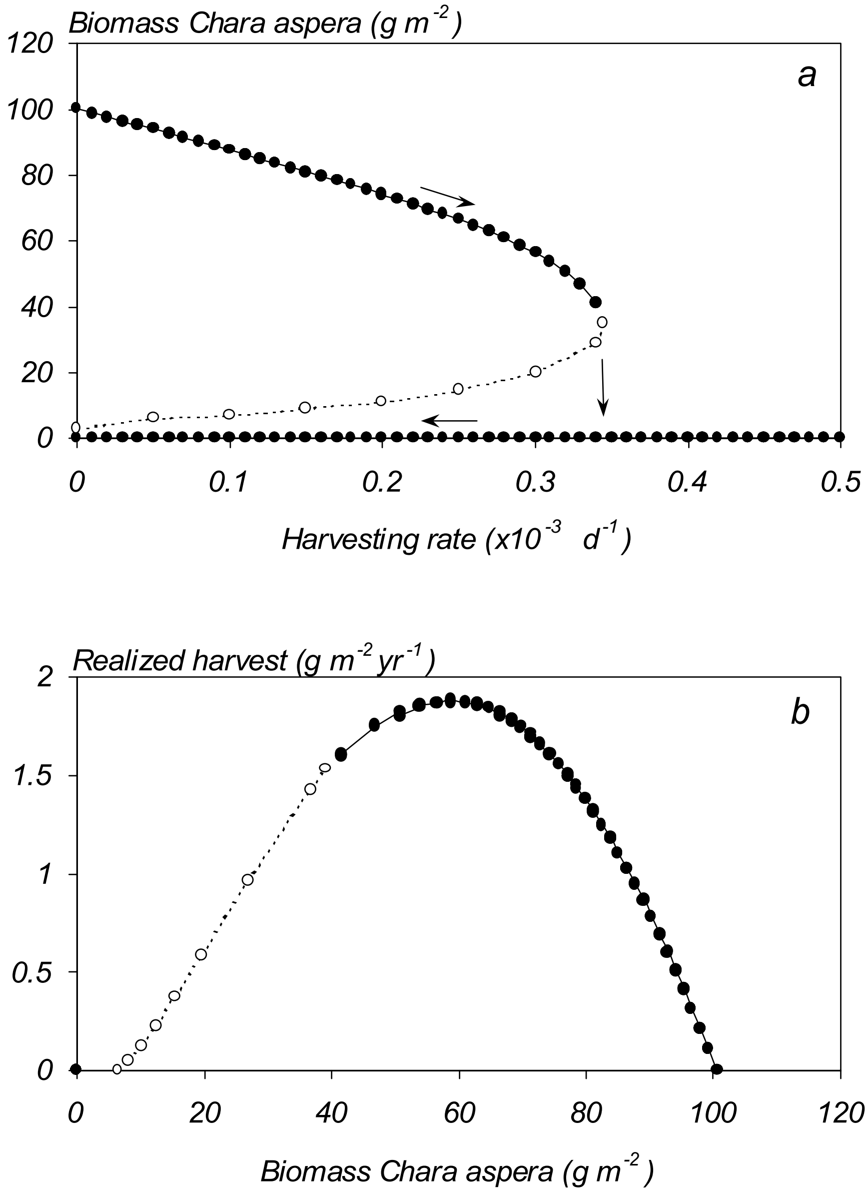


Fig. 6.8 *Effect of harvesting on Chara vegetation evaluated with the more realistic model Charisma, using a Holling type I functional response of harvesting at a vertical light attenuation of 4.5 m^{-1}. (a) The effect of different harvesting rates on the equilibrium summer biomass of Chara (day 183) (closed circles). The arrows indicate the direction of changing the harvesting rate, showing that there are two alternative equilibria. Open circles are estimates of the unstable equilibria generated by varying the initial biomass (b) The produced harvest per year and the realized equilibrium summer biomass. These combinations were generated by varying the harvesting rate. The open circles are also estimates of the unstable equilibria.*

The first analysis was done assuming relatively clear water (vertical light attenuation coefficient (K_D) of 2 m^{-1} outside the vegetation beds). Under this regime, the system has no multiple equilibria (Chapter 4). For the first analysis we used a harvester with a type I functional response (Fig. 6.7). The equilibrium summer biomass decreases almost linearly with increasing harvesting rate (Fig. 6.7a), which is remarkably well in line with the logistic growth model (Fig. 6.3b). We can also reconstruct Fig. 6.3a with the complex model, but only in an indirect way by plotting the realized harvest per year against the realized summer biomass with different harvesting rates (Fig. 6.7b). Also this figure closely resembles the yield curve from the logistic growth model (Fig. 6.3a). The conclusions are thus identical to those from the logistic model: under these conditions and parameter settings, vegetation can be set to any desired level and the maximum biomass yield occurs with an intermediate vegetation biomass, which is therefore probably the most costly situation to maintain.

The model Charisma produces alternative equilibria if the vertical light attenuation coefficient is between 3.9 and 6.4 m^{-1}, with the parameter settings of *C. aspera* in Lake Veluwe (Chapter 4). If in this range of vertical light attenuations (for instance $K_D = 5\ m^{-1}$) the harvesting rate is increased stepwise, the vegetation suddenly collapses at a certain critical harvesting rate (Fig. 6.8a). The biological explanation is that at this point vegetation biomass becomes too modest to improve transparency enough to allow sufficient plant growth. If harvesting is stopped after such a vegetation collapse, the vegetation is not able to recolonize the lake, because the system has switched to an alternative stable state without vegetation and with a high turbidity.

The unstable equilibria (open dots) between the alternative stable states could not be found exactly, but their location was estimated numerically by finding the minimum initial summer biomass from which the vegetation can develop. Like in the case of clear water, the graph is qualitatively the same as the one produced by the simple model (Fig. 6.5b). The reconstructed yield function (Fig. 6.8b) shows a remarkable similarity with the production line of the minimal model (Fig. 6.5a) as well. (The unstable equilibria in Fig. 6.8b are estimated by setting the initial biomass on the estimated unstable equilibria and calculating the summer biomass and the realized harvest in the subsequent simulated year. The negative part could, for obvious reasons, not be reproduced).

A more complete image of the effect of harvesting and turbidity on the stable states of the system is obtained by constructing a 'bifurcation plot' (Fig. 6.9a). This plot is constructed by repeating the above analysis for several different light attenuation coefficients. By plotting only the points where the vegetation will recover ('transcritical bifurcations') and the points where vegetation collapses ('fold bifurcations'), a map of the zone with two alternative stable states in the parameter space (Fig. 6.9a) is produced. With increasing harvesting rates the zone where alternative equilibria occur, becomes smaller, shifts to lower attenuation coefficients and vanishes at a certain point ($K_D = 2.2$). This special point where the fold bifurcation collides with the transcritical bifurcation is called a 'Cusp point' in non-linear dynamical systems theory (see e.g. Strogatz, 1994). Beyond this point, the transcritical bifurcation becomes non-catastrophic, which means that this bifurcation is a gradual transition, in our case, moving from a vegetated state to a state without plants.

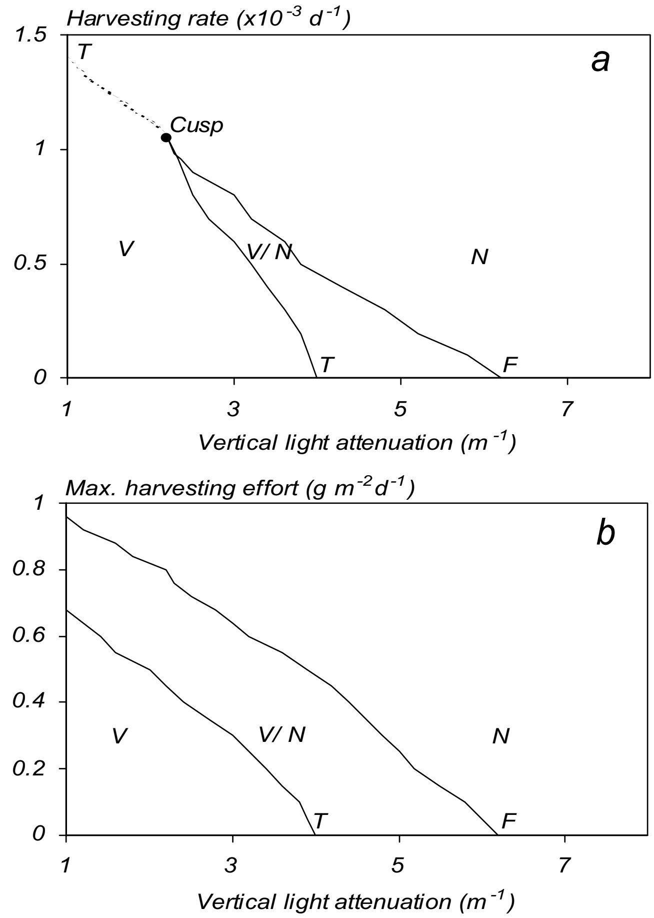


Fig. 6.9 *Bifurcation plot of the harvesting rate and the vertical light attenuation coefficient (a) and of the maximum harvesting rate with a functional response type II with the vertical light attenuation coefficient (b). V = vegetated state; V/N = either vegetated or no vegetation as alternative equilibria; N = no vegetation; dashed line = non-catastrophic bifurcation, solid line = a catastrophic bifurcation; T = transcritical bifurcation, F = fold bifurcation; Cusp = Cusp point. See explanation in the text.*

We also constructed a bifurcation plot using a harvester with a Holling type II functional response (Eq. 6.4). In this case there is no Cusp point (Fig. 6.9b). The alternative states remain present even in clear water (vertical light attenuation of 1). Under these conditions, the clearing effect of macrophytes can not be responsible for the alternative stable states, since the plants can not reduce the turbidity below 1 m^{-1} in the model. Under these conditions it is possible to reproduce Fig. 6.6 for the complex model (not shown), therefore it is very likely that the same mechanism is responsible for the presence of alternative stable states. If the biomass is below a critical value, the harvester can over-exploit the vegetation and the biomass decreases to zero. Above this critical value, harvesting becomes too inefficient to keep the vegetation low. Consequently, the vegetation can increase and establish a higher equilibrium. Thus, the alternative stable states shown in Fig. 6.9b are caused by both the over-exploitation feedback and the positive feedback by the clearing effect of macrophytes.

Discussion

Our model analyses suggest that it may be impossible to realize a substantial reduction of submerged plant biomass in shallow lakes by harvesting without risking the complete loss of submerged vegetation. Some harvesting strategies are intrinsically destabilizing the system, because they may result in a switch to an overexploited state, analogous to that obtained in overgrazed pasture systems (Noy-Meir, 1975). Even careful harvesting protocols may cause complete loss of vegetation in eutrophic lakes, as a result of a positive feedback of the increasing turbidity that results in a further decrease in vegetation growth. In those lakes, it will be difficult to know *a priori* what should be a safe vegetation biomass to avoid a switch to a turbid phytoplankton-dominated state without plants. One problem, indicated by the models used, is that maintaining a plant population at an intermediate biomass is costly, as this should be done exactly at the point at which regrowth is maximal, and consequently the required harvest effort is the highest. These results suggest that it may often be a more efficient strategy to assign entire lakes for recreational use and others for nature conservation, though this is often not applicable.

This conclusion is supported by earlier analyses using a simple economic model (Chapter 5), showing that even if an intermediate vegetation biomass can be obtained by harvesting, it may not always represent a situation which is desirable from the point-of-view of the benefit of community of lake users. In particular, if the vegetation is floating or canopy-forming so that even a low biomass causes considerable nuisance, aiming at an intermediate biomass is a bad strategy from an economic point-of-view (Fig. 6.2). It should be stressed that in practice the political solution of a conflict of interests, does often not coincide with the optimum environmental economic solution, as presented here, due to various socioeconomic mechanisms (Scheffer et al., 2000). For instance, there can be a bias due to differences in the organizational power of groups of lake-users. Furthermore, there is often a tendency to choose a compromise, even if this is not the solution with the maximum overall welfare of the society (Scheffer et al., 2000).

Obviously, our simple analyses do present a rather black-and-white image of the problem of controlling vegetation nuisance. In specific cases, compromise solutions may be possible without aiming at intermediate biomass. It may be possible for instance to control vegetation in small restricted parts of a lake designated for swimming or boating, without affecting overall lake ecosystem dynamics too strongly. Also, if the vegetation consists of a mixture of canopy-forming plants and species with a low growth form, it may be effective to harvest selectively the canopy-forming species, by mowing at a certain height above the lower plant canopy. Charisma simulation runs have been made for the case with a mixed vegetation of *C. aspera* and *Potamogeton perfoliatus* L. in the shallow eutrophic Lake Veluwe (Coops et al., submitted). In the lake, canopy-forming *P. perfoliatus* caused extensive nuisance to recreational navigation, whereas *C. aspera*-dominance would meet the interests of both navigation and conservation. Preliminary model simulations with the model Charisma suggest that one such mowing event may be sufficient to substantially reduce the biomass of the canopy-forming species for 2 - 4 years (Coops et al., submitted). The low speed of recovery of the canopy-forming species (*P. perfoliatus*) is caused by competition with the lower growing species (*C. aspera*). An analogous manipulation of the outcome of competition by selective harvesting has been shown elsewhere with a simple model (McClanahan, 1995). Likewise, a species shift has been observed after non-selective harvesting in ditches (Best, 1993). Though these results indicate that it should be possible to use selective harvesting successfully, it is still difficult to predict the outcome of such strategy. The model Charisma can be extremely sensitive to parameter settings when modeling the competition between two species (Chapter 3). Furthermore, it is not yet clear how harvesting affects the biomass. The plants may regrow rapidly, even to a higher density than before harvesting (Kimbel and Carpenter, 1981; Engel, 1990), sometimes referred to as a 'pruning effect' (Serafy et al., 1994). Even if biomass regrowth within one season is fast, there can still be a significant effect on the biomass in the next season (Kimbel and Carpenter, 1981).

The harvesting strategies we analyzed here are simple and not very realistic. The continuous cutting strategies have been selected for simplicity and used to illustrate basic principles. We did not analyze the effect of cutting of the vegetation in a few discrete annual events. The timing of such events is essential (Van Vierssen et al., 1994). If cutting occurs just before the plants form overwintering structures, the effect on the next years' generation would be much larger (Engel, 1990; Dall'Armellina et al., 1996). Furthermore, a harvesting strategy that anticipates on the vegetation biomass reduces the risk of switching to the alternative turbid equilibrium, as was shown by the stabilizing effect of a stopping rule added to the Holling type II strategy (Fig. 6.6c, d, e). Including prudent anticipation in management strategies, however, may appear impracticable. For a long-term effect the number of surviving overwintering structures will be crucial, but this amount is hard to predict from the vegetation biomass during the growing season.

Our analysis illustrates that combining different model approaches can be helpful for obtaining a better understanding of a problem. Our modeling approaches each have their own strengths and shortcomings (Scheffer, 1998). The minimal model is easier to understand, but may leave out many relevant aspects. The rather complex model Charisma is much more realistic, although, because of its complexity, it is often difficult to understand the reasons for obtaining certain results. By combining both approaches, we gained an understanding of the main mechanisms and obtained an impression of their realism and relative importance. The fact that we obtained the same results in both model approaches provides some credibility to the apparently oversimplified minimal model. The approach of simultaneously addressing macrophyte restoration issues with simple and elaborate models appears a promising way to solve also other and more complex questions regarding the functioning of ecosystems. It could help to bridge the gap between classical population ecology and the approach of individual-based modeling, which too often appear incompatible (Fahse et al., 1998; Grimm, 1999).

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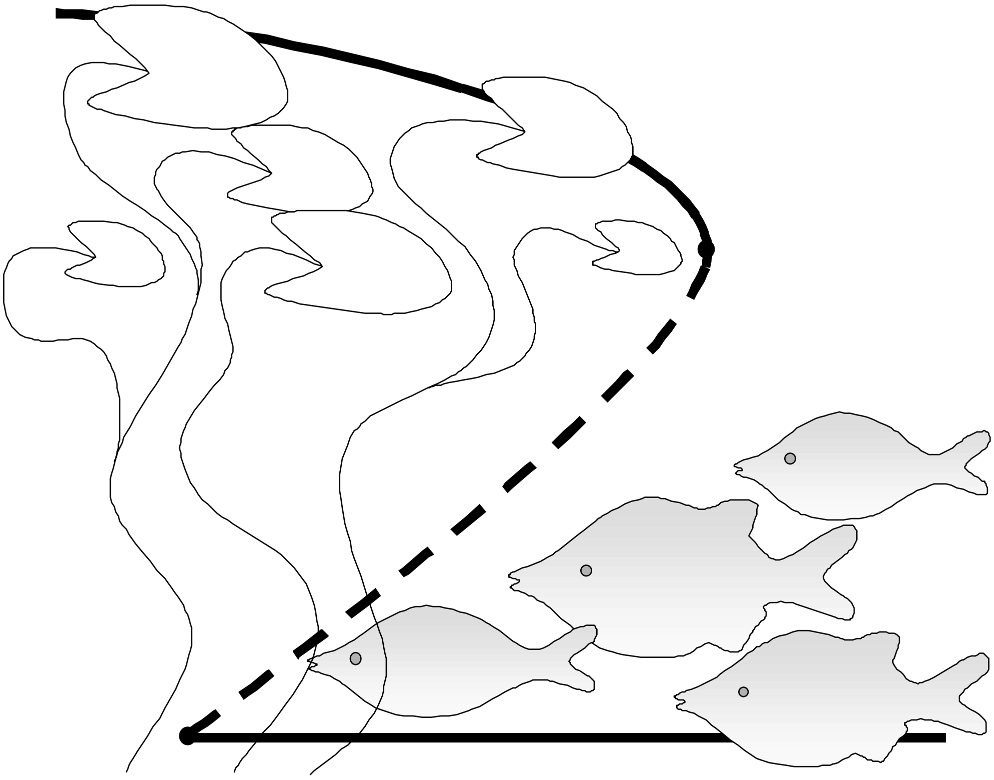
Part III: Modeling Fish Communities



Chapter 7
PISCATOR, an individual-based model to analyze the dynamics of lake fish communities

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Ecological Modelling, accepted for publication

Abstract

Unraveling the mechanisms that drive dynamics of multi-species fish communities is notoriously difficult. Not only the interactions between fish populations are complex, also the functional niche of individual animals changes profoundly as they grow, making variation in size within populations and even within cohorts highly important to consider. Not surprisingly, traditional aggregated populations models have proved to be limited in their capacity to describe dynamics of interacting fish species, and individual-based models have become popular for modeling fish populations. Nonetheless, the majority of the individual-based models describes either a single species or focus entirely on a certain life stage. We present the individual-based model Piscator, which describes a multi-species fish community, and demonstrate techniques to deal with the inherent complexity of such a model. We propose a novel procedure for calibration and analysis in which the complexity of the model is increased step-by-step. We also illustrate the use of a special Monte-Carlo sensitivity analysis to identify clusters of parameters that have roughly the same effects on the model results. As an example we use the model to analyze a fishery experiment in the Frisian Lakes (The Netherlands). Despite of high bream catches (40-50 kg $ha^{-1}yr^{-1}$), it was observed that the seine fishery had unexpected little effect on the bream population. Our simulation results suggest that if one takes community feedbacks and climatic variability into account, this effect can be explained. The main cause was, besides a reduction of piscivory due to a simultaneous gill-net fishery, a coincidental strong year-class just before the fishery started. The strong development of this year-class could be explained by three subsequent warm years, whereas yearly variations in recruitment were less important.

We also suggest that this relatively realistic model could play a role in ecological theory. It can be used to analyze the conditions for multi-year cycles and chaotic dynamics, phenomena that are usually predicted only from simple abstract models.

Introduction

Fish communities usually consist of several interacting species, and the interactions between these species are typically rather complex (Carpenter, 1988; Wilson et al., 1991). An important complicating factor is the so-called 'ontogenetic niche shift' (Werner and Gilliam, 1984). Food preference tends to be very different for various size and life stages of fish. At their early life stages, fish are largely planktivorous, whereas at some length they usually change to other food sources. The resulting dynamically shifting competition for food within and between species can be a bottleneck for the development of cohorts (Persson and Greenberg, 1990). Another complicating factor in fish dynamics is that piscivorous fish can have a strong top-down effect not only on other species but also on conspecifics by cannibalism between and within cohorts, making size dispersal within year-classes a crucial process (DeAngelis et al., 1979).

Not surprisingly, modeling the mechanisms that drive the dynamics of fish communities is a difficult task. Traditional aggregated population models are obviously limited in their ability to simulate interacting fish species. Individual-based models (Huston et al., 1988; DeAngelis and Gross, 1992) seem more suitable since, at least, they can deal with the individual variability which is so important in fish interactions. Indeed, the majority of the recently developed individual-based models describe fish populations (Grimm, 1999). Most of these models, however, are single species models (e.g., DeAngelis et al., 1991; Rose et al., 1993; Dong and DeAngelis, 1998) or are focussed on a certain life stage (e.g., Madenjian, 1991; Cowan et al., 1993). Only a few detailed models have been published about interactions between two or more fish species (Hagiwara and Mitsch, 1994; McDermot and Rose, 2000). In this paper, we present Piscator, an individual-based model designed to simulate interacting fish species.

The inherent complexity of fish communities and the large number of parameters make it hard to calibrate the model. Changing parameters of one species will often affect all other species in an unpredictable way. We developed a calibration procedure to deal this problem. It is a stepwise procedure, in which we first shut off all interactions between species. Functional responses and predation mortalities are replaced by fixed values. After a first calibration, we increase the complexity step-by-step by adding more interactions to the model. Furthermore, a Monte-Carlo sensitivity analysis is used to identify the parameters with the largest impact on the model. This analysis made it possible to find groups of parameters that have the same or opposite effects on the model results (Klepper, 1989).

As an example, we use the model analyze a fishery experiment in the Frisian Lakes (The Netherlands). We show the effect of different fishing scenarios on the biomass of the main species of the fish community. The interaction between the piscivorous pikeperch (*Stizostedion lucioperca* (L)) and the benthivorous bream (*Abramis brama* (L.)) is the main focus in this example.

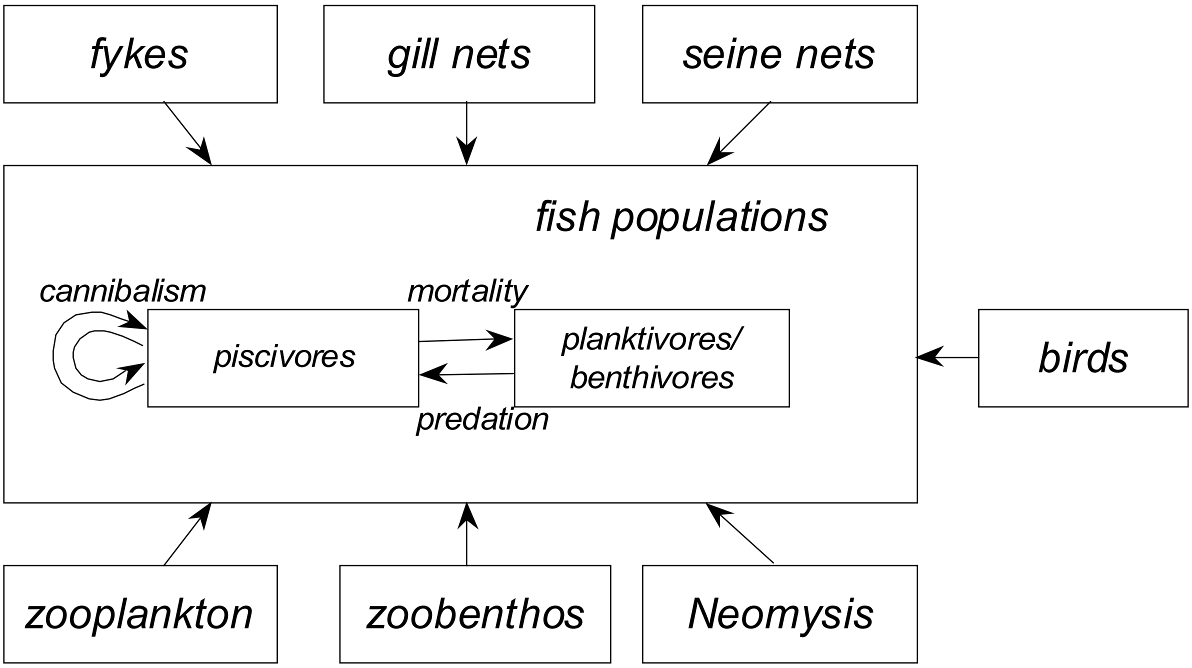

Fig. 7.1 *Overview of the components of the model PISCATOR.*

Model description

Overview

Piscator contains many components from which the user can flexibly select any desired sub-set. Although we do not use all components in the Frisian Lakes case, we give a brief description of the entire model here. For a complete overview of all options we refer to the user manual (Van Nes et al., 1996).

The basic components of the model are fish species, fisheries (fykes, gill nets and seine nets), piscivorous birds, zooplankton and zoobenthos (Fig. 7.1). The dynamics of the fish and fishery efforts are described in a detailed way, but the dynamics of larval stages of fish are not considered explicitly. The fish is modeled in an individual-based fashion. To model the large numbers of individuals in an efficient way, we use the concept of 'super-individuals' (Chapter 2). This implies that a limited number of representative 'super-individuals' is modeled. Each super-individual has an extra dynamic property: the number of individuals that it actually represents.

The food for the benthivorous and planktivorous fish (zooplankton, zoobenthos) can be entered as an external time series or modeled dynamically using a simple logistic growth model. The numbers of piscivorous birds are entered as fixed values. The model is not spatially explicit, but we use two (or more) habitats (e.g. littoral and pelagial) over which the fish and their predators and food are distributed. The distribution over those habitats is not modeled dynamically, but assumed to be dependent on the species and the length of the individual fish.

Fish

Reproduction

At a fixed day in the year, young fish are introduced in the model. Because the relation between the spawning stock and recruitment is usually very poor in Dutch lakes (e.g., Buijse et al., 1992), the number of young fish is treated as an external value, which can be either fixed or variable. Optionally, recruitment can be dependent on the spawning stock (see for details: Van Nes et al., 1996). To account for individual variability, the average growth rate of the newly created young fish is assumed to be variable and normally distributed. The variability is implemented by following 10-100 different size classes (= super-individuals) of young fish created each year.

Although the number of young fish is not dependent on the spawning population, the mature fish loose weight during the spawning period. The start of the spawning period is defined by a day-degree sum formula (Elliott et al., 1987):

$$\sum_{t=1}^{n}(T_t - 10) = d \tag{7.1}$$

Where T_t is water temperature (°C), n is the number of days between March the 1st and the start of spawning period and d is a parameter.

During the spawning period, the adult fish loose a fixed fraction of their weight, and some species (especially bream and smelt) can be more vulnerable to being caught by fykes.

Growth

The growth of fish is modeled as an increase in their weight. The length (L, cm) of a growing fish is adjusted according to an allometric relation.

$$L = a_l W^{b_l} \tag{7.2}$$

a_l and b_l are parameters. We used values that were determined for Tjeukemeer (Mooij et al., 1994).

The increase of the weight (W_t, g) of each individual fish is calculated daily by a bioenergetics equation (e.g., Rose and Cowan, 1993):

$$W_t = W_{t-1} \quad p\, C_{\max} A - R_{tot} \tag{7.3}$$

Where C_{max} is the maximum consumption rate without food limitation (g d^{-1}), p is the proportion of C_{max} realized, A is the assimilation efficiency and R_{tot} is the total respiration (g d^{-1}).

The metabolic losses are dependent on the food intake. At low food consumption (low proportion p of C_{max} realized), the respiration is assumed to be one third of the maximum metabolic respiration (Huisman, 1974).

$$R_{tot} = \frac{R_{\max}}{1 + 2(1 - p)} \tag{7.4}$$

The maximum respiration (R_{max} in g d^{-1}) is determined by multiplying the standard metabolism function with a temperature (T in °C) dependent activity factor (*Act (T)*):

$$R_{\max} = a_r W^{b_r} Q_{10}^{\frac{T-20}{10}} Act(T) \tag{7.5}$$

In which: a_r is a constant and b_r the exponent of the weight (W, g). At low temperatures the activity is very low (Winberg, 1956). This behavioral response comes on top of the temperature dependence of the basal metabolism. We assume a Hill function with temperature. The effect of activity ranges between 0.5 and 2:

$$Act = 0.5 + (2 - 0.5)\frac{T^3}{T^3 + H_T^3} \tag{7.6}$$

The maximum growth without food limitation is based on a regression equation fit on field data of Lake Tjeukemeer (Mooij et al., 1994; Mooij and Van Nes, 1998):

$$\left(\frac{dW}{dt}\right)_{\max} = \left(G_{mean} + T_1(T - T_0)\right)W^{b_c} \tag{7.7}$$

In which: G_{mean} (g d^{-1}) is the average growth of one gram fish at the mean temperature (T_0 = 17.5 °C in The Netherlands), T_1 is a first order temperature effect (d^{-1} °C^{-1}) and b_c is an exponent of ca. 2/3. The consumption (C_{max}) that is required to achieve the maximum growth is calculated back from the observed growth of the species with negligible food limitation (Eq. 7.3, with $p = 1$).

Food limitation is described as a Holling type II functional response. However, we changed the formulation slightly to account for the fact that larger fish feed more efficiently because they swim faster and search a larger area. We assume that the available food is dependent on an inspected volume that increases linear with the weight of the fishes. Larger fish also needs more food, but this additional need is roughly proportional with $W^{2/3}$ (Eq. 7.7). Therefore, the available food seems to be roughly proportional with the length of fish, and we come to the following formulation for the functional response (Van Nes et al., 1996):

$$p = \frac{C_r}{C_{\max}} = \frac{TotFB}{TotFB + H/L} S \tag{7.8}$$

In which $TotFB$ is the total available food biomass and S is a length-dependent factor that describes the suitability of the food type for the fish. Usually S is close to 1; only if the fish is about to switch in kind of food, the suitability of the food decreases. The fish may switch between four categories of food (fish, zooplankton, zoobenthos, and mussels) if the fish are within a certain length class (between *MinLen* and *MaxLen*) that is defined for all different species. We assume that the suitability of the food item changes continuously with fish length. The suitability factor for the food item i (S_i) is then the minimum of two Hill functions:

$$S_i = \min\left(\frac{MaxLen_i^{pow}}{MaxLen_i^{pow} + L^{pow}}, \frac{L^{pow}}{L^{pow} + MinLen_i^{pow}}\right) \tag{7.9}$$

We used a large power of these Hill function (default $pow = 8$) to obtain a relatively steep decrease in food suitability if the length of the fish is close to the upper border (*MaxLen*).

For all food categories the functional responses are evaluated. The food item with the maximum functional response is chosen. Only one category is consumed at a time.

The total food biomass (*TotFB*) of each category of food is obtained by the summation of the product of the weights (W_i) of all possible preys and the selectivity for each prey (Sel_{ij}).

$$TotFB = \sum_{j=0}^{n} \sum_{i=0}^{N_j} W_i Sel_{ij} \tag{7.10}$$

In which: n is number of species (j) of the food category and N_j number of individuals of species j.

The selectivity (Sel_{ij}) of different zooplankton species is a parameter. For fish predation, such species selectivity is used too. However, this selectivity factor is multiplied by a function of the length of the prey (L_{ij}) relative to the length of the predator (L_k), indicating the suitability of the prey:

$$Sel_{ij} = f\left(\frac{L_{ij}}{L_k}\right) S_j \tag{7.11}$$

It is assumed that a prey is suitable if their relative length is within certain limits (*Min* and *Max*). Between these limits the function f is 1. Below the lower limit (ca. 0.1) the suitability decreases linearly to zero. Also, above the maximum relative length (ca. 0.45) the suitability decreases linearly till 0, which is reached at 1 1/3 of the maximum limit. The limits are of each species are based on field observations in Lake Tjeukemeer (unpublished results E.H.R.R. Lammens and W.M. Mooij).

Mortality

If the respiration is larger than the growth, the fish loses weight, but the length is not reduced. If the expected weight on basis of their length is lower than a certain fraction (we take 0.7 on basis of Ivlev (1961)), starvation mortality takes place (Rose et al., 1996). The probability of dying then increases to a high value of ca. 0.1 d^{-1}.

The background mortality (m_b in d^{-1}) is a fixed parameter. All fish have a defined maximum age in the model. We have defined simply a 100% mortality if the fishes reach that age. The mortality takes place the same day that new fish are introduced.

Fishery

We have defined three types of fishery: fykes, gill nets and seine net fishery. The catch of all these nets (c_t in kg ha^{-1}) is modeled as a Holling type I functional response, which means that the catches increase linearly with the fish biomass:

$$c_t = N \sum_{j=0}^{n} \sum_{i=0}^{N_j} W_i e_{ij} \tag{7.12}$$

Where: e_{ij} is the efficiency of the net for species j; W_i is the fish biomass of species j (kg), this biomass is a function of mesh size, length of prey, specific selectivity and N is the number of nets (ha^{-1}), which may change during the season and is treated as an external variable. The efficiency is a function of the type of net and the fish, which is modeled differently for each type of fishery.

In gill nets is an optimal length of the fish (L_{opt} in cm) where the efficiency of the net is maximal, which is defined as follows:

$$L_{opt} = \frac{Mesh}{LM_i} \tag{7.13}$$

Mesh is the mesh size of the gill nets in cm, LM_i a specific conversion factor, which is defined for each species and dependent on the shape of the fish.

The efficiency of the gill net for fish i (e_{ij}) is defined as a Gauss curve of the relative deviation of the length to the optimal length, with a standard deviation of 0.1. Fish are vulnerable to being caught in gill nets in a narrow range of lengths (L_i in cm):

$$e_{ij} = e_{\max,j} \exp(-0.5 \frac{\left({}^{L_i}\!/_{L_{opt}} \right)^2}{0.1^2}) \tag{7.14}$$

$e_{max,j}$ is the maximum efficiency of the seine nets for species j.

The efficiency of the fykes (e_{ij}) is a combination of the maximum efficiency of the species ($e_{max,i}$) and a length selectivity:

$$e_{ij} = f(L_{ij})\, e_{\max,j} \tag{7.15}$$

The maximum efficiency may be different during the spawning period and the rest of the year.

It is assumed that a prey is suitable if their relative length is within certain limits (*Min* and *Max*). Between these limits the function f is 1. Below the lower limit the suitability decreases linearly to zero at another length limit (*AbsMin*). Also, above the maximum length the suitability decreases linearly till 0, which is reached at the absolute maximum limit. All these are parameters of each species.

For seine nets we assume that all fish larger than a certain threshold length are caught with equal probability. The threshold length is dependent on the mesh size (*Mesh* in cm) of the nets. For each species the efficiency can be defined:

$$\begin{aligned} &if\ \ L_i\ LM_{ij} > Mesh\ then \\ &\qquad e_{ij} = e_{\max,j} \\ &else \\ &\qquad e_{ij} = 0 \end{aligned} \tag{7.16}$$

In which: e_{ij} efficiency for individual i of species j; $e_{max,j}$ maximum efficiency of the net for species j; L_{ij} the length of the fish (cm) and LM_j a species dependent factor (dependent of the shape of the fish).

Piscivorous birds

Consumption by piscivorous birds can be included in the model in a simple way. The number of birds (N_i in ha^{-1}) and the daily individual consumption by birds (C_t in kg d^{-1}) are external variables. The consumption (B in kg ha^{-1} d^{-1}) of the birds is calculated as follows:

If $TotFB_t < FB_{crit}$ then

$$B = N_t C_t \tag{7.17}$$

else if $TotFB_t < FB_{min}$ then

$$B = N_t C_t \frac{TotFB_t - FB_{crit}}{FB_{\min} - FB_{crit}} \tag{7.18}$$

else

$$B = 0 \tag{7.19}$$

$TotFB_t$ is total food biomass (kg ha^{-1}), which is defined as the sum of all fish of a size range that is defined by two parameters (*MaxLen* and *MinLen*). If the food biomass (kg ha^{-1}) drops below the limit of FB_{crit} the birds move partly to another area for feeding. Below a second value (FB_{min}) all birds migrate.

Food species

For benthivorous and planktivorous fish, different kinds of food species are modeled. These species include for example: *Neomysis integer*, zooplankton, zoobenthos and *Dreissena polymorpha*, but we can define more similar food species. All these species can either be treated as external variables or included dynamically in the model as logistically growing species with a temperature dependent growth rate (r) and carrying capacity (K):

$$\frac{dF}{dt} = r\, Q_{10r}^{\frac{T-20}{10}} \left(1 - \frac{F}{K_t\, Q_{10k}^{\frac{T-20}{10}}} \right) F \tag{7.20}$$

Where F = biomass of the food species (kg ha^{-1}); t = time (d); r = growth rate at 20 °C, Q_{10r} = Q_{10} parameter for growth rate; T = temperature °C; K = carrying capacity at 20°C; Q_{10k} = Q_{10} parameter for growth rate.

Stepwise calibration

Understanding the dynamics of multiple interacting species can be very difficult, and models of as few as three interacting species without any size structure can already show a bewildering complex behavior (e.g., Gragnani et al., 1999). If many species are interacting in a model, it is also very difficult to calibrate parameter values. We designed a stepwise procedure comparable with the method of Rose et al. (1988). We start with shutting off all interactions between all species (Fig. 7.2). This is done by replacing mortality caused by predation by a predator independent mortality and making food consumption of fish independent on food availability. This is implemented as follows:

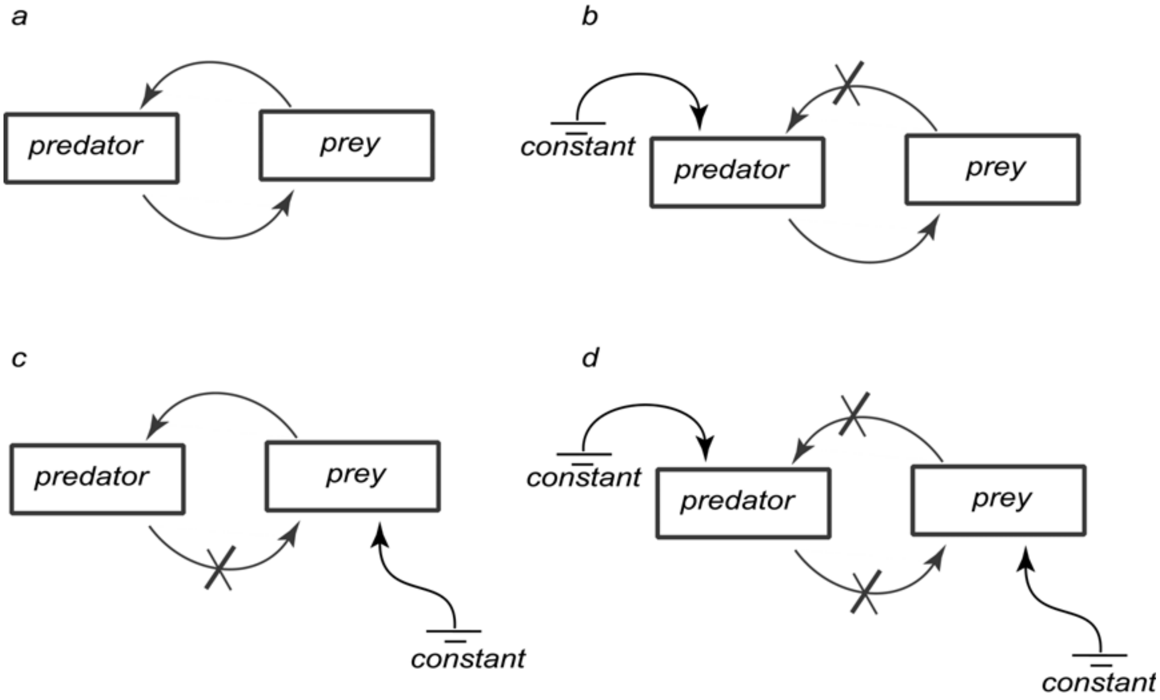

***Fig. 7.2** Three modes of simplifications in the predator-prey relationships in the model. a. The full feedback loop between predator and prey ('dependent growth/dependent mortality mode'); b. The food dependent consumption of the predator is replaced by a fixed consumption ('fixed growth mode'); c. The mortality of the prey caused by predation is replaced by a fixed mortality ('fixed mortality mode'); d. The predator is completely independent of the prey biomass and vice versa ('fixed growth/fixed mortality mode').*

1. The mortality caused by predation or grazing is replaced by an additional mortality (m_f, d^{-1}) dependent on temperature (T in °C) and fish length (L in cm):

$$m_f = \left(m_{f,adult} + \left(m_{f,young} - m_{f,adult} \right) \frac{h^p}{h^p + L^p} \right) Q_{10}^{\frac{T-20}{10}} \qquad (7.21)$$

2. The consumption is made independent on the food availability. The fishes consume a fixed proportion of their maximum consumption rate, which is dependent on the size of fish and temperature.

The simplified model can be considered as a collection of single species models without interactions. Changing parameters of one species does not change the biomasses and numbers of other species. The model was first calibrated in this 'fixed growth/fixed mortality' mode. When the model results described the data adequately, the relations between the species are introduced gradually by making the species growth dependent on food. In the next round of calibrations, only parameters related to the food selection are allowed to be changed by the user, until there is a reasonable result. The next step in the procedure is to reset the growth to the fixed mode, and make the mortality dependent on the predator consumption. After calibration, both growth and mortality are made dependent on the other species. If one of these calibrations fail, we returned to the first calibration step, changing the fixed mode mortality or the fixed functional response. The iterative process may stop if the result in the 'dependent growth/dependent mortality' mode is satisfying.

In both modes the model saves detailed information about the causes of mortality and the food sources of all species, which has proven to be very helpful to understand the causation in the model.

Parameterization for the interaction between bream, pikeperch and fishery in the Frisian Lakes

As an example of the use of the model we apply it to a case study of effects of a changed fishery in the Frisian Lakes. The Frisian Lakes form an extensive water system of shallow lakes, interconnected by canals with a total surface area of 14 000 ha in the northeast of the Netherlands (Maasdam and Claassen, 1998; Dekker et al., 2001). The fish population has been monitored from 1985 till 1995 (Lammens et al., 1990; Lammens, 1999b) and is dominated by bream, which represents about 70% of the biomass. The other 30% consists mainly of pikeperch, smelt (*Osmerus eperlanus* (L.)), roach (*Rutilus rutilus* (L.)), ruffe (*Gymnocephalus cernuus* (L.)) and perch (*Perca fluviatilis* (L.)).

From 1990 till 1995 an experimental seine fishery has been performed in the Frisian lakes (Lammens, 1999b), aimed at removing large bream (> 15 cm) in order to improve the feeding conditions of European eel (*Anguilla anguilla* L.), the most important commercial fish. This fishery was accompanied by a gill net fishery for the commercial profitable large pikeperch (> 60 cm) to finance the bream fishery (Lammens, 1999b). The pikeperch fishery was also predicted to change the size composition of the main piscivore (pikeperch) in such way that the population would consist of many small specimens that would exert a higher predation pressure on small planktivorous fish, which would be beneficial for the water quality (Lammens, 1999b). The effect of the fishery on the bream population was smaller than expected. Only in the early summer the bream population was reduced (Lammens, 1999b).

Parameterization

We first tuned the parameters to reproduce the composition of the fish community before and during the fishing experiment. Subsequently, we explored the effects of other fishery scenarios on the interaction between pikeperch and bream.

No data on zoobenthos and zooplankton were available. Therefore and for simplicity, the food intake of planktivorous and benthivorous fish (bream, smelt roach and ruffe) was set to the fixed mode (independent on food concentration). However, the growth of the piscivorous pikeperch was made dependent on the availability of prey. We focussed on the interaction between bream and pikeperch; therefore the mortality of these two species was made dependent on the predation. Also the mortality of smelt, being an important food source is made dependent on the predation. Roach and ruffe were given a fixed mortality.

We further simplified by introducing young fish (10-15 super-individuals) not earlier than the moment that the monitoring data were available (October). The number of young fish was thus an external variable, derived from annual censuses.

The growth parameters of each fish species were calibrated based on detailed information about Lake Tjeukemeer, which is one of the Frisian Lakes (Mooij et al., 1994; Mooij and Van Nes, 1998).

For temperature we used daily water temperature data of the nearby Lake Veluwe (unpublished data RIZA). The initial size and structure of the populations were in accordance with the field situation at the start of the monitoring.

Monte Carlo sensitivity analysis

We applied a multivariate sensitivity analysis (Klepper, 1989; Klepper et al., 1994) to assess the effect of the parameters on the model outcomes. The basis for this method is a Monte Carlo sensitivity analysis, at which a certain simulation run is repeated many times. For each run a parameter set is drawn, by randomly and independently selecting all parameter values within certain ranges. After the runs, sensitivity coefficients ($s_{i,j,t}$) are calculated by linear regressions between the parameter values (p_i) and the model output j at time t ($M_{j,t}$) of all runs (Klepper, 1989).

$$s_{i,j,t} = \frac{\partial M_{j,t}}{\partial p_i} \frac{\Delta p_i}{M_{j,i}} \tag{7.22}$$

The resulting sensitivity coefficients ($s_{i,j,t}$) give the relative change of the model output i at time t ($M_{i.t}$) as a consequence of changing the parameters over a range of $\Delta p_{i.}$.

The overall effect of each parameter ($s_{tot,\ i}$) on all model results can be characterized by the sum of the sensitivity coefficients:

$$s_{tot,i} = \sqrt{\left(\sum_{j,t} \left(s_{i,j,t} \right)^2 \right)} \tag{7.23}$$

The sensitivity coefficients comprise a huge sensitivity matrix, which can be hard to understand. Therefore, Klepper (1989) introduced a multivariate analysis of this matrix. By conducting a hierarchical cluster analysis, clusters of parameters that have the same or opposite effect on the qualitative model results are distinguished. As similarity measure, the absolute sine of the angle between the vectors of sensitivity coefficients is used. Additionally, from each cluster we plotted from each parameter the sensitivity coefficients of each model result as a time series of the simulated period to visualize the common features of the parameters in each cluster.

We also added 100 dummy parameters that did not have any effect on the model outcomes. These dummy parameters were set to 1 and varied in the same way as the model parameters. This way it is possible to select the parameters that have an effect significantly different from zero. This is done by comparing the total sensitivity of each model parameter with the 99% percentile of the sensitivity coefficients of the 100 dummy parameters. Only parameters that have significantly stronger effect on the model than the dummy variables were included in the cluster analysis.

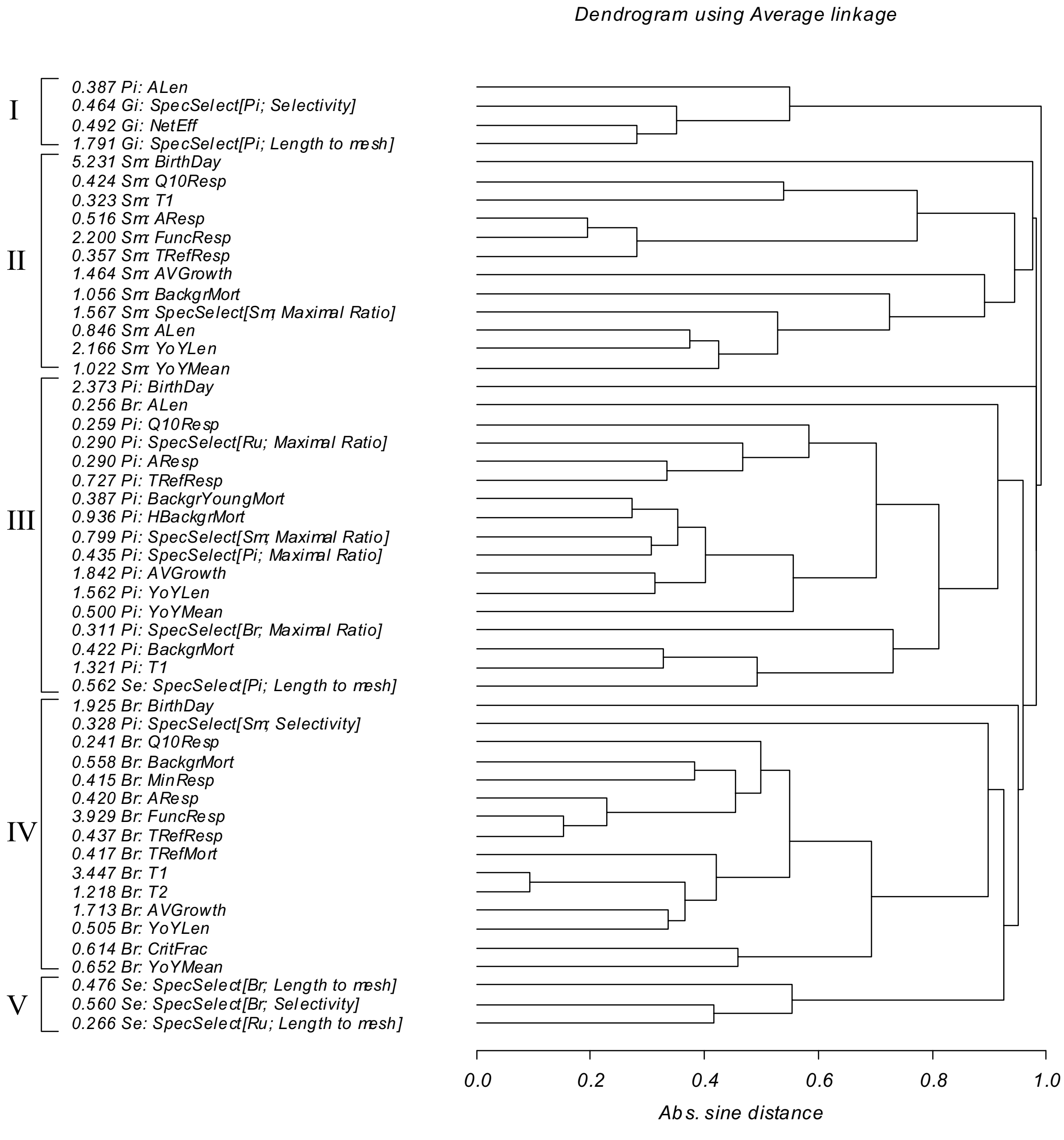

Fig. 7.3 *Cluster analysis of parameters on the basis of their sensitivity indices. Parameters with the same or opposite effect on the model results (biomass, numbers on 3 days per year) are grouped together. The value before each parameter is the length of the vector of the sensitivity coefficients (Klepper, 1989), which is a measure of the total strength of the effect. The 60 parameters that are shown have a significantly stronger total effect than 99% of 100 dummy variables. Pi = Pikeperch; Br = Bream; Ro = Roach; Sm = Smelt; Ru = Ruffe; Gi = Gill nets; Se = Seine nets. The abbreviations of the parameters are explained in Table 7.1.*

Table 7.1 *Brief description of the parameters.*

Parameter	Description	Unit
ALen	A in allometric regression	-
BLen	Exponent B in allometric regression	-
FixedMort	Fixed mortality	d^{-1}
FixedYoungMort	Maximal fixed mortality	d^{-1}
FuncResp	Fixed functional response	fraction
HFixedMort	Half saturation of fixed mortality	cm
PFixedMort	Power in length dependent fixed mortality	-
Q10Mort	Temperature dependent mortality (both background and fixed mode)	-
FoodSwitch	Crit.length species and funct.resp. for each food	-
SpecSelect	Overall selectivity; min ratio predator/prey; max ratio predator/prey	-
AResp	Constant in respiration equation	-
AVGrowth	Growth of one gram fish at 17	$g\ d^{-1}$
b_cons	Exponent in consumption equation	-
b_resp	Exponent in respiration equation	-
HActiv	Half saturation of activity (NAN = no activity)	°C
MinResp	Minimum respiration factor	-
Q10Resp	Temperature factor in respiration	-
T1	First order temperature correction	$d^{-1}\ °C^{-1}$
T2	Second order temperature correction	$d^{-1}\ °C^{-2}$
TRefResp	Constant in respiration equation	°C
nHabitatChoices	Number of changes in habitat distribution	-
BackgrMort	Background mortality	d^{-1}
BackgrYoungMort	Background mortality of young fish	d^{-1}
CritFrac	Critical weight loss for starvation mortality	fraction
HBackgrMort	Half-saturation of the length dep. background mortality	cm
MaxAge	Maximum year class	yr
MaxLength	Maximum length above which senescence mortality takes place	cm
MaxLength2	Absolute maximum length of the fishes	cm
PBackgrMort	Power of the length dependent backgr. mortality	-
Q10BackgrMort	Temperature dependence of background mortality as Q10	-
StarvMort	Starvation mortality	d^{-1}
TRefMort	Reference temperature for Q10Mort	°C
BirthDay	Reproduction day	dayno
BirthDaySum	Temp. sum from spawning defining the introduction of 0+ fishes	d °C
BirthDayTemp	Reference temperature for BirthDaySum	°C
CVGenPar	Coefficient of variation (SD/Mean) of 'genetic parameter'	fraction
EggWeight	Mean weight of eggs	g
IncubationPeriod	period between start of spawning period and birthday	d
MaturityAge	Age when fishes start spawning	yr
MinMaturityWeight	Minimal weight of spawning fish	g
NSuperInd	Number of super-individuals per year class	-
SpawnDuration	Duration of spawning period	d
SpawnWeightLossSlope	Weight loss during spawn	fraction
YoYHEggs	Half-saturation number of eggs (NAN is no limitation)	No. ha^{-1}
YoYImport	Import of 0+ fishes	No. ha^{-1}
YoYLen	Initial length of 0+ fishes	cm
YoYMean	Mean number of 0+ fishes	No. ha^{-1}
YoYNumDistr	Distr. of the number of 0+ fishes	-
YoYSD	Standard deviation of No of 0+ fishes	No. ha^{-1}
ZoopSelect	Overall selectivity for zooplankton	fraction

Results

Sensitivity analysis

For our sensitivity analysis we used the parameter settings of the Frisian lakes as basis, but with a constant yearly recruitment and a reduced number of super-individuals for computational reasons. We generated 10 000 sets of parameters, by varying 380 parameters affecting the fish species and fishery (smelt, pikeperch, perch, bream, ruffe, roach, gill nets and seine nets) at random and independently within ranges of ±10%, using a uniform distribution. We excluded nominal parameters and parameters that would have a negligible range (integer parameters with values < 5 and real parameters with the value 0) and some exponents of equations (b_c, b_r and b_l) that are well known and obviously will have large impact on the results. With each parameter setting four years were simulated, and the model results (population biomass, numbers) were stored annually at day 152 (1 June), day 213 (1 August) and day 274 (1 October). All simulations started with an equilibrium biomass distribution of fish obtained by a separate model run of 100 years with default parameter settings.

We excluded the parameters of roach and ruffe from the cluster analysis because these species were in the 'fixed mortality-fixed growth' mode. Of the 283 remaining parameters 66 were significantly better than the dummy parameters ($p < 0.05$), a result which depends upon the number of iterations affecting the power of the analysis. Cluster analysis of the 51 most significant parameters ($p < 0.01$) resulted in five distinct clusters of parameters with a comparable effect (I-V in Fig. 7.3).

The first cluster (I) contains a parameter defining the length-to-weight ratio of pikeperch and parameters defining the efficiency of gill nets. These parameters have a strong effect on the gill net catches and a strong opposite effect on the pikeperch biomass (Fig. 7.4a). The reason that length-to-weight ratio of pikeperch has a similar effect as the gill-net parameters, is that this parameter causes pikeperch to reach the critical size for being caught faster.

The next cluster (II) is formed by several parameters of smelt. As a representative example of the effects in this cluster, we show the effects of the parameter for the food conditions of smelt (the fixed functional response of the fixed growth mode) (Fig. 7.4b). This parameter has strong effects on the smelt biomass and numbers. Surprisingly the effects on biomass and numbers are opposite: if the biomass increases, the numbers decrease. The latter can not be ascribed to pikeperch predation as this species declines in response to the enhanced smelt growth. A potential explanation would be that large smelt becomes piscivorous and cannibalistic.

Cluster III consists mainly of pikeperch parameters. These parameters typically have an effect on the pikeperch biomass or numbers. This species, being the dominant piscivore, has a negative effect on all other species, which is reflected in opposite sensitivity coefficients on the numbers of all other species (Fig. 7.4c).

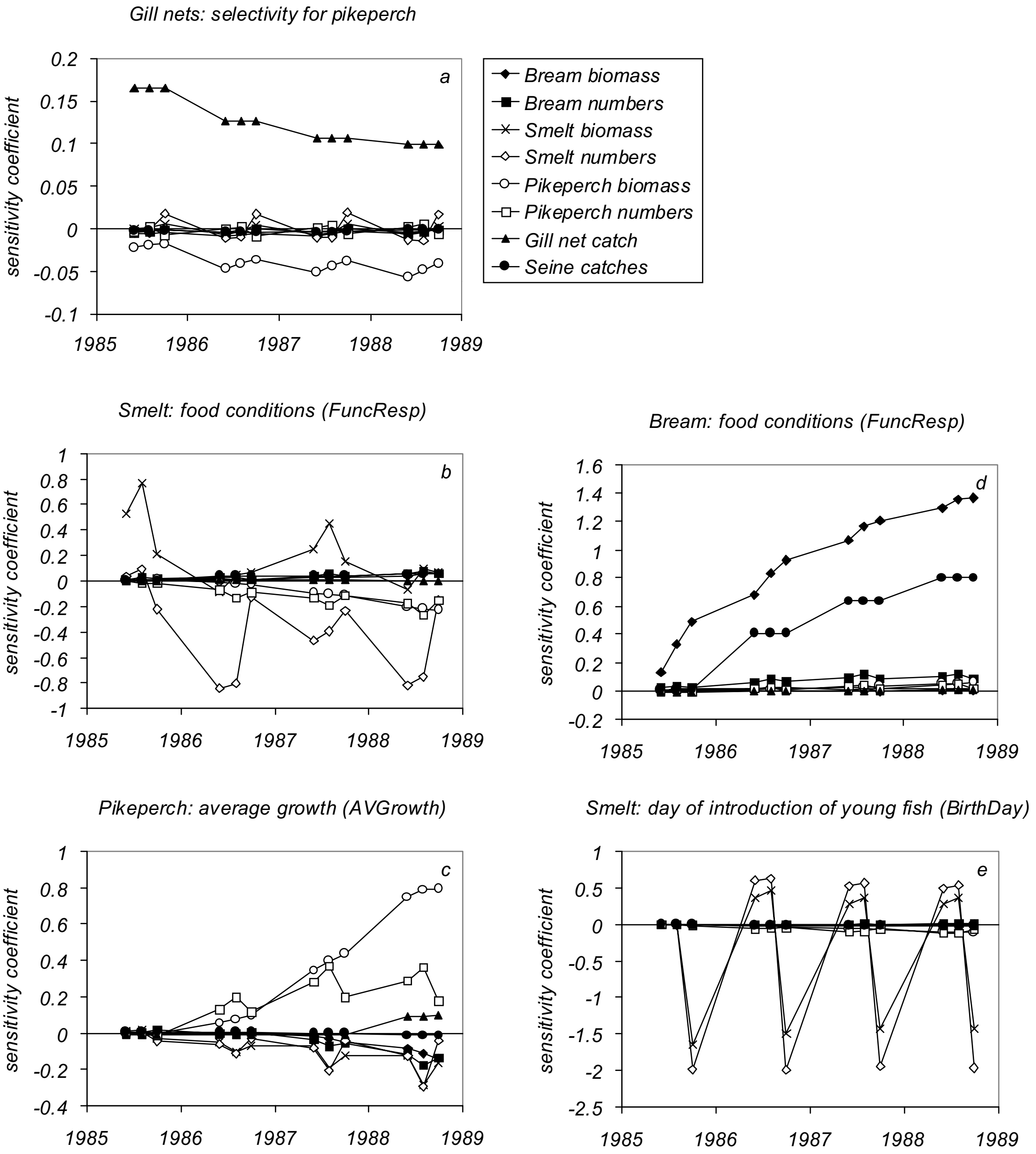

Fig. 7.4 *Time course of the relative effect (expressed as sensitivity coefficient) of variation in parameters on various model variables for simulations starting in 1985. The panels (a-e) show effects of representative parameters selected from each the five clusters marked in Fig. 7.3 respectively.*

Several bream parameters comprise cluster IV. These parameters characteristically have a strong effect on the bream biomass and the seine catches. The pikeperch biomass is hardly affected by the increase of bream (Fig. 7.4d).

The last cluster (V) consists of three parameters of the seines. These have a strong effect on the seine catches and an opposite effect on the numbers and biomass of bream.

It is striking the parameter '*BirthDay*' has a very large effect for all species, and is poorly related to the effects of all other parameters. This parameter defines the day on which new fish enter the model, which causes a distinct peak in numbers of fish and also a peak in biomass. A closer look at the sensitivity coefficients (Fig. 7.4e) shows that the effect is mainly due to the fact that the timing of the birth of the young fish can have a very strong effect on the fish biomass on nearby sampling days. The sudden increase of fish biomass caused by the introduction of young fish is sometimes just before or just after the last sampling day (day 274). This has large consequences for the measured biomass on that date, but is irrelevant in biological terms. This match or mismatch of a discontinuity in the output with the sampling timing illustrates a problem with the measuring of the sensitivity of a parameter that defines the timing of a discontinuity or a peak in the model outcomes (Klepper, 1989).

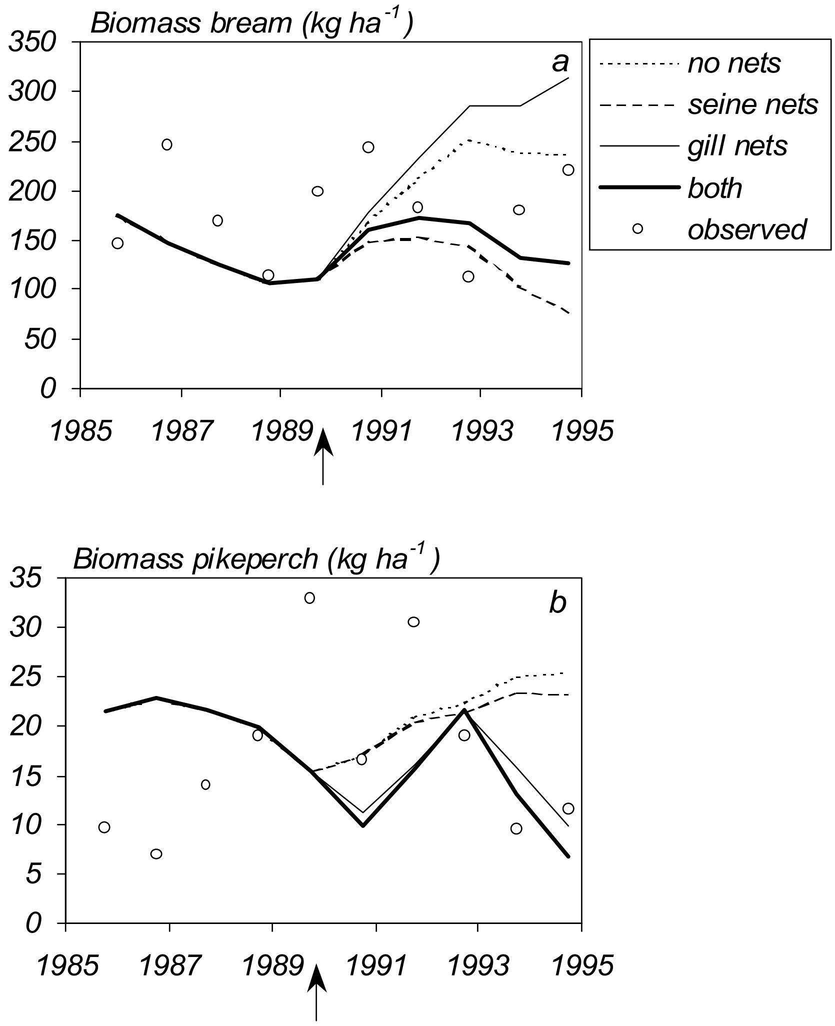

Fig. 7.5 *Simulated biomass on 1 November of pikeperch (a) and bream (b) calculated with four scenarios. The arrows indicate the start of the fishery experiment.*

The interaction between bream and pikeperch in the Frisian Lakes

During the simulated period there were two kinds of fishing regimes in the Frisian Lakes. We start the simulations with five years (from 1985 to 1990) without fishing. The next five years (starting in October 1989) two types of fishing were introduced in winter (October - March):

a. Approximately 0.4% of the lake area is fished daily with seine nets (knot-to-knot mesh size 3 cm).
b. Two types of gill nets are used: one with a knot-to-knot mesh size 7.5 cm and one with a 10 cm mesh. Both nets were deployed with an intensity of 0.01 nets ha^{-1}.

Though we did not manage to reproduce the variations in the bream and pikeperch data (Fig. 7.5), the average biomass is simulated reasonably. However, also in the monitoring data of the annual biomass there is a large unknown variability. Particularly the pikeperch data have a large uncertainty because the estimates were based on relatively few caught individuals. In addition to overall biomass estimates, the simulated annual catches from seines and gill nets had a reasonable fit with estimated catches (Chapter 8). Also, the simulated size distributions were realistic (Fig. 7.7).

Fig. 7.6 presents the dynamics of the causes of mortality of pikeperch bream and smelt. In the first period without fishing, the main mortality causes for pikeperch are the background mortality and cannibalism (Fig. 7.6a). Furthermore, there was one short period of mortality of an old strong year-class (senescence) around the onset of fishery. In the period with seine and gill net fishery, both types of fishery contribute to the decline in the population. For bream (Fig. 7.6b), the main causes of mortality are background mortality, seine fishery and predation by pikeperch. Smelt is hardly affected by fishery (Fig. 7.6c), apart from the background mortality, predation by pikeperch and cannibalism are the main causes of mortality.

To study the potential effects of fishery further, we analyzed three other fishery scenarios (Fig. 7.5):

1. Without fishery;
2. With seine fishery only (returning caught pikeperch)
3. With gill nets only.

Without fishery, both simulated pikeperch biomass and bream biomass increase. Seine fishery (returning caught pikeperch) causes the bream biomass to be reduced somewhat stronger than with both types of fishery, as the predation by pikeperch is stronger. Fishery with (pikeperch specific) gill nets only, has the opposite effect: pikeperch biomass is reduced and bream increases strongly. Fig. 7.7 shows the effect of the different fishery scenarios on the simulated populations in more detail. In the initial (1985) situation, both bream and pikeperch had a strong year class that dominated the length frequency distribution. In 1989 there is a new strong year class of both species that develops further if there is no fishery (Fig. 7.7c, d). If we simulate fishing with both kinds of nets combined (Fig. 7.7a, b), this year class of both species is substantially reduced within a few years. Hardly any pikeperch > 60 cm is left with this scenario. These graphs also illustrate that the simulated seine nets remove a wide size range of bream (Fig. 7.7f), whereas pikeperch is removed by the gill nets only if the individuals become large enough (Fig. 7.7e).

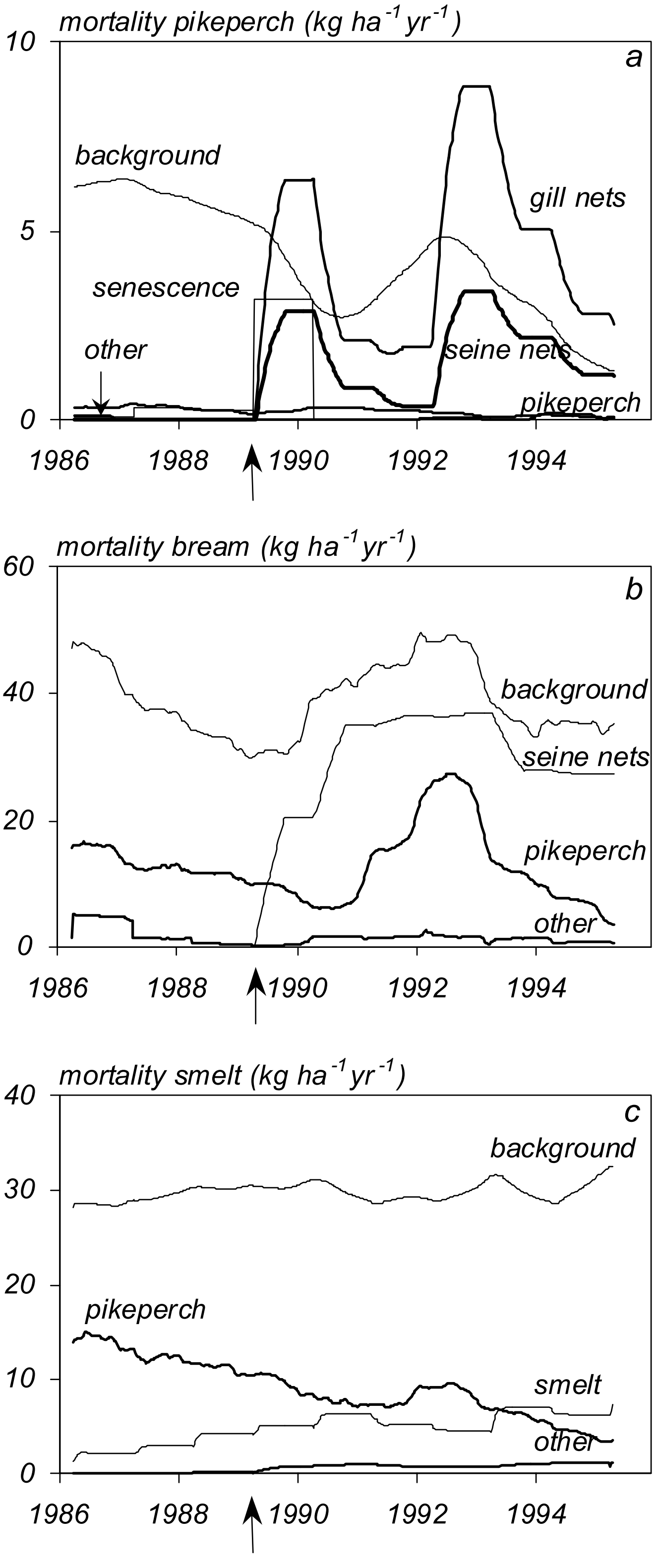

Fig. 7.6 *The causes of mortality for bream (a), pikeperch (b) and smelt (c) in the Frisian lakes. The mortality values are shown as moving averages with an averaging window of 1 year. Seine nets and gill nets were introduced in October1989 (indicated with an arrow).*

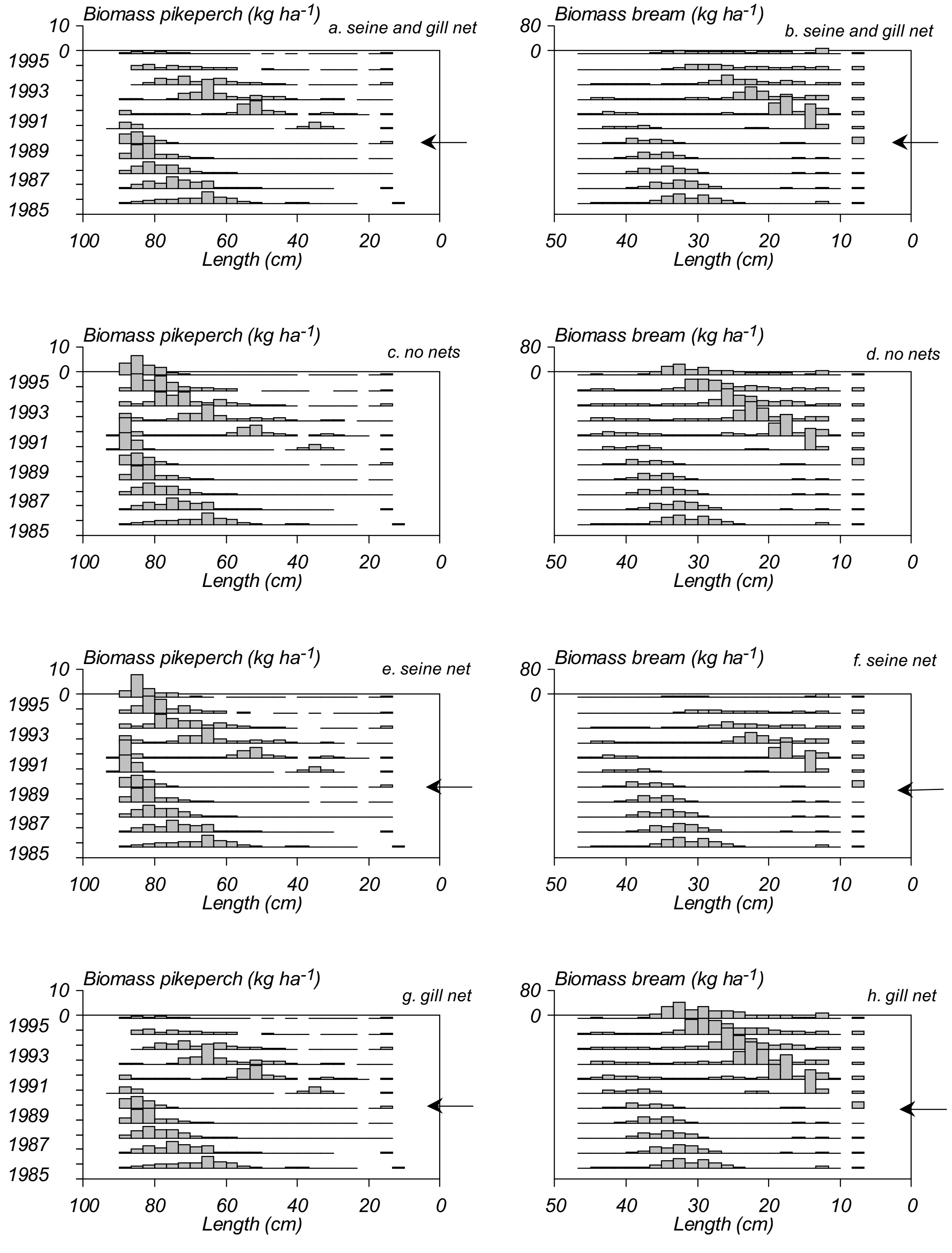

Fig. 7.7 The development of the pikeperch (a, c, e, g) and bream (b, d, f, g) population before and after the fishery (from 1991 on) with the four fishery scenario's. a-b: seine and gill net fishery in winter period; c-d: no fishery; e-f: with seine fishery in winter; g-h: gill nets in the winter. The arrows indicate the start of the fishery experiment.

In summary, the simulations suggest that the employed fishery in the Frisian Lakes was effective as the population of bream would have increased strongly without fishery. Lammens et al. (Chapter 8) proposed two hypotheses for this development. Firstly, in 1989, just before the experiment, the reproduction of both species was very high. Secondly, the mean water temperature from 1990 till 1992 was relatively high (Chapter 8). To distinguish between these possible effects we did simulation runs without fishing in which we eliminated these variable external factors. We simulated two additional scenarios, one with the same average recruitment for each year and one with the same average recruitment and also the same sinusoidal temperature scenario for each year. The results suggest that the variation in recruitment could indeed contribute to the increase in biomass of bream, but that the yearly variation in temperature was main cause of the good development of the strong bream year class (Fig. 7.8).

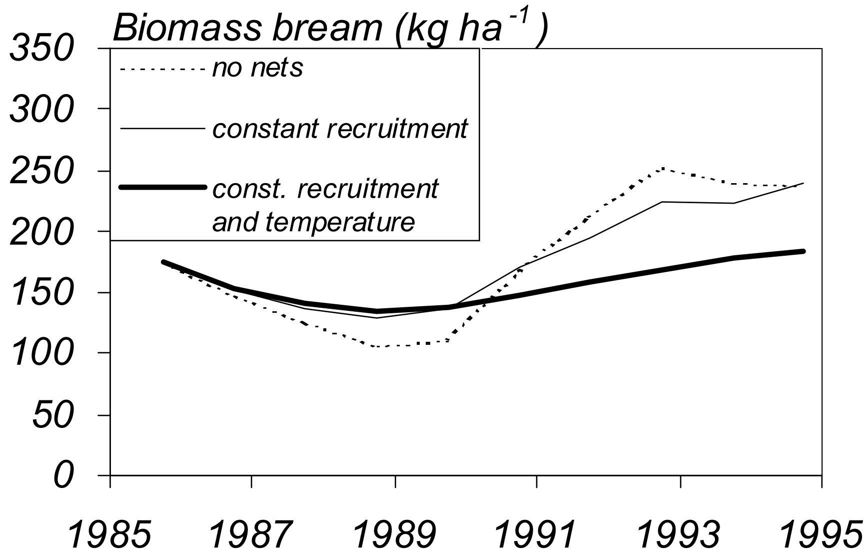

Fig. 7.8 The effect of the observed annual variation in recruitment and temperature on the development of the bream biomass without fishery.

Discussion

Multi-species models are notoriously complex to understand and Piscator is no exception. Our strategy of starting with simplified versions of the model proved to be helpful for determining base line values of the parameters. However, with each new implemented relation between species, the dynamics of the model often changed considerably. Although informative, the process of analyzing and comparing different versions can indeed be quite laborious.

The Monte-Carlo sensitivity analysis proved to be an efficient way of sorting out the effects of the numerous parameters in the model. The multivariate analysis of the sensitivity matrix not only detected the most important parameters, it also gave insight in the functioning of the model. Especially the visual inspection of the sensitivity coefficients

(Fig. 7.4), is a good starting point for further analysis of the model behavior with changing parameters. However, it should be stressed that a Monte-Carlo sensitivity analysis also has important limitations. If non-linearity's and parameter interactions are strong, like in our case, a sensitivity analysis is valid only in a small region round the chosen parameter combination and the current environmental conditions (Drechsler, 1998). Although a Monte Carlo sensitivity analysis scans a larger part of the parameter space than the simple sensitivity analysis by one-by-one changing of parameters, it is still important to keep this limitation in mind. The high sensitivity coefficients of the 'BirthDay' parameter illustrates another problem with sensitivity analysis: a parameter that causes a slightly different timing of a peak in model outcomes, has a very large sensitivity coefficient, even though this might be irrelevant to the model user (Klepper, 1989).

Even though Piscator is a large model with many parameters, there are still many processes not included in the model or modeled in a highly simplistic way. Several important processes have been omitted or simplified, merely because we lack sufficient insight in the mechanisms. For instance, we have no data about the bottlenecks in the larval life stages of fish. Therefore, we omitted these stages and simply added young fish at a certain moment of the year, independent of the standing stock. Another simplification is that we did not describe the competition for food sources such as zooplankton and zoobenthos realistically, because we modeled these groups of species in a highly simplified way. Likewise, we neglected feedback mechanisms in the fishery, such as optimizing strategies of fishermen and dependence of the fishing effort on the fish biomass. At other points, almost indispensable mechanisms are included in the model, despite a lack of data. For instance, in the description of the food selection there are some parameters that are hard to substantiate, such as the parameters that define the functional response with respect to the available food biomass (Eq. 7.8) and the parameters defining the ontogenetic food switches (Eq. 7.9).

In summary, the model is complex yet incomplete and despite the use of clever techniques it remains difficult to parameterize and analyze. Although this suggests a dim perspective for Piscator and related models, we feel that there are at least two important niches for models of this type.

Firstly, models such as Piscator may be used to generate or substantiate detailed specific hypotheses about mechanisms that generate patterns in fish communities. As an example consider the use of the model, for analyzing the Frisian lakes fishery experiment. The model simulations offered an explanation for the at first sight surprising observation that it was possible to remove 40-50 kg ha^{-1}yr^{-1} bream without much effect on the total biomass of bream. The lack of effect was partly caused in the simulations by the simultaneous reduction of the large pikeperch by the gill nets, implying a reduction of the predators of bream. In addition the model suggested that fishery effects in the Frisian case were compensated by the good development of the year-class that hatched just before the experiment, and by the prosperous development of this cohort caused by high water temperatures in the period 1990 – 1992. Indeed, Piscator has been found useful to quantify and explain qualitative hypotheses of fish biologists about fish dynamics in several Dutch lakes (Frisian lakes (this study and Lammens (Chapter 8)), IJsselmeer (Lammens, 1999a), Lake Veluwe (Chapter 8 and 9) and Lake Volkerak (Chapter 8)).

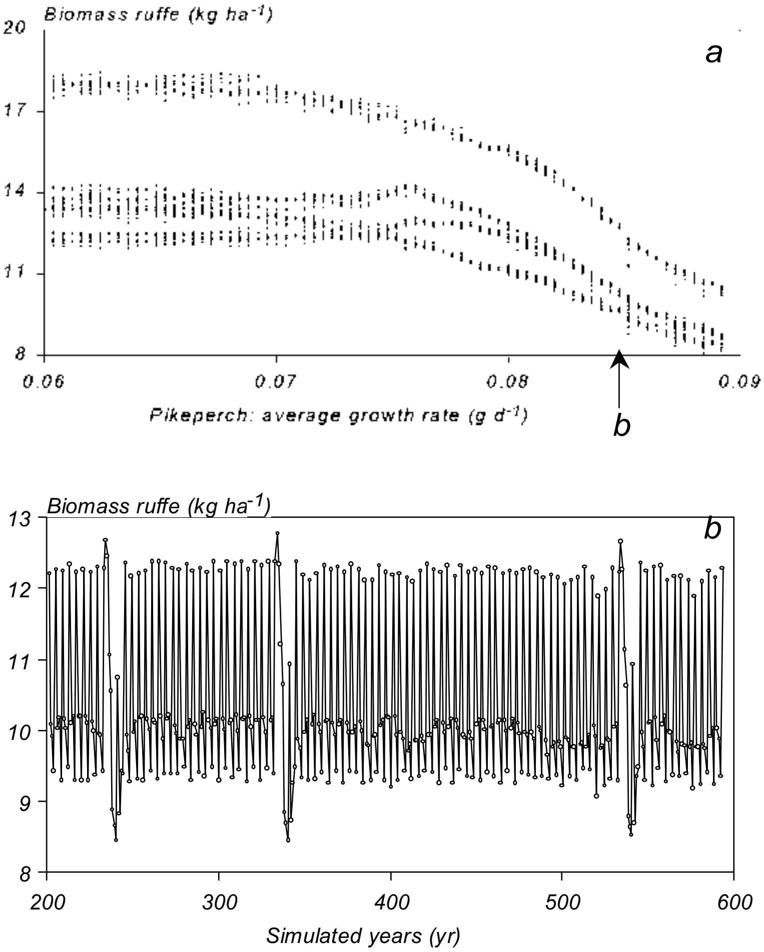

Fig. 7.9 *Example of more complex behavior of the model based on unpublished results of the fish community in Lake IJsselmeer. a. Dots represent the biomass of ruffe in October of 50 subsequent years, with various settings of the growth rate of pikeperch. The picture was created by increasing this parameter in small steps. Dynamics for each new parameter setting were left to stabilize for 50 simulation years before plotting the 50 next years. The growth and mortality of all species were dependent on predation and food biomass, and temperature or recruitment were kept constant. b. Example of a chaotic time series (after 200 years of stabilizing with a growth rate of pikeperch of 0.0852 g* d^{-1}*, indicated with an arrow in a). At irregular intervals the 4-year cycle destabilizes for about 12 years.*

These studies have helped, for instance to estimate the effect of cormorants on the fishery in IJsselmeer (Lammens, 1999a) and to substantiate the idea that natural growth of the bream population (without immigration) could explain the growth of the bream population in the recently created Lake Volkerak.

Secondly, we feel that models such as Piscator are useful to bridge the gap between reality and theoretical results obtained from highly abstract minimal models that are hard to test. For instance, many simple models of interacting (often planktonic) species have been shown to display extremely complex ranges of behavior, including alternative attractors, cycles and chaos (Gragnani et al., 1999). However, such behavior can well result as an artifact of the oversimplified formulation of the models (Scheffer and Rinaldi, 2000). In Piscator, complex multi-year cycles and chaos can also arise, especially if we do not use the many optional ways to uncouple species interactions and allow recruitment to depend upon parent populations (see an example in Fig. 7.9). The fact that such dynamics may arise in such a model shows that they are not mere artifacts of leaving size structure, multiple prey availability and seasonality out of consideration. Furthermore, the flexible structure of the model and the detailed graphical output of the model, allow one to unravel the precise causes of complex model behavior further, generating detailed testable hypotheses.

In conclusion, though we realize that fish interactions are complex, we feel that modeling interactions between fish species is a useful exercise that can help unraveling driving mechanisms and can assist fishery biologists in making management decisions.

Acknowledgements

We are much indebted to the monitoring crew of the Frisian lakes: Koos Swart, Bauke Vlink and others. We thank the Frisian Union of Fishermen for cooperation in the registration of the catches in the Frisian lakes. We are grateful to Willem Dekker, Peter Mous, Tom Buijse, Wim van Densen, Mennobart van Eerden and Wolf Mooij for their valuable advises during the creation of the model.

Chapter 8
Differences in exploitation of the bream population in three Dutch lakes and their relation to water quality

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Freshwater Biology, accepted for publication

Abstract

1. The development of the bream population was analyzed in three differently exploited lakes: the Frisian lakes (10 000 ha), Lake Veluwe (3000 ha) and Lake Volkerak (4500 ha). A model is used to analyze the effect of fishery on the population. Apart from direct effects on the bream population, indirect effects of fishery on transparency, chlorophyll-a, vegetation and macrofauna were analyzed.
2. In Lake Veluwe, the bream population was reduced from ca. 100 to 20 kg ha^{-1} after five years of fishing. The mortality caused by the fishery was estimated at 38% of bream > 15 cm on top of the 13% natural mortality for bream > 17 cm. The decline of the bream population was followed by a clearing of the lake and an accelerated expansion of the *Chara*-beds present in the shallow parts. The expansion of the *Chara*-beds occurred simultaneously with an increase of transparency in the open water, an increase of density of zebra mussels and a decrease of chlorophyll-a level.
3. The newly created Lake Volkerak showed the opposite of what happened in Lake Veluwe. The unexploited bream population started to develop in 1988 and reached a biomass of ca. 140 kg ha^{-1} in 1998. The transparency of the lake decreased from a maximum of 3 m to ca. 1 m. In the same period, the chlorophyll-a level increased from 5 μg l^{-1} to 45 μg l^{-1}. Vegetation coverage developed in the first years to 20% of the total area, but decreased to 10% with increasing turbidity.
4. The seine fishery in the Frisian lakes did not seem to affect the bream population, despite high catches of 40-50 kg ha^{-1}. The calculated natural mortality of fish larger than 15 cm was ca. 15%, and the fishery mortality was another 26%. The high loss was compensated by good recruitment and higher growth rates due to the higher temperatures in the period of fishing. There was only a slight decrease in chlorophyll-a level and a slight increase of transparency.

Introduction

Bream (*Abramis brama)* is usually a dominant fish species in eutrophic lakes in Europe, particularly in the Netherlands (Lammens, 1989). With increasing eutrophication, submerged vegetation decreased and new habitat for bream was created: turbid open water. Since the beginning of the 1970's, bream have dominated most Dutch lakes and although nutrient loads have decreased significantly since the late 1980's (Meijer, 2000), there are no signs that the bream stocks have responded to this. Until recently, bream was not exploited commercially. There was a limited removal of bream as by-catch in eel fishery, mainly in spring during spawning. Bream was also removed as by-catches in gill-nets, used to exploit pikeperch (*Stizistedion lucioperca*) and perch (*Perca fluviatilis*) commercially until 1976, when this was forbidden in the Netherlands (Steinmetz et al., 1990).

Since the 1990's, the position of bream in the fishery market has changed considerably: the demand for bream by angling clubs in Belgium has increased and at the same time the eel fishery has decreased steadily. Therefore, several commercial fishermen switched to bream fishery. In the Frisian lake district, commercial fishermen were allowed to fish with seines for bream during a period of five years and in Lake Veluwe commercial fishermen have been fishing bream since 1993. In Lake Volkerak the opposite happened: in this new man-made lake, the bream population developed in ten years from zero to a high-density population. In this lake fishermen were not allowed to fish bream.

We evaluated the effect of the fishery on the bream population by comparing the natural mortality before the fishery started, with the additional mortality caused by the fishery. We used a model to estimate the mortality and to analyze the results of the fishery in Lake Veluwe and the Frisian lakes. Then, we evaluated the effect on the ecosystem by comparing system variables such as transparency, chlorophyll-a level and vegetation coverage in the same periods. In Lake Volkerak, we followed the development of the bream population since the origin of the lake and at the same time monitored the same system variables as in the other lakes.

Description of the lakes

The Frisian lake district consists of 13 lakes with a total surface area of 10 000 ha, varying in size from 200 to 2000 ha (Fig. 8.1). The depth of the lakes is on average 1.5 m and there is only little variation between the lakes. The transparency is 30-40 cm with chlorophyll-a levels of 100-150 $\mu g\ l^{-1}$. All lakes are interconnected by channels and fish can migrate freely between the lakes.

Lake Veluwe has a surface area of 3400 ha with an average depth of 1.5 m. In the 1990's, the transparency in the lake was ca. 50 cm with chlorophyll-a levels of 25-75 $\mu g\ l^{-1}$. The vegetation coverage increased from ca. 5% in 1990 to ca. 60% in 2000.

Lake Volkerak was created in 1987 by closing a dam in the eastern part of the Eastern Scheldt, enclosing 4500 ha, with an average depth of 5.2 m. Transparency was 3 m in 1990 and decreased to ca. 1 m at the end of the 1990's. Vegetation coverage varied between 0 and 20%.

***Fig. 8.1** Locations of the three study sites (Volkerak, Veluwemeer and Frisian Lakes).*

Materials and methods

The bream population

The bream population was monitored with two type of trawls: one with an effective opening of 7 m, a height of 1 m and a cod-end mesh size of 12 mm (knot-to-knot). This trawl was used for shallow parts (< 1 m). The other trawl had an effective opening of 10 m, a height of 4 m and a cod-end mesh size of 10 mm, mainly used for lake parts > 1 m. Both nets were trawled with a speed of ca. 1.5 m s^{-1} during 10 min per haul. Bream were counted and measured to the nearest 0.5 cm. Where necessary, the total catch was subsampled by weight. The biomass of the bream population was calculated per ha; the catch was divided by the surface area covered and corrected for size-dependent catch efficiency according to Lammens & Klein Breteler (1995) and Klinge (1999) In the Frisian lakes (10 000 ha), we monitored at 40-45 locations once a year in September - October during 1985-1994. The interconnected lakes were considered as one system, as fish moved freely between these lakes during winter, spring and summer for various reasons (e.g., overwintering, spawning and feeding). Moreover, the seine fishery took place in all these lakes. In Lake Veluwe 25-30 locations were sampled once a year in September during 1992-1999 and in Lake Volkerak 25-30 locations were sampled once a year in October during 1988-1998.

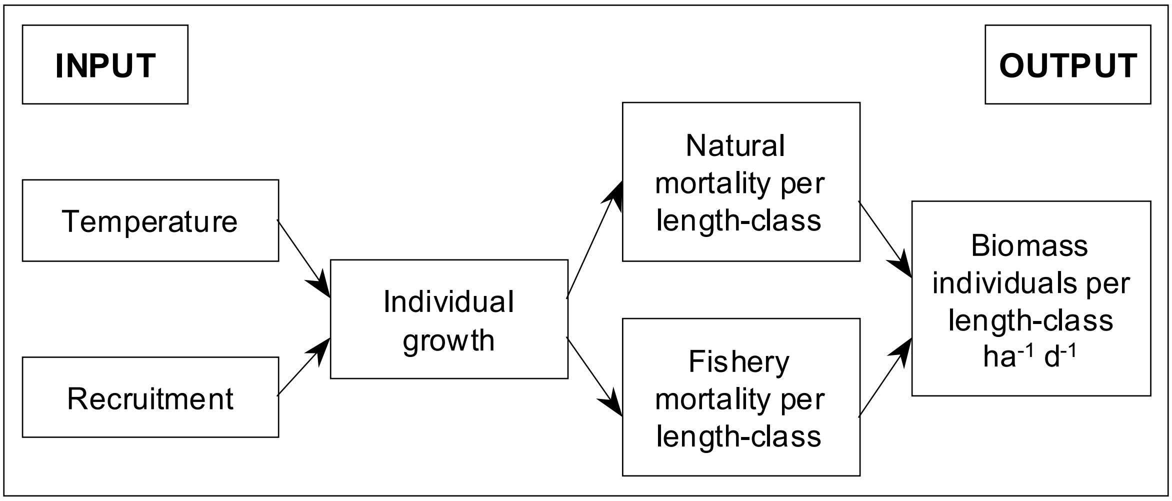

Fig. 8.2 *Schematic representation of input and output of the model.*

Transparency and chlorophyll-a levels

Transparency was measured monthly in the open water with a Secchi disc. For chlorophyll-a level determination, 5-6 separate samples (5 liters total) were collected from the open water with a tube sampler (perspex tube of 1.5 m, diameter 5 cm, which was closed with a perspex stopper below). The samples were collected in a single jar and the concentration of chlorophyll-a was measured by ethanol extraction according to Dutch standards (NEN), which comply with international standards (ISO).

Monitoring the vegetation

Between 1969 and 1987, aquatic macrophytes in Lake Veluwe were monitored irregularly. Mostly this was done by mapping the outlines of vegetation beds of *Chara* spp., *Potamogeton pectinatus* and *P. perfoliatus*. From this, the total area covered could be derived. Since 1987, all aquatic macrophytes were recorded much more accurately in this lake. The coverage of the vegetation was estimated in quadrates located in a 100 x 100 m grid over the lake (Coops and Doef, 1996; Van den Berg et al., 1999).

In Lake Volkerak, the coverage of the vegetation was estimated by divers. In plots of 10 x 10 m, the percentage coverage by vegetation was estimated for the whole depth range in the lake and converted to the total coverage for the lake.

Monitoring the zebra mussels

In Lake Veluwe, zebra mussels were sampled with a box core (780 cm^2) at 25 locations in the open water. At every location, three samples were taken and numbers (> 7 mm) per sample were counted.

The commercial fishery

The seine fishery was conducted during the winter months (November-March), when the eel fishery was not paying. The fishermen used seines of 680 m in length, which were operated with winches using 1500 meter ropes connected to the wings of the seine. The mesh size of the cod end was 40 mm, knot-to-knot. Usually, two to three hauls were made per day with a speed of 10-20 cm s^{-1}. Per haul, the total bream catch was weighed and the total amount removed per ha per year could be calculated.

Modeling the bream population

The model describes the dynamics of the bream population in numbers and biomass per length-class and year-class on a daily basis. Growth, mortality and recruitment are the basic components of the model. The model is individual-based, meaning the model population is composed of individuals with specific characteristics such as age, length, and growth rate. In this specific model, the growth and mortality are calibrated using the recruitment and temperature as the most important input variables (Fig. 8.2). The model is described in more detail in Chapter 7. We used the growth curves of bream that were fitted by Mooij & Van Nes (1998). Allometric functions (Mooij et al., 1994) were used to convert biomass to length. Recruitment and calibration are specific for these lakes and are described here.

Recruitment

The monitoring provided densities and biomasses in September-October. Next to growth and mortality, we needed figures on recruitment for modeling. For recruitment, we used the densities of 0+ bream as found in the lake. The dynamics of the first year were left out of the analysis.

Calibration

The parameters for growth and mortality had to be calibrated in order to fit the growth and mortality in the lake with the growth and mortality in the model. The parameterization of model was done in three steps:

1. calibrating the growth curve for each of the three lakes;
2. calibrating the mortality in the un-fished conditions;
3. calibrating the mortality including the fishery of seines.

We used the Controlled Random Search (CRS) technique (Price, 1979) to find the best fit in each of these three steps. As goodness-of-fit criterion, we used the least sum of squares to establish the best fit, and used a conservative stop criterion. For temperature, we used data sets of daily measured or interpolated (Mooij and Van Tongeren, 1990) water temperatures of sampling points in each lake.

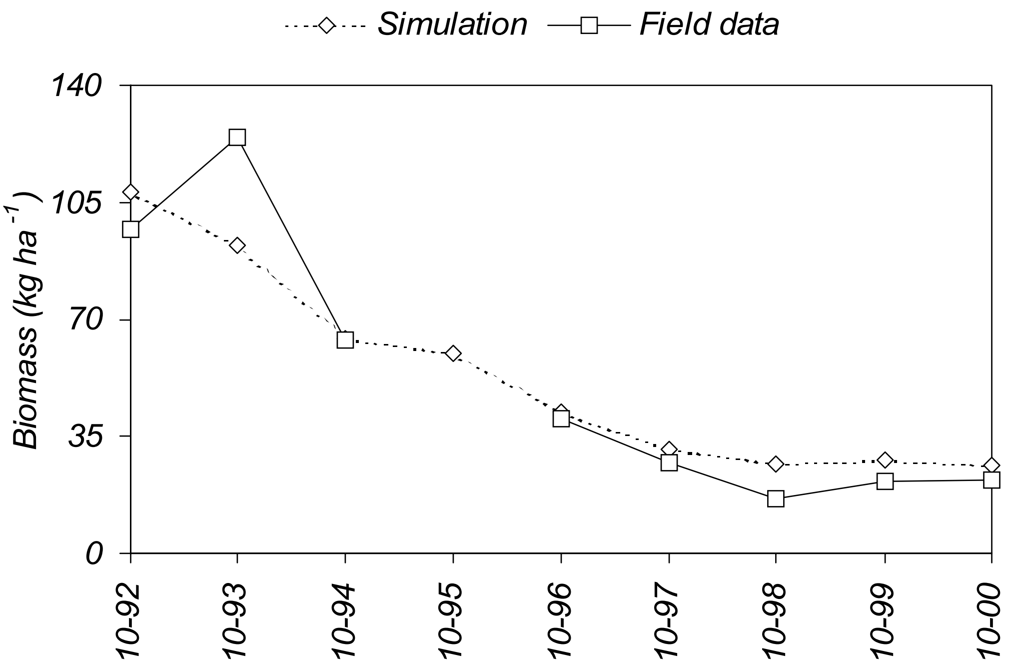

Fig. 8.3 *Simulated and measured biomass of bream (kg ha^{-1}) in Lake Veluwe in the period 1992-2000.*

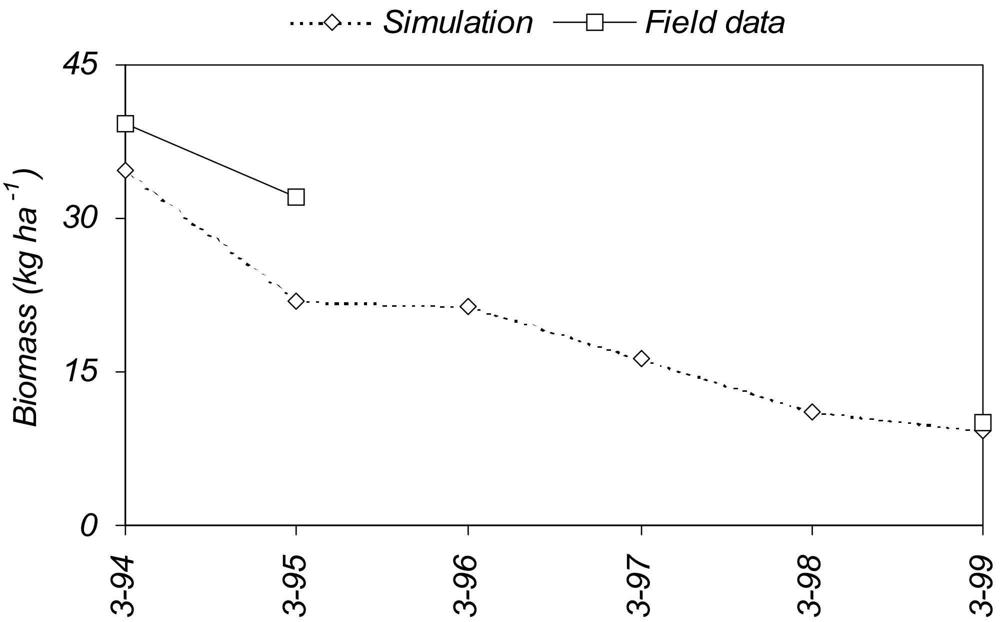

Fig. 8.4 *Simulated and measured catches of bream (kg ha^{-1}) in Lake Veluwe in the winters of the successive years in the period 1994-1999.*

To calibrate growth curves of each of the three lakes, we used published length data of the year classes (Lammens, 1982; Backxs, 1989; Lammens, 1996). We varied the growth rate between 0.7 and 1 of the maximal growth.

To calibrate the mortality we used 0+ densities as input and used CRS to fit the simulated biomass with the biomass in the field. We fitted the mortality of young and adult fishes and the age of the gradual switch between these two mortalities (see Chapter 7: $m_{f\,young}$, $m_{f\,adult}$ and h_f).

We calibrated the mortality caused by seine fishery (= catch effort (N), for selectivity S = 1) to fit the simulated change in biomass with the observed change by CRS and using the least sum of squares to establish the best fit. It was assumed that the estimated growth and mortality were not affected by the seine fishery.

Results

Lake Veluwe

The biomass of the bream population was ca. 100 kg ha^{-1} in the beginning of the 1990's, but decreased to ca. 20 kg ha^{-1} at the end of the 1990's (Fig. 8.3). The best fit of measured and simulated biomass in the period before the seine fishery started, was obtained with an estimated growth of 88% of the maximal growth and an estimated mortality of ca. 65% per year for small bream and ca. 13% for large bream with a gradual switch around 17 cm (see methods for calibration of model). The mortality due to seine fishery was estimated to be 38% of the population > 15 cm, superimposed on the natural mortality. The catches of the commercial fisherman were somewhat higher than the independently simulated catches necessary to reduce the population to ca. 20 kg ha^{-1} (Fig. 8.4).

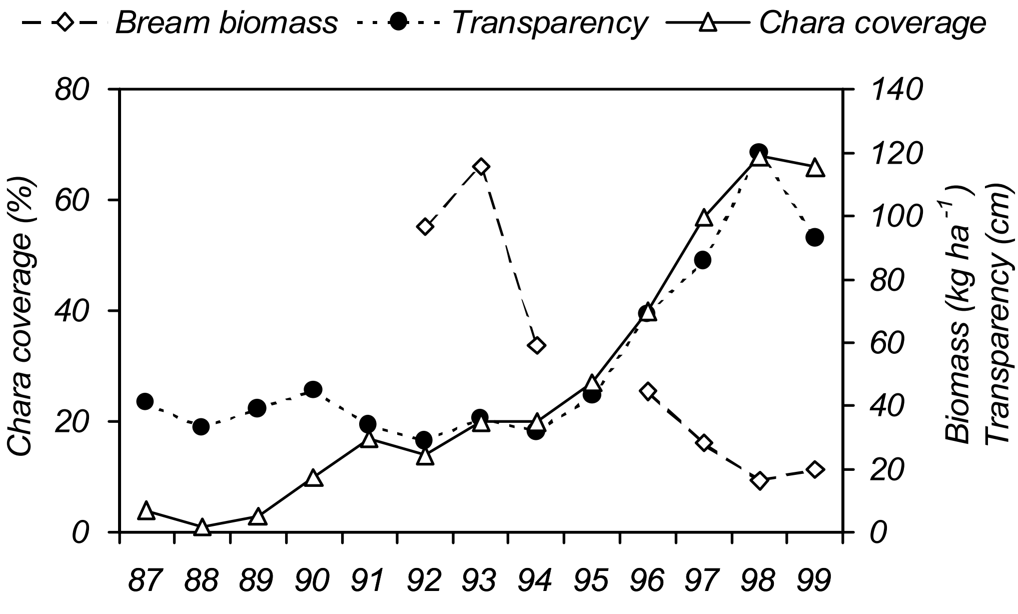

Fig. 8.5 Percentage coverage of Chara sp., transparency (cm) and biomass of the bream population (kg ha^{-1}) in Lake Veluwe in the period 1987-1999.

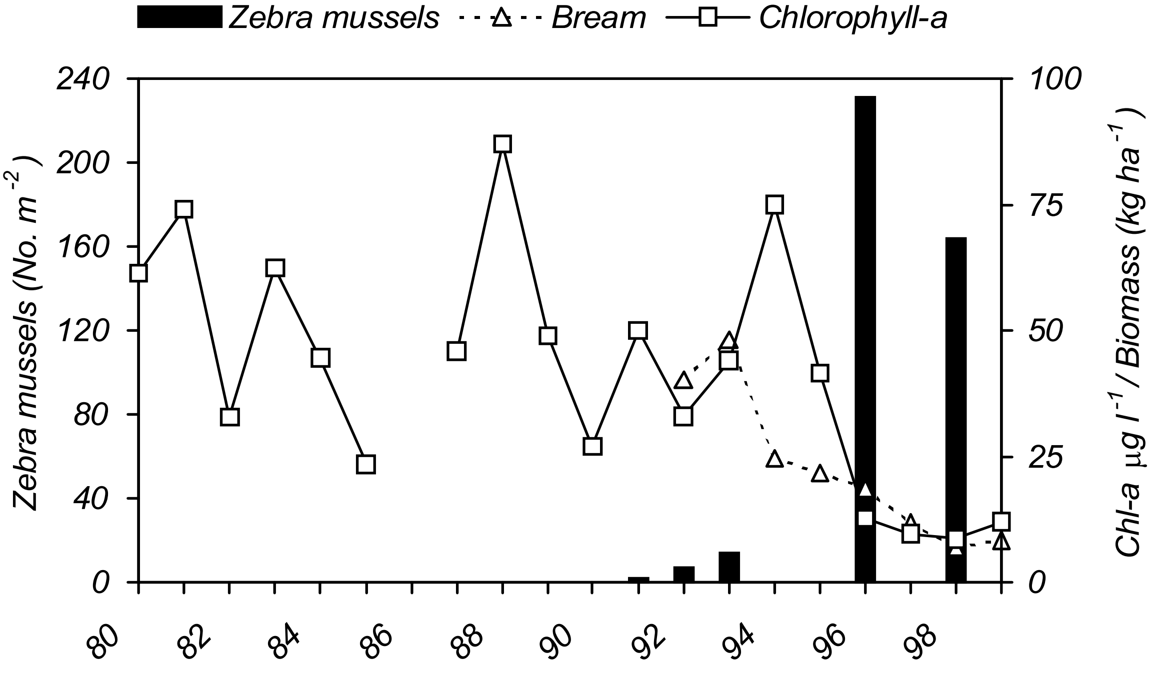

Fig. 8.6 Chlorophyll-a concentration (µg l^{-1}), biomass of bream (kg ha^{-1}) and the density of zebra mussels (No. m^{-1}) in Lake Veluwe in the period 1980-1999.

The decrease of the bream population was followed by a clearing of the lake from 40 to 100-120 cm and a rapid expansion of the *Chara*-beds from 15 to 65% coverage (Fig. 8.5).

The chlorophyll-a level decreased from ca. 50 µg l^{-1} (1980–1995) to ca. 10 µg l^{-1} after 1995. The decrease followed two years after the decrease of the bream population and coincided with the rapid increase of the zebra mussel density (Fig. 8.6).

Frisian lakes

The biomass of the bream population varied between 100 and 250 kg ha^{-1} in the period between 1985 and 1994 and showed a 4-year cycle (Fig. 8.7). The best fit of the measured biomass for the first five years, when there was no fishery, could be obtained with an estimated growth of 88% of the maximal growth and an estimated mortality of ca. 70% per year for small bream and ca. 15% for large bream, with a gradual switch around 15 cm (see methods for calibration of model). The best fit for the second period was obtained by an estimated fishery mortality of 26% of the population > 15 cm by fishing with seines superimposed on the natural mortality (Fig. 8.7). The catches of the commercial fisherman were somewhat higher than the independently simulated catches, necessary to fit the population to the measured biomass (Fig. 8.8).

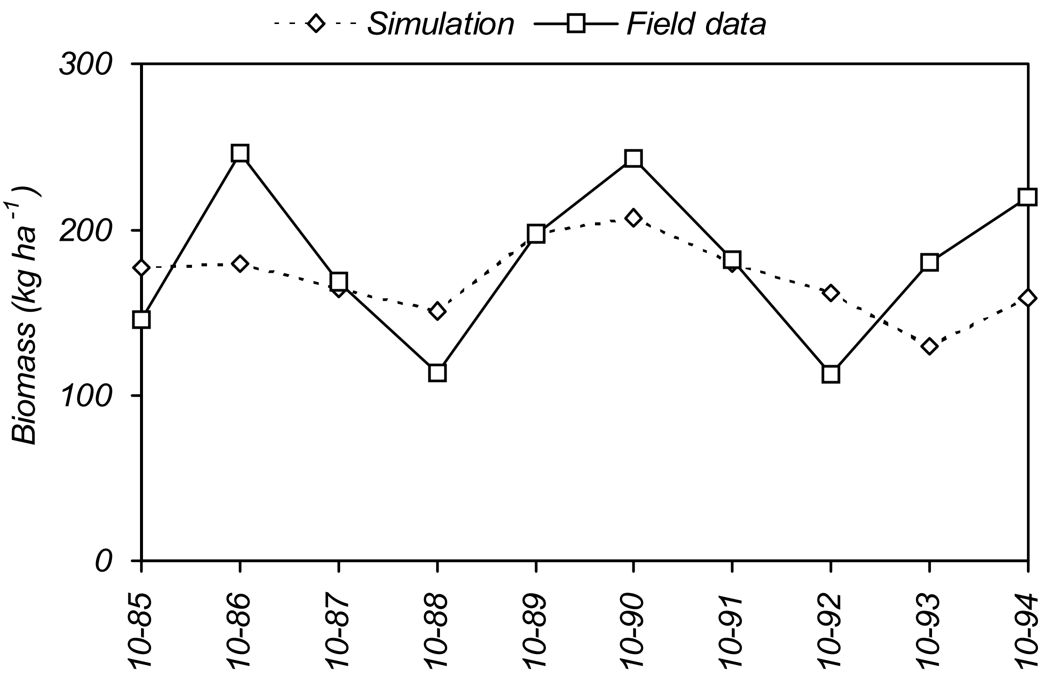

Fig. 8.7 *Simulated and measured biomass of bream (kg ha^{-1}) in the Frisian Lakes in the period 1985-1994.*

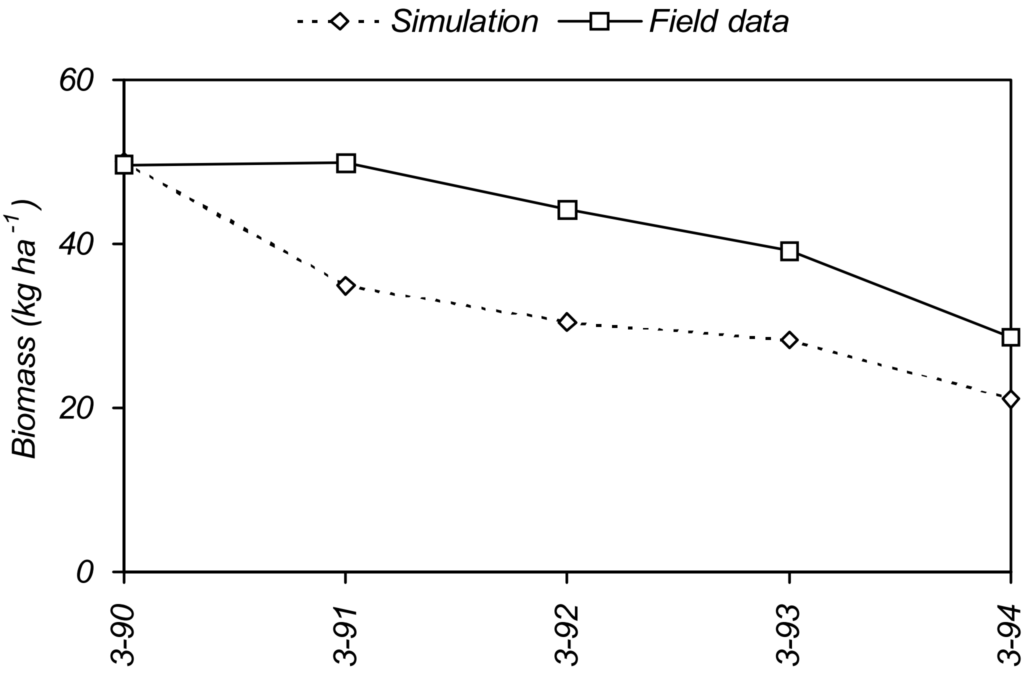

Fig. 8.8 *Simulated and measured catches of bream (kg ha^{-1}) in the winters of the successive years in the period 1990-1994 in the Frisian Lakes.*

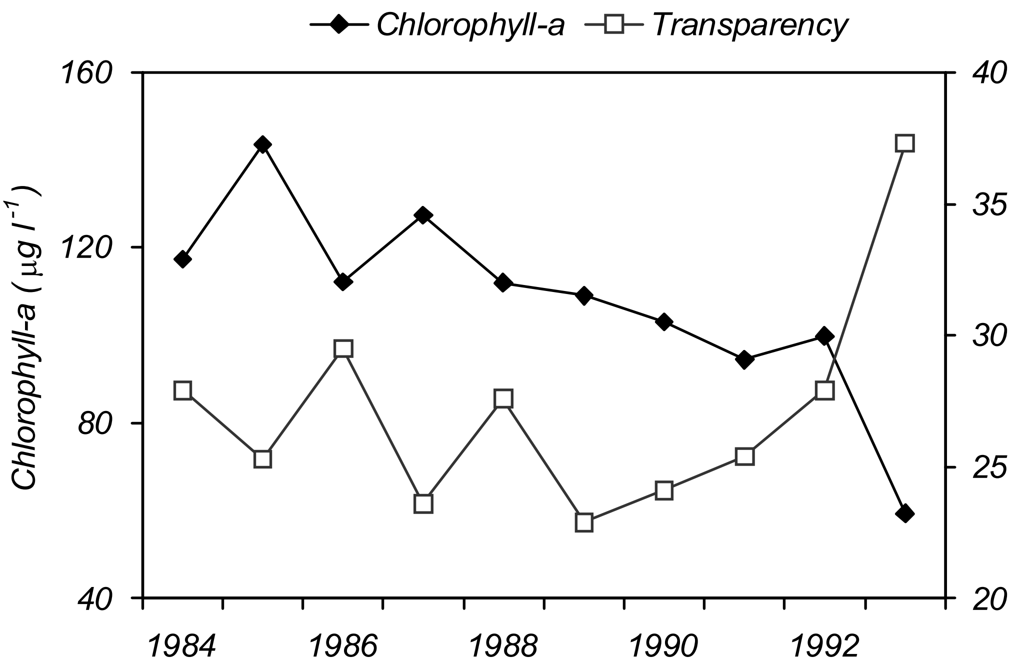

Fig. 8.9 *Chlorophyll-a (μg l^{-1}) and transparency (cm) in the Frisian lakes.*

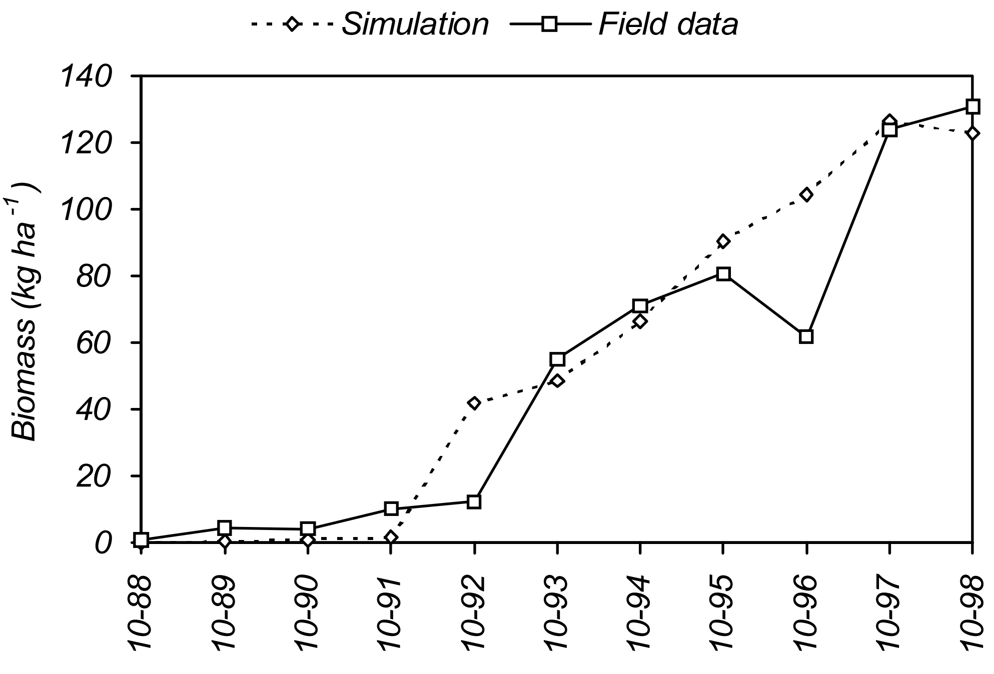

Fig. 8.10 *Simulated and measured biomass of bream (kg ha^{-1}) in Lake Volkerak in the period 1988-1998.*

The chlorophyll-a level decreased slightly from ca.120 µg l^{-1} in 1984 to ca.100 µg l^{-1} in 1992. In 1993, there was a sudden decrease to ca. 70 µg l^{-1}. Transparency was stable until 1993, when it increased from 28 to 38 cm (Fig. 8.9).

Lake Volkerak

The biomass of the bream population increased from ca.1 kg ha^{-1} in 1988 to 140 kg ha^{-1} in 1998 (Fig. 8.10). The best fit of the first period could be obtained with an estimated growth of 99% of the maximal growth and an estimated mortality of ca. 69% per year for small bream and ca. 14% for large bream with a gradual switch around 15 cm (see methods for calibration of model).

While the bream population developed into the dominant species in the lake, the transparency of the lake decreased from a maximum of 3 m in 1990 to ca. 1 m in 1998 (Fig. 8.11). In that time, the chlorophyll-a level increased from a minimum of 5 µg l^{-1} to a maximum of 45 µg l^{-1}. Vegetation started to develop in the first years to 20% coverage of the total area in 1992, but decreased to 10% as transparency decreased (Fig. 8.12).

Discussion

Although it was not the intention, a biomanipulation experiment was carried in Lake Veluwe, the Frisian lakes and Volkerak: in the first two lakes by removing a part of the bream population by fishery, in the latter by the development of the bream population in a new lake. In all cases, the bream population was monitored together with other ecosystem variables such as transparency, chlorophyll-a levels and zebra mussel density. The monitoring showed that the changes in the bream population coincided with changes in transparency, chlorophyll-a level and zebra mussels in Lake Veluwe and Volkerak and that changes in the Frisian lakes were small. We used a model to analyze whether the changes in the bream population were caused by fishery and whether the development of the bream population in Lake Volkerak was merely autonomous.

Lake Veluwe

Lake Veluwe showed quite significant effects of the fishery of the bream population and ecosystem variables. After five years of fishing, the bream population was reduced from ca. 100 to 20 kg ha^{-1}. Until the end of the 1990's, it was unclear whether this was the impact of the fishery. The generally accepted cause of the decrease of the bream population was the increase of the *Chara*-beds, which resulted in a smaller foraging area for the bream population (Van den Berg, 1999; Meijer, 2000). A visit to the local commercial fisherman provided insight into the amount of bream caught on a yearly basis. We used a model to calculate if the amount of bream removed by this fisherman would be sufficient to cause the decrease in the population measured in the lake.

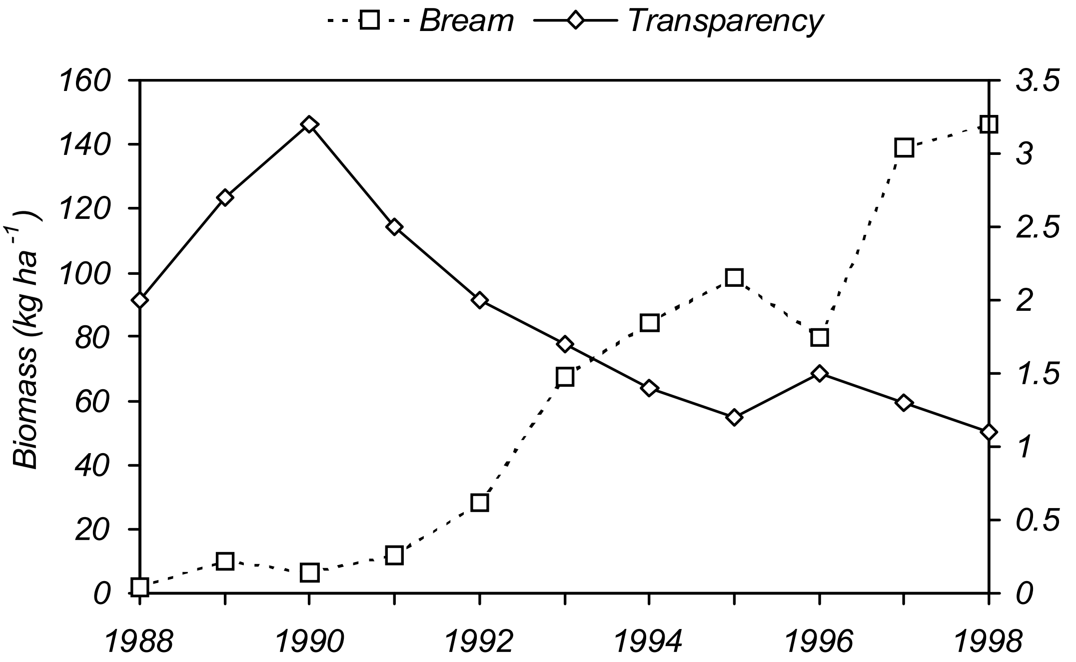

Fig. 8.11 *Biomass of bream (kg ha^{-1}) and transparency (m) in Lake Volkerak in the period 1988-1998.*

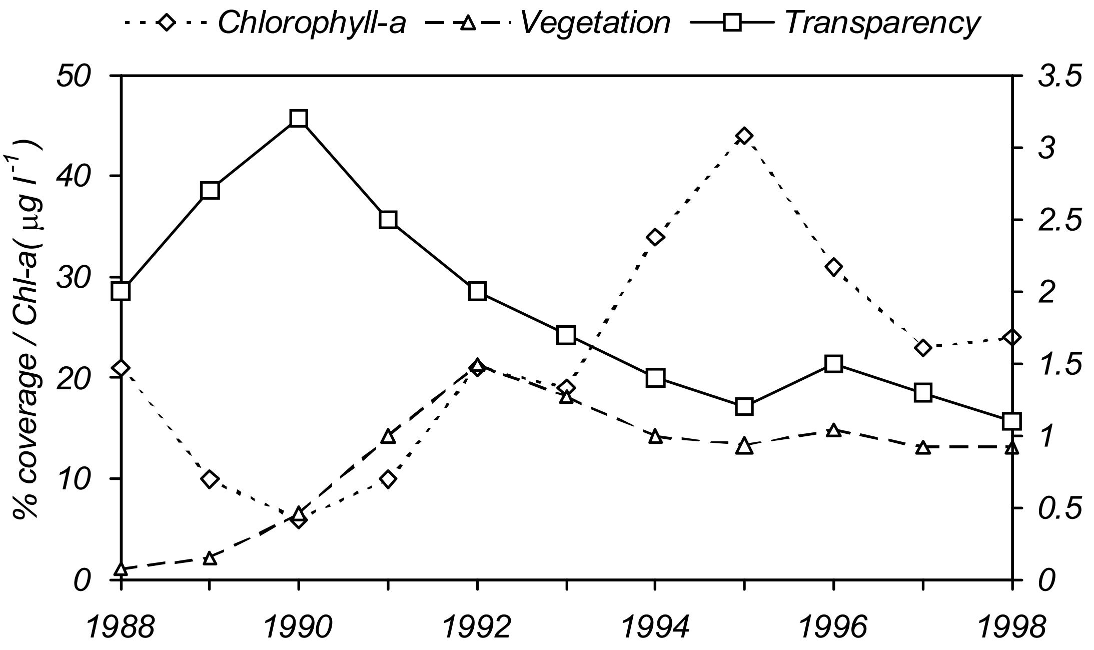

Fig. 8.12 *Transparency (m), percentage coverage of vegetation (%) and chlorophyll-a (μg l^{-1}) in Lake Volkerak in the period 1988-1998.*

First, the natural mortality of the bream population was calculated before the fishery was introduced. It was assumed that the feeding conditions for bream were constant. Measured recruitment for bream and measured water temperatures were used as input for the model. In the model, recruitment took place on October 1 and therefore the mortality of young fish did not include the period before October 1. In that case, the mortality for young fish would have been more than 99% (Mooij, 1992). When fish are young, they are especially vulnerable to predation, but when larger than 15-20 cm, the chance of being eaten by a predator becomes small and the main causes for mortality are disease, starvation and spawning. Then, the estimated mortality is ca. 15% per year. This value made the best fit with the field data and was used to estimate the fishery mortality. However, both mortalities are probably not independent and natural mortality will be probably lower when fishery mortality is high, as feeding conditions are improved by a reduction of the fish stock.

The mortality caused by the fishery was estimated at 38% of bream population > 15 cm on top of the 13% natural mortality for bream > 17 cm. At the start of the fishery, ca. 40 kg ha^{-1} was removed during the winter months and this was somewhat higher than the amount needed in the model to reduce the population to the low level of 20 kg ha^{-1}. As discussed before, this can be explained by a decrease of natural mortality in the lake in response to the fishery due to improved feeding conditions. This would also lead to an increased growth rate in the lake. The model, however, used fixed parameters and this resulted in a lower catch needed to cause the decrease in the population.

The decline of the bream population was followed by a clearing of the lake and accelerated expansion of the *Chara*-beds present in the shallow parts (Fig. 8.5). Of course we don't know what would have happened if there was no fishery at all, but without the reduction of the bream population it is very difficult to find a plausible explanation for what happened. Before the fishery, there was a high transparency only within the *Chara*-beds (Scheffer et al., 1994). The increase of the *Chara*-beds occurred simultaneously with the increase in transparency in the open water, necessary for the *Chara*-expansion. The increase in transparency can only be related to the decline of the bream population and to the following rapid increase of zebra mussel density and decrease of chlorophyll-a concentration.

Lake Volkerak

Lake Volkerak showed the opposite of what happened in Lake Veluwe. This lake was originally part of a salt water system, the Eastern Scheldt Estuary. It was isolated by a dam in 1987 and was a complete freshwater system at the end of that year (Breukers et al., 1997). The bream population started to develop in 1988 and reached a biomass of ca. 140 kg ha^{-1} in 1998. While bream population developed into the dominant species of the lake (Breukers et al., 1997), the transparency in the lake decreased from a maximum of 3 m to ca. 1 m. In the same period, the chlorophyll-a level increased from a minimum of 5 μg l^{-1} to a maximum of 45 μg l^{-1}. Vegetation started to develop in the first years to 20% of the total area, but deceased to 10% with increasing turbidity.

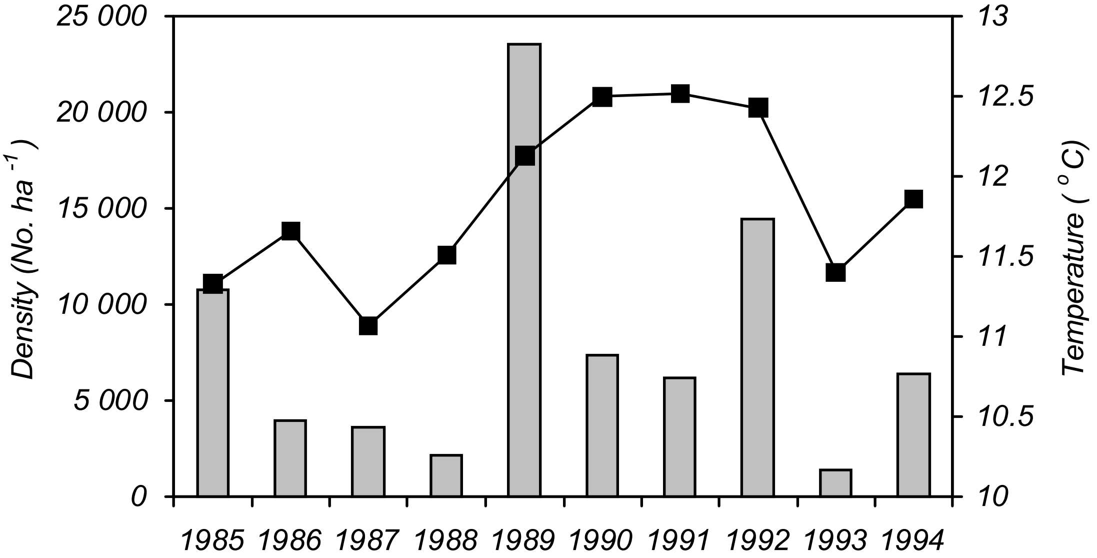

Fig. 8.13 *Recruitment as numbers of 0+ bream after the growing season (bars) and the mean yearly temperatures in the Frisian lakes in the period 1985-1994.*

The application of the model suggested that the time needed for the development of the bream population in Lake Volkerak was a matter of natural development. The natural mortality in Volkerak was comparable to that in Lake Veluwe and Frisian lakes. There were no indications that adult bream immigrated; only larvae were passively imported from outside the lake (Ligtvoet et al., 1991). Only the growth was much higher (almost maximal) than in the other lakes. The time needed for the development of the bream population corresponded with the time the lake needed to become eutrophic, with high chlorophyll-a levels and low transparency. The lake was already potentially eutrophic from the beginning of its existence (Breukers et al., 1997), but needed the bream to express it.

Frisian lakes

The seine fishery in the Frisian lakes did not seem to affect the bream population. Although high catches of 40-50 kg ha^{-1} were realized, the difference in biomass of the bream population before and after the fishery was started, was not significant ($p > 0.05$, Kruskall-Wallis). The fishermen could hardly believe that the bream population was not affected by the fishery, as it was obvious that a large part of the population was removed, even more than in Lake Veluwe. So it was unclear what happened in the Frisian lakes. The model results showed the best fit with the field data if the fishery mortality was 26%, which was sufficient to realize a catch somewhat lower than the real catch, but it was relatively less than in Lake Veluwe (38%). The higher recruitment and temperature in the second period (Fig. 8.13) contributed to compensate the losses by fishery. Apart from that, the natural mortality must have been lower because of the fishery, as the model predicted lower catches of fish to explain the observed biomasses (Fig. 8.8). We could not reproduce the cyclic pattern of biomass changes in the lake with the model. If growth and mortality varied in this period (they were constant in the model), they may have contributed to this pattern, reflecting the feeding conditions in the lake.

The slight improvement of the water quality during the last year of the fishery indicated that there was some effect of the fishery. The fish population was reduced in winter and increased during summer. By the end of the summer, when we conducted the monitoring, the losses of the fishery were compensated, but at least in the first half of the summer, the biomass must have been lower than in the years before. The slight decrease in chlorophyll-a levels and increase in transparency can be explained in this way.

The role of bream in eutrophic lakes

Bream is one of the dominant fish species in eutrophic lakes and lowland rivers (Lammens, 1989). It is specialized in benthivorous feeding, taking mouthfuls of bottom sediment and retaining the organisms (chironomids, oligochaetes, benthic crustaceans) by 'sieving' (Lammens and Hoogenboezem, 1991). If the biomass of the bream population is large, the effect on turbidity is great. Breukelaar et al. (1994) demonstrated that transparency decreased from 1 m to ca. 40 cm and chlorophyll-a levels increased from 5 $\mu g\ l^{-1}$ to ca. 40 $\mu g\ l^{-1}$, when the bream biomass increased from 0 to 100 kg ha^{-1} in ponds of 1 m depth. Ten Winkel & Meulemans (1984) showed that *Chara* beds rapidly developed in areas in Lake Maarseveen from which bream had been excluded.

The relation of bream with zebra mussels may comparable to this process, as zebra mussels are prevented to settle as long as bream is actively feeding in the bottom sediment. Disturbing the sediment is known to have a negative impact on the settlement of zebra mussels (Martel, 1993; Martel et al., 1994; Bially and MacIsaac, 2000).

Today, a large area of Lake Veluwe is covered with *Chara* beds and the total foraging area has considerably decreased, and therefore the carrying capacity of the lake for bream has decreased as well. If the fishery would be terminated, the bream population would increase again, but it is unlikely that it would attain its original density. The habitat has changed and the stability of this habitat will largely depend on the interaction between bream, *Chara*, zebra mussels and nutrient loads. In the Frisian lakes, vegetation is still absent and as long as bream is dominant in these lakes, it is not likely that vegetation will develop in the present eutrophic conditions. In Lake Volkerak the bream population reached a biomass comparable to that in the Frisian lakes in just 10 years. The dominance of the bream is reflected in the decrease of transparency, the increased chlorophyll-a concentration and reduced vegetation coverage.

Acknowledgements

We are much indebted to the monitoring crew of Witteveen & Bos and Aquaterra: Jouke Kampen, Marcel Klinge, Joost Backx who did most of the fish monitoring in Lake Veluwe and Lake Volkerak and to Koos Swart and Bauke Vlink for the Frisian lakes. We thank Henk Timmer for his cooperation to reconstruct the bream catch in Lake Veluwe and the Frisian Union of Fishermen for cooperation in the registration of the catches in the Frisian lakes. We are grateful to Marie-Louise Meijer, and Harry Hosper who stimulated and guided research in Lake Veluwe.

Chapter 9

The effect of commercial fishery on the bream population and relation to the rapid expansion of *Chara* beds in Lake Veluwe

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submitted for publication

Abstract

1. The fish community in Lake Veluwe (3400 ha) changed in composition and biomass, simultaneously with the development of the *Chara* beds. The number of fish species increased considerably and the total biomass decreased to ca. 35% of the original biomass. The change in the fish biomass followed the introduction of a commercial fishery and was in its turn followed by a rapid expansion of the *Chara* beds.
2. A fish model was used to describe the development of the bream population in Lake Veluwe before and after the commercial fishery started. We calculated the natural mortality using data on growth, recruitment and size distribution and discriminated between natural and fishery mortality. The model predicted that without fishery the biomass of the bream population would hardly change and that the fishery could explain the change in the biomass and size composition.
3. The rapid expansion of the *Chara* beds was not likely without the fishery as the *Chara* needs transparency up to the bottom and undisturbed sediment. The reduction of the bream population created favorable conditions for zebra mussels to settle which in turn created the clear water, necessary for the further development of the *Chara* beds.

Introduction

In a period of ten years (1989-1999), Lake Veluwe (3000 ha) changed from a turbid lake with only little vegetation into a clear lake with ca. 60% vegetation cover, mainly consisting of *Chara* beds (Van den Berg, 1999; Meijer, 2000). The development of *Chara* beds coincided with a change in the fish stock. Particularly bream showed a strong decrease in density being reduced from ca. 100 kg ha^{-1} in 1993 to ca. 25 kg ha^{-1} in 1998 (Meijer, 2000). The first hypothesis about the development of the fish stock stated that the increase of the *Chara* beds reduced the feeding area of bream and caused the decrease of the population (Van den Berg, 1999). In 2000 we found out that since 1993 commercial fishermen removed large quantities of bream to compensate for their decreasing income, as catches of eel diminished steadily.

The purpose of the present study is to evaluate whether the fishery can explain how the bream population developed and how the bream population interacted with the increase of the *Chara* beds. For the evaluation we used an individual-based model to describe the effect of fish removal on the total community. Apart from that, we tried to explain if there are alternative explanations for the rapid decrease of the bream population.

Materials and methods

Describing the fish community

The fish community was monitored with two type of trawls: one with an effective opening of 7 m (wonder trawl), height of 1 m and cod-end mesh size of 12 mm, used for shallow parts of maximally 1 m. The other trawl has an effective opening of 10 m, height of 4 m and cod-end mesh size of 10 mm, mainly used for parts deeper than 1 m. Both nets were trawled with an speed of ca. 1.5 m s^{-1} during 10 min per haul. From 1991 to 1999 fishing was done in or around the first week of October and always at night. Homogeneously distributed over the lake, 25-30 locations were fished. The fish were identified per species, counted and measured to the nearest 0.5 cm. Where necessary, the total catch was subsampled by weight.

Modeling the fish community

Growth

The growth of the fish species was modeled using the equation below. The growth of a fish in optimal feeding conditions is related to its weight and to temperature (Mooij and Van Nes, 1998).

For each species a growth curve is established according to the following equation:

$$\left(\frac{dW}{dt}\right)_{\max} = \left(G_{mean} + T_1\left(T - T_0\right) + T_2\left(T - T_0\right)^2\right) W^{b_c} \tag{9.1}$$

Mooij & Van Nes (1998) fitted the parameters G_{mean}, T_1 and b_c for bream. The second order term (T_2) is usually negligible. It is mainly added as a check for non-linearity during the optimizing process. See Mooij & Van Nes (1998) and Chapter 7 for explanation of all parameters.

G_{mean}	0.044
T_1	0.0063
b_c	0.67

We used allometric functions (Mooij et al., 1994) to convert biomass to length.

Natural mortality

The natural mortality is considered temperature dependent. We used a Q_{10} formulation to describe this dependency. Furthermore, we discriminated between the mortality of two size classes (young and adult) and formulated the total mortality as (Fig. 9.1):

$$m_f = \left[m_{f\,adult} + (m_{f\,young} - m_{f\,adult}) \frac{h_f^2}{h_f^2 + L^2} \right] Q_{10}^{\frac{T-20}{10}} \qquad (9.2)$$

In which: m_f = mortality (d^{-1}); $m_{f\,adult}$ = adult mortality (d^{-1}); $m_{f\,young}$ = young mortality (d^{-1}); h_f = parameter, the length where the mortality is halfway young and adult (cm); L = length (cm); Q_{10} = temperature effect; T = temperature (°C)

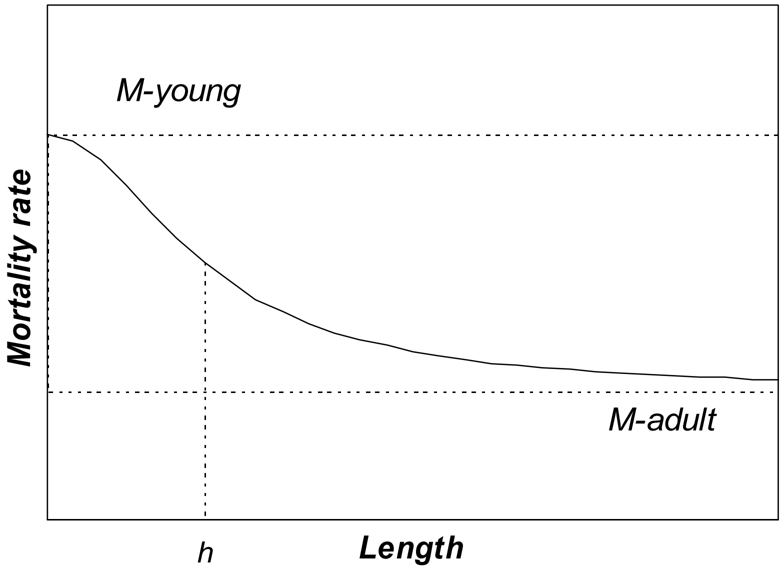

***Fig. 9.1** The graphical representation of mortality of young and 'adult' fish*

Mortality caused by fishery

The catch of seines is modeled as a functional response type I:

$$c_t = N\ TotFB_t \qquad (9.3)$$

In which: c_t = catches of seines at day t (kg ha^{-1}); $TotFB_t$ = total vulnerable fish biomass: a function of mesh size, length of prey, specific selectivity (kg ha^{-1}); N = Intensity of fishery (area fished per lake area).

The fishery takes place daily during the winter months. The ‘availability’ of fish for the seine is defined by a selectivity index:

$$TotFB = \sum_{j=0}^{n} \sum_{i=0}^{N_j} W_i \; Sel_{ij} \tag{9.4}$$

In which: n = number of fish species in the current habitat; N_j = number of individuals of species j (ha^{-1}); W_i = individual biomass (kg); Sel_{ij} = selectivity of individual i of species j, function of mesh width and fish length and fish species (ranges between 0 and 1).

We assume that all fishes larger than a threshold length, are caught with equal probability. For each species an efficiency can be defined:

$$if \;\; L_i \;\; LM_j > Mesh \quad then \quad Sel_{ij} = S_j \quad else \quad Sel_{ij} = 0 \tag{9.5}$$

In which: L_i = length of fish i (cm); LM_j = length-mesh conversion of species j (dependent of the shape of the fish, as a rule of thumb 1/4); S_j = specific selectivity (a value between 0 and 1).

Recruitment

The monitoring provided us densities and biomasses in September-October. To simulate the population we needed next to growth and mortality, figures about recruitment, assuming that migration was negligible. For recruitment we used the densities of 0+ bream as found in the monitoring. The dynamics of the first year was left out of the analysis.

Calibration

The parameterization of model was done in three steps: (1) calibrating the growth curve for each of the three lakes; (2) calibrating the mortality in the un-fished conditions and (3) calibrating the mortality using the seines.

We used Controlled Random Search (CRS) technique (Price, 1979) to find the best fit in these three steps. As goodness-of-fit criterion we used the least sum of squares to establish the best fit, and used a conservative stop criterion. For temperature, we used data sets of daily measured or interpolated (Mooij and Van Tongeren, 1990) water temperatures of sampling points in the lake.

To calibrate growth curves of each of the three lakes, we used published length data of the year classes (Backx, 1989). We varied the growth rate between 0.7 and 1 of the maximal growth.

To calibrate the mortality we used 0+ densities as input and used CRS to fit the simulated biomass with the biomass and length-frequency distribution in the field. We fitted the three mortality parameters ($m_{f\,young}$, $m_{f\,adult}$ and h_f).

We calibrated the mortality caused by seine fishery (= catch effort (N), for selectivity S = 1) to fit the simulated change in biomass with the observed change by CRS and using the least sum of squares to establish the best fit. It was assumed that the estimated growth and natural mortality were not affected by the seine fishery.

Results

The fish community in Lake Veluwe is dominated by bream, ruffe, roach and perch. Eighteen other fish species were found, but their contribution to the total fish biomass was limited. The biomass of the bream population decreased from ca. 120 kg ha^{-1} in 1992 to ca. 20 kg ha^{-1} in 1999 (Fig. 9.2).

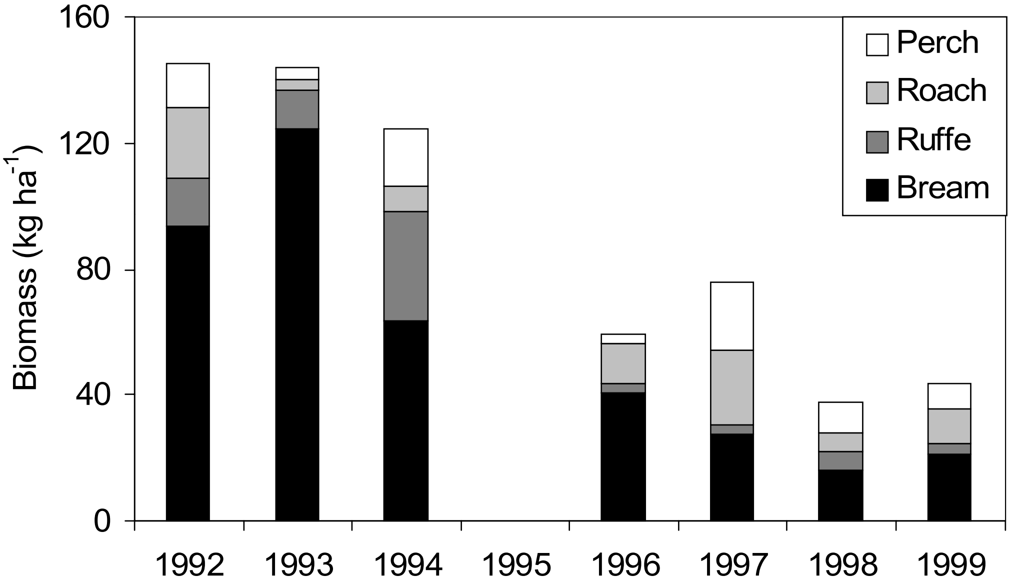

Fig. 9.2 *Biomass and species composition of dominant fish in Lake Veluwe.*

We only modeled the bream population, as bream is the dominant species in the fish community. Moreover, this species showed the major decrease in the total biomass and was the main target of the commercial fishery. In 1992 and 1993, the bream population was dominated in biomass by bream > 25 cm. After 1993, bream > 15 cm quite rapidly disappeared out of the population and the total biomass decreased (Fig. 9.3). The strong year class of 1995 did not get the opportunity to build up a large biomass.

Modeling the bream population

The simulation of the bream population expressed as the size distribution in October 1992 and 1993 was not significantly ($p > 0.05$, Kolmogorov-Smirnov test) different from the ones found in 1992 and 1993 (Fig. 9.4). Growth was calibrated as 0.88 of the maximal growth, mortality for adults was estimated to 0.13 per year, for juveniles mortality was 0.65 up to a length of 17 cm. As recruitment in the model started in the first week of September, the juvenile mortality did not include the period from birth to September. The period after 1993 was simulated as two different scenarios: excluding fishery and including fishery.

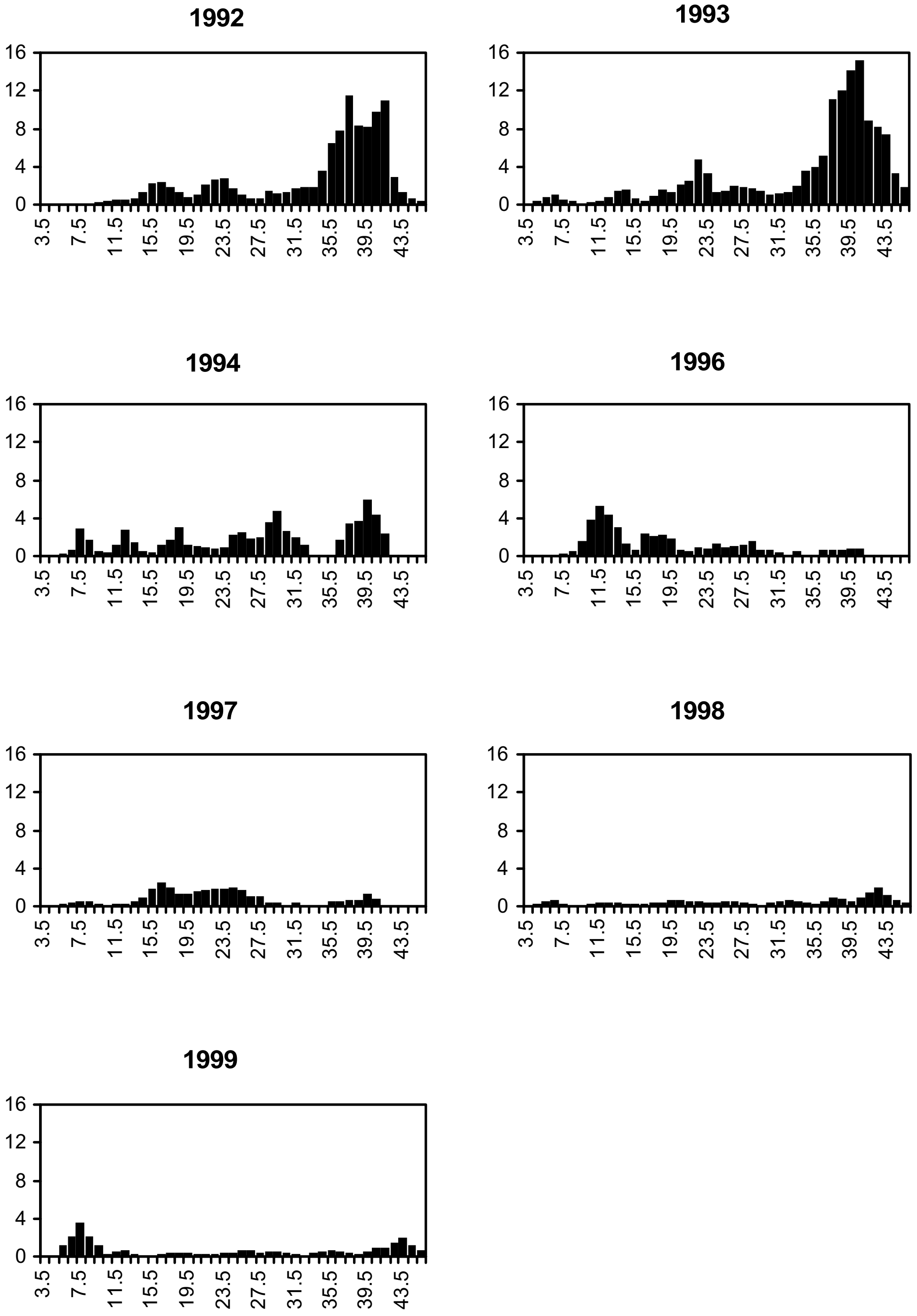

Fig. 9.3 *Measured biomass of bream plotted for 1 cm length-classes for 7 successive years, 1995 excluded.*

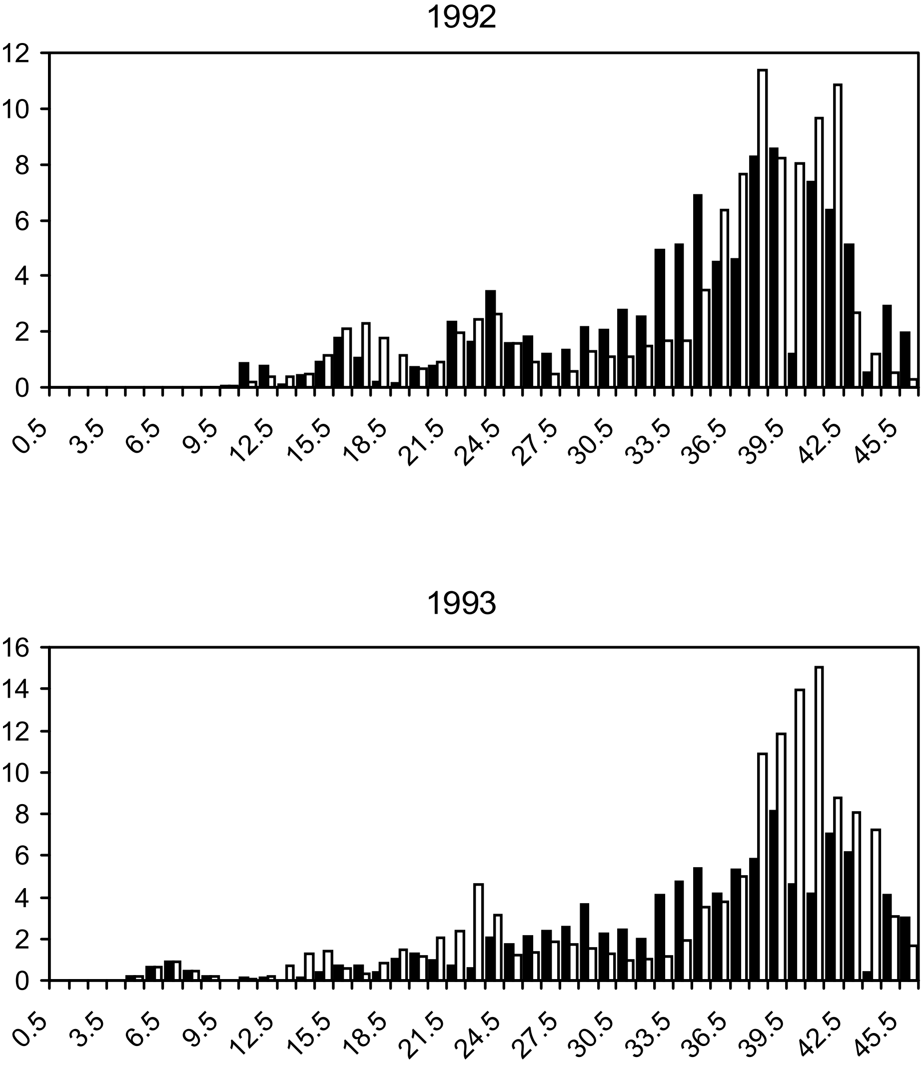

Fig. 9.4 *Simulated and measured biomass of 1 cm length-classes bream in 1992 and 1993. Open bars represent field data; black bars model results.*

Modeling the bream population without seine fishery

Simulating the development of the bream population without the fishery, the model results showed a large deviation from the field data the years after 1993 (Fig. 9.5). The model results show that large bream kept dominating the biomass of the population. The simulated biomass varied between 120-130 kg ha^{-1} between 1994 and 1999, but decreased to ca. 20 kg ha^{-1} in the lake. In comparison to the simulated population bream > 15 cm disappeared quickly out of the population and showed a higher mortality than the ones measured before 1994.

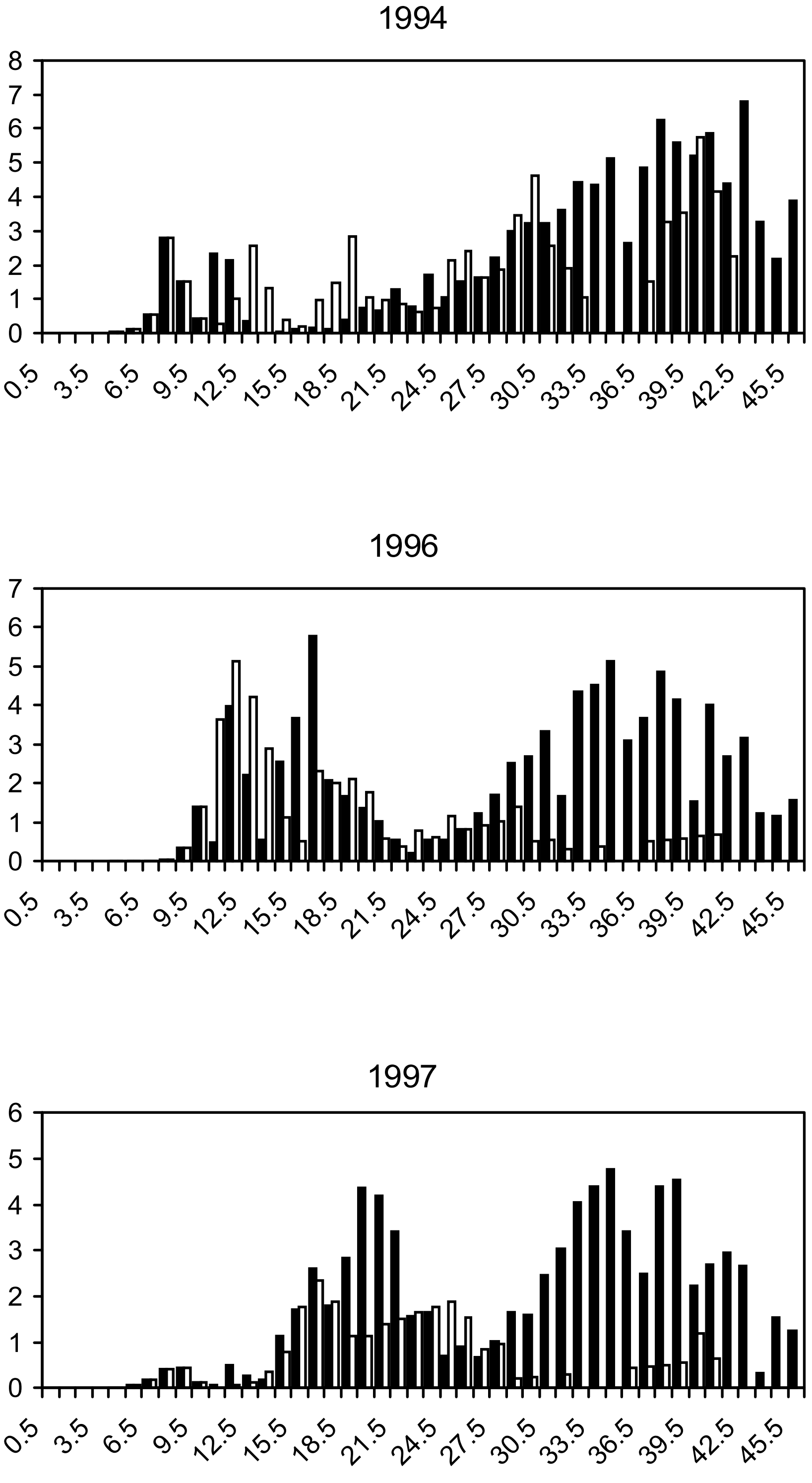

Fig. 9.5 *(continued on next page)*

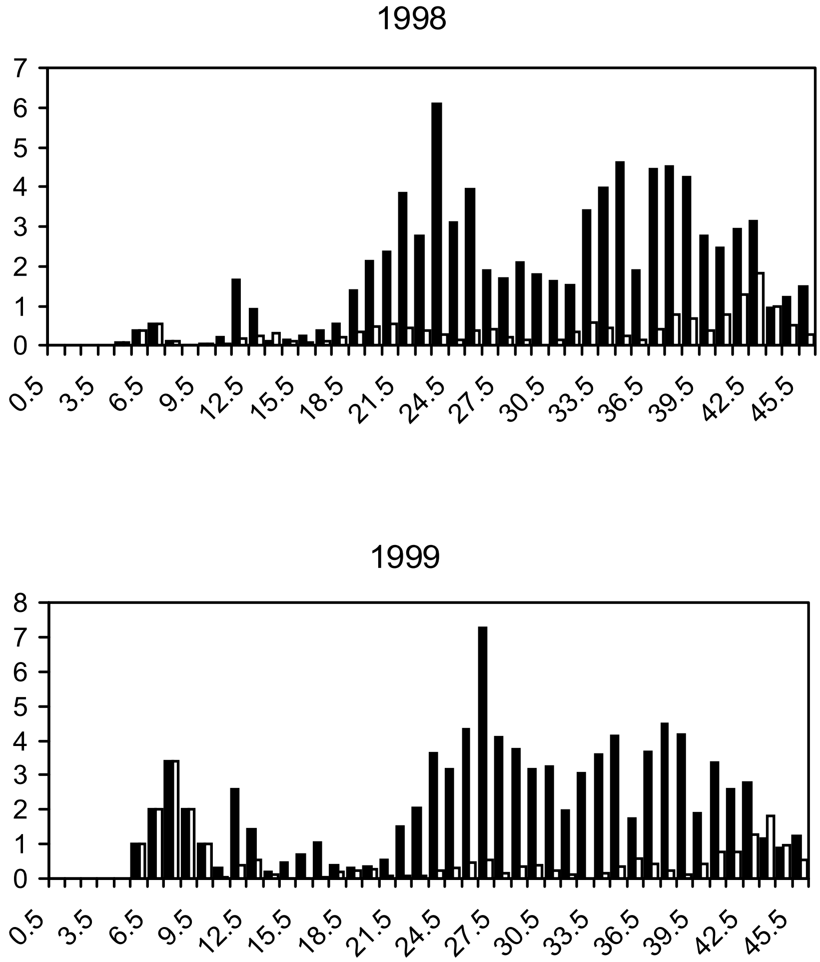

***Fig. 9.5** Simulated and measured biomass of 1 cm length-classes bream in 1994 - 1999 in the absence of fishery. Open bars represent field data; black bars model results.*

Modeling the bream population with seine fishery

In the other scenario we modeled the development of the bream population subjected to seine fishery. The bream population was simulated after calibration of the fishery mortality. The simulation of the bream population expressed as the size distribution in October 1994 - 1999 was not significantly ($p > 0.05$, Kolmogorov-Smirnov test) different from the field population in 1994, 1996 and 1997, but was significantly ($p < 0.05$, Kolmogorov-Smirnov test) different in 1998 and 1999 (Fig. 9.6).

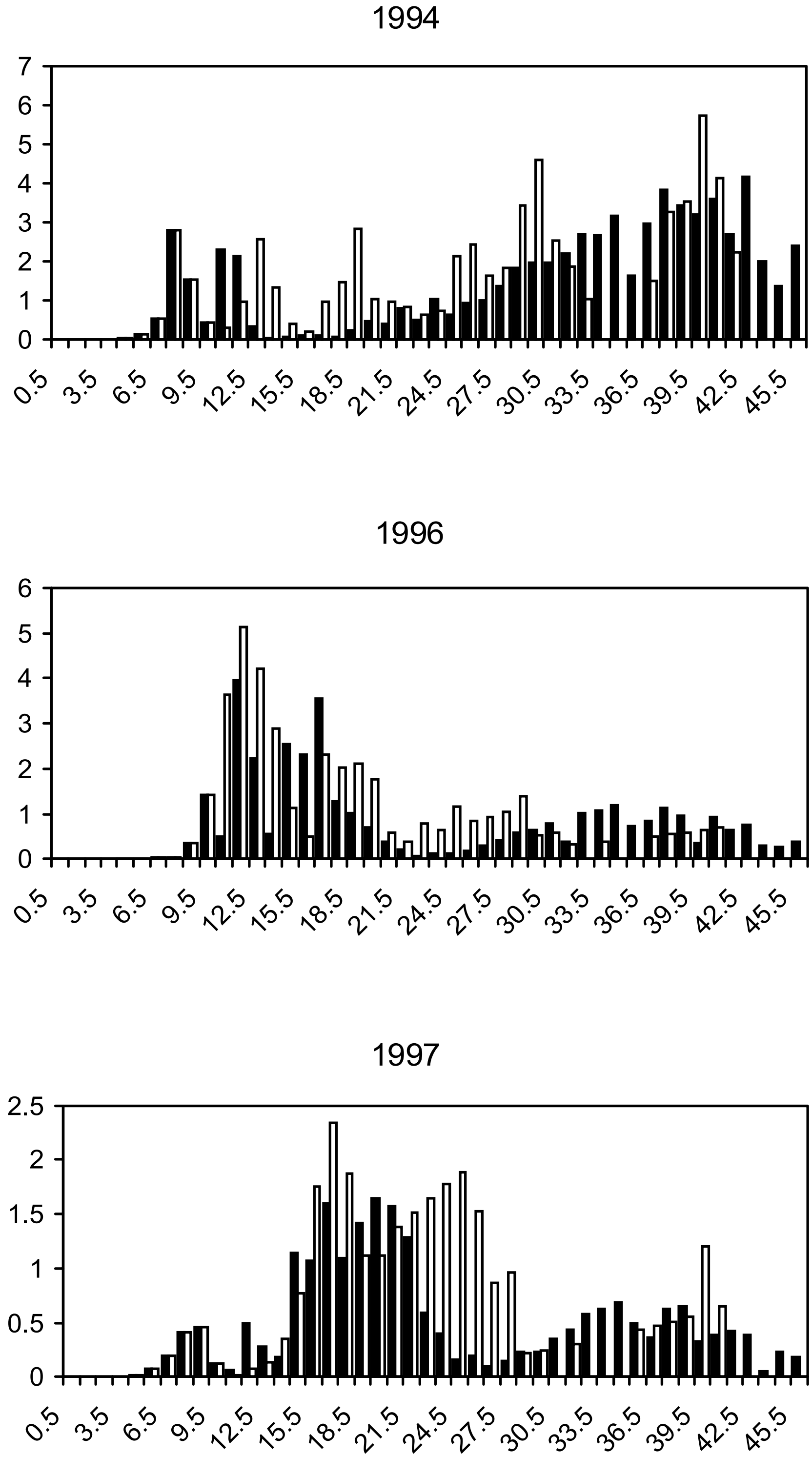

Fig. 9.6 *(continued on next page)*

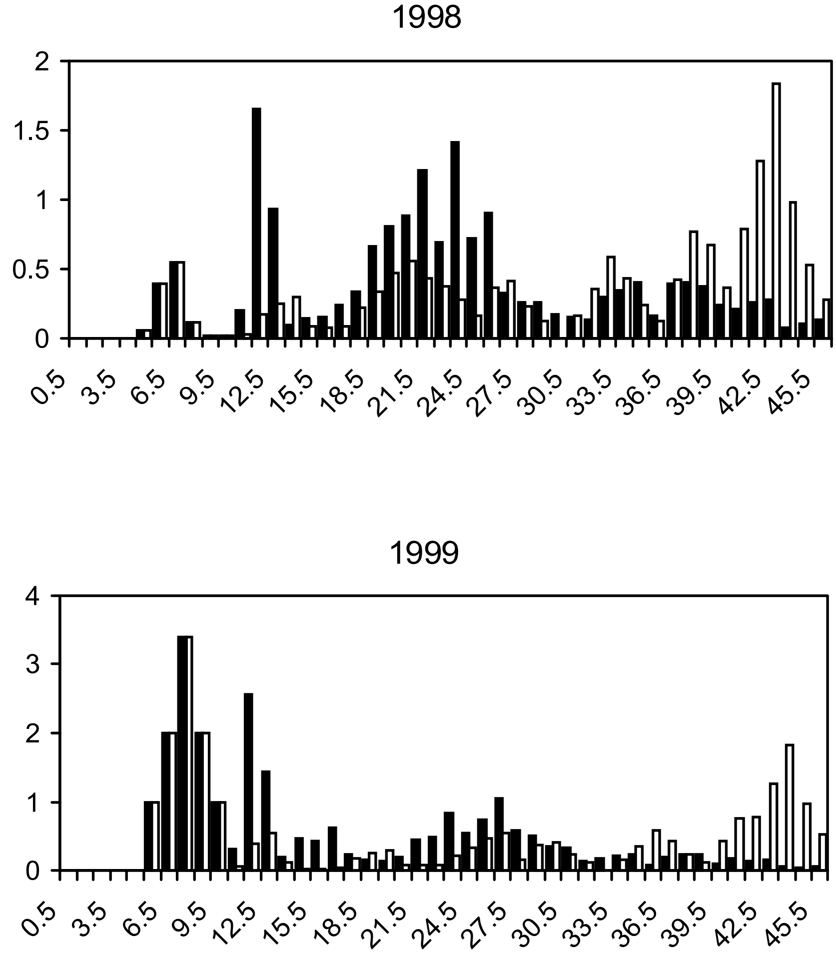

Fig. 9.6 *Simulated and measured biomass of 1 cm length-classes bream in 1994 - 1999 in the presence of fishery. Open bars represent field data; black bars model results.*

The simulated catches of bream showed a good correspondence with the actual realized catches (Fig. 9.7)

Discussion

The fish community in Lake Veluwe changed in composition and biomass simultaneously with the development of the *Chara* beds (Meijer, 2000). The number of fish species increased considerably and the total biomass decreased to ca. 35% of the original biomass. The first hypothesis about this change stated that the expansion of the *Chara* beds diminished the total habitat area for the bream population in particular, and benthivorous fish in general. The *Chara* beds cover the bottom completely (Van den Berg, 1999) and make it impossible for large fishes as bream to forage in this habitat. This would be a strong hypothesis if we were sure that there were no other sources of mortality. However, we learnt from a commercial fisherman that he started fishing bream in the winter of 1993 and continued until 1997. There was a good market for this fish and his income had gradually decreased the last decade because of decreasing eel. Looking into his financial administration, we could reconstruct the amount of bream he caught in Lake Veluwe.

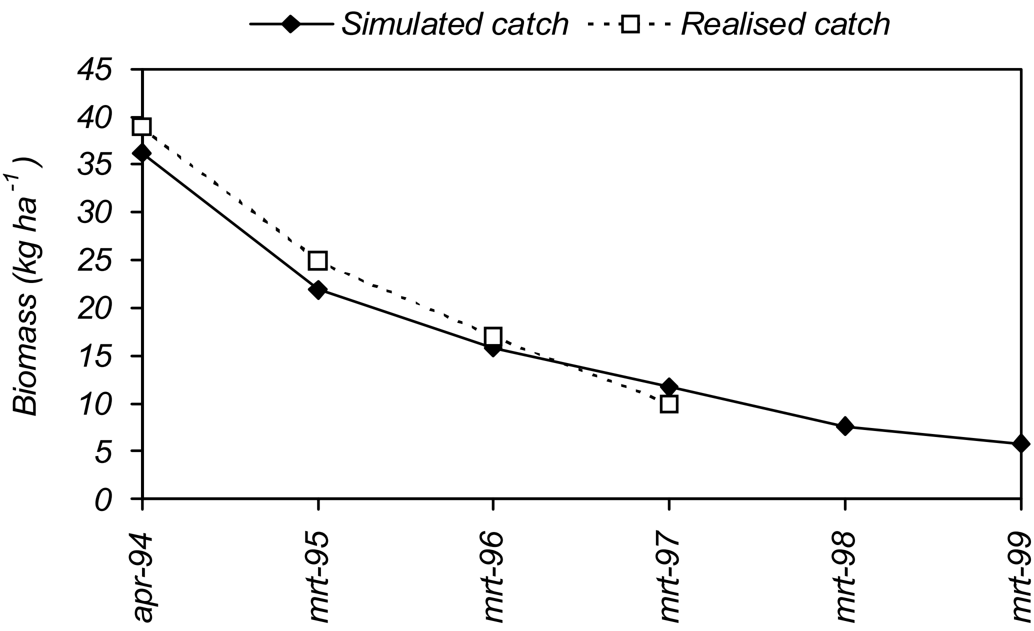

Fig. 9.7 *Simulated and realized catches of bream*

We developed a fish model describing growth, mortality and recruitment as main processes to build up the population. To simulate the development up to 1992 and 1993 we estimated the natural mortality with data about recruitment and growth. It was quite clear that the mortality needed to reduce the bream population was much higher than the natural mortality and that the surplus corresponded well with the mortality caused by fishery. The fit of the length-frequency distribution in the field and model was quite good in the period 1992-1997. In 1998 and 1999 there was a significant deviation between field and model. The fisherman explained that the density in the last two years was too low to make the business pay and therefore the bream population had the opportunity to increase again.

The strong expansion of *Chara* beds occurred after the removal of the bream population (Meijer et al., submitted). In the years after the bream fishery the density of zebra mussels increased from only a few to ca. 400 m^{-2} as an average for the open water (Meijer et al., submitted). Simultaneously the transparency in the area outside the *Chara* beds strongly increased because of decreasing chlorophyll-a levels, and the *Chara* beds expanded from ca.20% coverage to more than 60% (Meijer et al., submitted). Meijer et al. (submitted) discussed the mechanism of this chain of events. It was most likely that the rapid development of the zebra mussels was responsible for the clearing of the open water. According to Noordhuis et al. (1992) a density of 400 mussels m^{-2} would be able to filter a water column of 1.5 m (depth of the open water area) in ca. 3 days, which is likely to affect the algal biomass. Clear impacts on density and composition of the phytoplankton were recently demonstrated by Bastviken et al. (1998) and Horgan & Mills (1997).

The rapid expansion of the *Chara* beds was stimulated by the clearing of the open water, but probably at the same time by the decreased foraging activities of bream which used to disturb the bottom sediments continuously. Ten Winkel & Meulemans (1984) demonstrated that *Chara* beds rapidly developed in areas in Lake Maarseveen, which were excluded from bream. The negative impact of bream on zebra mussels may be related to active foraging in the bottom sediments. Martel et al. (1993; 1994) and Bially & MacIsaac (2000) showed that disturbing the sediment has a negative impact on the settlement of zebra mussels. As a consequence bream may prevent the settlement of zebra mussels.

Of course, we cannot be sure what would have happened if there was no fishery at all, as we know that the *Chara* beds already started to develop at the end of the 1980's before the fishery started. After many years of effort to reduce the nutrient load the transparency improved in the second half of the 1980's from about 20-30 cm to 40-50 cm (Meijer et al., submitted) and caused bottom transparency in some shallow parts. In these parts *Chara* started to develop. As bream usually avoid shallow areas, two main conditions for *Chara* were fulfilled at that time: light and little or no disturbance. From this point there was a very slow peripheral development of the *Chara* up to 20% coverage of the lake (Van den Berg, 1999). In this area there was a high transparency, whereas in the open water area transparency was low. In the beginning of the 1990's there was a general feeling that the development of the *Chara* beds would stop as the deeper parts were too turbid to allow plant growth. Although there was a plea to remove the bream population it was not done from a management point-of-view, as the lake manager was not fully confident. However, the commercial fisherman did the job because it was commercially interesting, but without informing us.

At the moment a large area of Lake Veluwe is covered with *Chara* beds and the total foraging area has considerably decreased, therefore the carrying capacity for bream has decreased as well. If the fishery would be terminated the bream population would increase again, but will not attain its original density. The habitat has changed and the stability of this habitat will largely depend on the interaction between bream, *Chara*, zebra mussels and nutrient loads.

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Summary

Individual-based models (IBM's) have become a popular tool in ecology during the last ten years. These models have individual animals or plants as basic units and generate patterns of distribution or abundance resulting from the interaction between individuals. This approach has important advantages. To mention few:

- The biological principle that each individual is different can be incorporated, resulting in a higher realism.
- Parameters needed in the models as well as the predicted variables are typically of the type measured by experimental biologists.
- Model behavior is often rather robust to variation in formulation of the processes.

For these reasons the expectations were high for the contribution of these models to ecological theory. However, a recently published review of 50 individual-based animal population models concludes that the results of the first ten years have been disappointing. The main reason is that most individual-based models are very complex and special techniques needed to cope with this complexity have only occasionally been applied. In this thesis, two individual-based models are presented analyzed with a suite of special and often novel techniques. The result is an enhanced understanding of some mechanisms that may regulate the dynamics of fish communities and aquatic macrophytes, but also a strategy to deal with complexity of this kind of models which has evolved along the way.

The first chapter introduces this strategy to cope with model complexity. This chapter first reviews the pros and cons of large complex models versus the simple abstract models, which have contributed so much to the development of ecological theory. Subsequently, a strategy to improve our understanding of the way in which complex models generate their results is presented. The strategy consists of three phases: ‘scrutinizing’, ‘simplifying’ and ‘synthesizing’. The first step is a thorough analysis of the model behavior with respect to a selected set of parameters (‘scrutinizing’). Secondly, similar analyses are done with several simplified versions of the model (‘simplifying’). In this step, relationships between state variables or species that may potentially cause incomprehensible behavior, are replaced by fixed values or highly simplified relations. The last step is to explain the differences between the full and the simplified versions and to discuss the results in the light of the existing ecological theory, field patterns or other models (‘synthesizing’). It is argued that this way of combining analyses of simple and more elaborate models is a powerful way to gain understanding of complex systems.

The second chapter describes a simple technique to handle a practical problem with individual-based models. The typically large number of individuals that is needed in such models, requires impractically large computation times. The solution of simply reduce the number of individuals in the model, can lead to loss of variation, irregular dynamics, and large sensitivity to the value of random generator seeds. As a solution to these problems, this chapter proposes to add an extra variable feature to each model individual, namely the number of real individuals it actually represents. This approach, using representative individuals, which were called ‘super-individuals’, is used throughout the thesis. An important advantage of this approach is that it adds flexibility to the model, allowing the

modeler to zoom from a real individual-by-individual model to a cohort representation or ultimately an all-animals-are-equal view without changing the model formulation. This way, the super-individual concept offers easy possibilities to simplify the model in order to verify whether individual variability is an essential ingredient for the observed model behavior.

In the next section of the thesis (Chapters 3-6), models of aquatic vegetation are described and analyzed. In Chapter 3, the individual-based model ‘Charisma’ is presented. In this model, the vegetation can be modeled in an individual based, spatially explicit way. Also, the growth of several competing species can be studied, an issue that had hardly been addressed so far. The model behavior easily becomes rather complex and puzzling if we study more than one species. This probably reflects real complexity in nature, but poses a challenge for calibrating and understanding the model. To control this complexity, feedback loops and processes were eliminated to trace the causes of the complex behavior of the model. The resulting ‘realistic yet transparent’ model appeared useful in many aspects for bridging the existing gap between theory and reality. As an example, an analysis of competition between the charophyte *Chara aspera* Deth. ex Willd. and pondweed *Potamogeton pectinatus* L. is presented. The model suggests that alternative equilibria may arise as a result of two positive feedbacks: the enhancement of transparency by macrophytes and a feedback caused by bicarbonate competition. Monte-Carlo uncertainty analysis revealed a particular phenomenon related to the existence of such multiple attractors. If the variation of the parameters is large enough to cause a switch between alternative equilibria, a variation of ±10% in all parameters may lead to a variation of predicted summer biomass as large as ±90%. Such amplification of sensitivity is restricted to certain regions of the parameter space. Corollaries in terms of real macrophyte dynamics are that under some conditions, small environmental variation may blow up to large changes in vegetation abundance, and that sensitivity to disturbances may vary strongly depending on the conditions.

In Chapter 4 the model Charisma is applied to analyze the conditions for occurrence of alternative stable states in shallow lakes dominated by charophytes. Submerged plant dominance with clear water versus a turbid state with few submerged plants has been hypothesized to represent alternative stable states in eutrophic shallow lakes. However, so far this qualitative prediction had been derived largely from highly simplified minimal models, which leave out important aspects such as seasonality and spatial heterogeneity. The more realistic model Charisma does confirm prediction of alternative stable states, but shows that the range of conditions over which alternative stable states exist, is highly sensitive to the strength of the assumed effect of plants on turbidity and to the maximum growth rate of the plants. In line with earlier theory, shallow lakes with a ‘flat’ depth profile are predicted to have the strongest hysteresis. In lakes with a depth gradient, the response to changes in turbidity is predicted to depend strongly on horizontal mixing of the water between vegetation stands and the open water. In such lakes hysteresis disappears with strong horizontal mixing of water. By contrast, in case of little mixing, local alternative stable states are predicted to occur. Further analysis indicates that from an evolutionary perspective there is an optimum biomass allocation strategy with respect to investment in overwintering structures. Too little investment reduces chances to regain dominance in the subsequent year, whereas too much investment in dormant overwintering structures such as seeds and tubers reduces photosynthesis. The predicted optimal investment is close to what is observed for Sago pondweed and stoneworts in Lake Veluwe. Analyses also suggests that a spring clear-water phase can have a considerable boosting effect on annual plant growth, especially if it occurs at the end of May or in June as is indeed the case in many lakes.

Chapter 5 addresses a socio-economical dimension related to the growth of aquatic vegetation. Often, dense beds of submerged macrophytes may cause a nuisance to boaters and swimmers, and obstruct water flow. Management of aquatic vegetation is, therefore, often aimed at reducing the biomass of the plants. If the nuisance is caused by exotic invasive species, there usually is no controversy with nature conservation aims. In shallow lakes, however, the interests of recreational users may conflict with nature conservation because the promotion of indigenous submerged vegetation is considered an important tool for lake restoration. Aiming at intermediate vegetation biomass seems a good solution for this controversy at first sight. However, it is argued that such a compromise is not always the best policy from a welfare economic point-of-view. In this chapter a simple graphical model is presented, showing that the overall benefit for all ecosystem users may be minimal at the intermediate vegetation biomass. It is concluded that in such cases it will be better to realize a management strategy aimed at keeping some lakes (or parts of lakes) free of aquatic plants, whereas allowing others to be densely vegetated.

Chapter 6 elaborates on this problem. In the previous chapter, it was concluded that in some cases a management strategy aimed at an intermediate vegetation biomass can be optimal from an economic point-of-view. In Chapter 6, it is shown that such a compromise-oriented strategy can be unfeasible for ecological reasons. This result is obtained from two very different models: a minimal logistic model of plant growth, which is easy to understand, and the relatively complex and realistic simulation model Charisma. Both models predict that if the ecosystem has no alternative stable states it is possible to set vegetation to any desired sustainable level if an appropriate harvesting strategy is chosen, although the costs can be quite high because the yield is maximal precisely at intermediate vegetation biomass. By contrast, if the ecosystem has alternative stable states, harvesting is risky as the vegetation may collapse entirely if it is reduced below a certain, in practice unknown, threshold level. Also, even moderate harvesting tends to reduce the resilience, making the ecosystem more vulnerable to collapse into an unvegetated turbid state in response to adverse conditions such as unfavorable weather conditions or bird grazing.

The last part of the thesis deals with the modeling of multi-species fish populations. The majority of existing individual-based models address fish dynamics, which is not surprising in view of the importance of variation in size of the individuals for several processes, including predation and cannibalism in fish. However, almost all of these models focus on single species and neglect the interactions between different species which are highly important in most fish communities.

In Chapter 7 the individual-based model Piscator, which describes a multi-species fish community, is presented, and several techniques to deal with the inherent complexity of such a model are demonstrated. A novel procedure for calibration and analysis is introduced in which the complexity of the model is increased step-by-step. Also, a special Monte-Carlo sensitivity analysis is used to identify clusters of parameters that have roughly the same effects on the model results. As an example the model was used to analyze the effect of different fishing scenario's on the bream population of the Frisian Lakes (The Netherlands). Our analysis suggests among other things that warm summers and piscivory may have very dominant effects on fish community dynamics. Indeed, our results indicate that effects of profound changes in fishery can only be understood if one takes climatic variability and community feedback mechanisms such as piscivory and competition into account. We also use this relatively elaborate and realistic model to demonstrate that interactions within fish communities may plausibly lead to multi-year cycles and chaotic dynamics, phenomena that are usually predicted only from highly simplified abstract models.

In Chapter 8, Piscator is used to analyze the factors determining the dynamics of bream populations in three lakes: the Frisian lakes (10 000 ha), Lake Veluwe (3400 ha) and Lake Volkerak (4500 ha). Apart from direct effects of fishery on the bream population, indirect effects of fishery on transparency, chlorophyll-a, vegetation and macrofauna were analyzed. In Lake Veluwe the bream population was reduced from ca. 100 to 20 kg ha^{-1} after five years of fishing. The mortality caused by the fishery was estimated at 38% of bream > 15 cm on top of the 13% natural mortality for bream > 17 cm. The decline of the bream population was followed by a clearing of the lake and an accelerated expansion of the *Chara*-beds and an explosion of zebra mussels (*Dreissena polymorpha*). The newly created Lake Volkerak showed the opposite development to what happened in Lake Veluwe. The unexploited bream population started to develop in 1988 and reached a biomass of ca. 140 kg ha^{-1} in 1998. The transparency in the lake decreased from a maximum of 3 m to ca. 1 m. In the same period the chlorophyll-a level increased from 5 μg l^{-1} to 45 μg l^{-1}. Vegetation coverage developed in the first years to 20% of the total area, but decreased to 10% with increasing turbidity. In the Frisian lakes, seine fishery did not seem to affect the bream population despite high catches of 40-50 kg ha^{-1}. The calculated natural annual mortality of fish larger than 15 cm was ca. 15%, whereas the fishery mortality added 26% of the mean biomass. The high loss was compensated by good recruitment and higher growth rates due to the higher temperatures in the period of fishing. There was only a slight decrease of chlorophyll-a and a slight increase of transparency.

In Chapter 9, the analysis of the development of the bream population in Lake Veluwe is extended further. The natural mortality was calculated using data on growth, recruitment and size distribution. The model predicts that without fishery the biomass of the bream population would hardly change and that the fishery could indeed explain the change in the biomass and size composition. It is argued that the rapid expansion of the *Chara* beds and the coinciding decrease in turbidity which were previously ascribed merely to decrease in nutrient loading would have been unlikely without the fishery.

Samenvatting

Individu-gebaseerde modellen zijn in tien jaar tijd populair geworden in de theoretische ecologie. Deze modellen zijn gebaseerd op een wiskundige beschrijving van de individuen van planten of dieren. De benadering heeft belangrijke voordelen, zoals:

- Het biologische relevante principe dat elk individu verschillend is, kan in het model worden ingebouwd, waardoor het beter de realiteit benadert.
- Zowel de benodigde parameters als de modeluitkomsten zijn vaak het soort gegevens dat door experimentele biologen wordt verzameld.
- Het gedrag van individu-gebaseerde modellen blijft vaak ongeveer hetzelfde als de formulering van de processen wordt veranderd.

Om deze redenen waren eind jaren '80, toen deze modellen voor het eerst in de ecologie op grotere schaal werden toegepast, de verwachtingen hooggespannen. Een recent literatuuroverzicht van 50 individu-gebaseerde modellen stelt echter dat de bijdrage van dit soort modellen aan de ecologische theorievorming tot nu toe teleurstellend was. Dit is volgens dit artikel te wijten aan de doorgaans grote complexiteit van deze modellen, en aan het feit dat hier bij de analyse onvoldoende rekening mee is gehouden.

Een centraal thema van dit proefschrift is het ontwikkelen en gebruiken van speciale modelleertechnieken om beter met de complexiteit van de modellen om te gaan. Deze technieken worden toegepast in een waterplantenmodel en een model dat vispopulaties beschrijft.

Het eerste hoofdstuk introduceert de modelleerstrategie die tijdens het onderzoek ontwikkeld is. Het hoofdstuk begint met een kort overzicht van de voor- en nadelen van complexe modellen vergeleken met simpele abstracte modellen, het soort modellen dat van oudsher veel heeft bijgedragen aan de ecologische theorievorming. Daarna volgt de presentatie van een strategie die het belang van grote complexe modellen zou kunnen vergroten. Deze strategie bestaat uit drie fasen: onderzoeken (‘*scrutinze*’), vereenvoudigen (‘*simplify*’) en interpreteren (‘*synthesize*’). De eerste stap is een diepgaande analyse van hoe het modelgedrag beïnvloed wordt door een geselecteerde verzameling parameters (‘*scrutinize*’). Daarna wordt dezelfde analyse herhaald met verschillende vereenvoudigde versies van het model (‘*simplify*’). Tenslotte worden in de laatste stap (‘*synthesize*’) de verschillen tussen de volledige en de vereenvoudigde versies verklaard en bediscussieerd in het licht van de bestaande ecologische theorie, veldpatronen en andere modellen. In het hoofdstuk wordt beargumenteerd dat het combineren van analyses van eenvoudige en realistischere modellen een goede methode is om meer inzicht te krijgen in complexe systemen.

Hoofdstuk 2 behandelt een ander probleem dat samenhangt met individu-gebaseerde modellen. Het aantal individuen dat in zulke modellen beschreven wordt, kan erg groot zijn, waardoor de berekeningen te langzaam gaan. De benadering om eenvoudigweg minder individuen te beschrijven, kan leiden tot een minder realistische beschrijving doordat door toevalsprocessen (zoals individuele sterfte) de populatiedynamiek onrealistisch en onregelmatig kan worden. Als oplossing voor deze problemen wordt in dit hoofdstuk het ‘super-individu’ geïntroduceerd, een concept dat in het verdere onderzoek is toegepast. Aan de eigenschappen van elk gemodelleerd individu wordt een extra eigenschap toegevoegd, namelijk het aantal echte individuen dat gerepresenteerd wordt. Een belangrijk voordeel van deze benadering is dat het model er flexibel door wordt. Zonder grote ingrepen in modelformulering, kan het aantal individuen worden gevarieerd van een echt individu-gebaseerde benadering tot een jaarklassenbenadering en uiteindelijk zelfs tot een benadering waarbij alle individuen gelijk zijn. Hierdoor biedt deze techniek ook de mogelijkheid om na te gaan of individuele variatie essentieel is voor het modelgedrag.

In het volgende deel van het proefschrift (hoofdstuk 3 - 6) worden modellen van waterplanten beschreven en geanalyseerd. In hoofdstuk 3 wordt het individu-gebaseerde model ‘Charisma’ gepresenteerd. In dit model kunnen optioneel ruimtelijke processen worden opgenomen, door de planten op een denkbeeldig raster (= grid) te modelleren. Bovendien kan in dit model de concurrentie tussen verschillende soorten worden bestudeerd, een onderwerp dat nog nauwelijks aandacht heeft gehad bij eerder beschreven studies van waterplantenmodellen. Als er meer dan één soort wordt bestudeerd, kan het modelgedrag snel moeilijk te begrijpen worden. Dit is waarschijnlijk een afspiegeling van werkelijke complexiteit, maar het kan daardoor wel moeilijk zijn om het model te kalibreren en het gedrag helemaal te begrijpen. Om die complexiteit het hoofd te bieden zijn verschillende versies van het model bestudeerd, waarbij terugkoppelingen in het model zijn weggelaten of belangrijke processen buiten beschouwing zijn gelaten. Op deze wijze kunnen de oorzaken van het modelgedrag goed getraceerd worden. Als voorbeeld wordt in het hoofdstuk een analyse van de concurrentie tussen de kranswiersoort *Chara aspera* Deth. ex Willd. en schedefonteinkruid (*Potamogeton pectinatus* L.) gepresenteerd. De modelanalyses geven aan dat alternatieve evenwichten kunnen ontstaan door twee positieve terugkoppelingen: de verbetering van de helderheid door waterplanten, en een terugkoppeling die veroorzaakt wordt door de concurrentie om bicarbonaat. Een Monte-Carlo onzekerheidsanalyse toonde dat alternatieve evenwichten ook grote gevolgen kunnen hebben voor de gevoeligheid van het model voor onzekerheden in de parameterwaarden. Een relatief kleine onzekerheid van ±10% in alle modelparameters kan soms leiden tot een variatie van de voorspelde zomerbiomassa van maar liefst ±90%. Zo'n versterking van de gevoeligheid van het model treedt echter niet altijd op; het is beperkt tot bepaalde parametercombinaties. De consequentie voor het werkelijke ecosysteem kan zijn dat onder bepaalde omstandigheden, kleine schommelingen in milieuomstandigheden kunnen worden opgeblazen tot grote verschillen in vegetatiebiomassa, en dat deze gevoeligheid sterk kan afhangen van de omstandigheden.

In hoofdstuk 4 wordt het model Charisma toegepast om de voorwaarden voor het ontstaan van alternatieve evenwichten in ondiepe meren te analyseren. Aan de hand van sterk versimpelde minimodellen is in de literatuur voorspeld dat er in ondiepe meren twee alternatieve evenwichten kunnen voorkomen: een troebel evenwicht met nauwelijks waterplanten en een helder evenwicht, waarbij waterplanten domineren. Dit fenomeen is met Charisma onderzocht, waarbij met het model de omstandigheden van het Veluwemeer zijn nagebootst waarbij alleen de kranswiersoort *Chara aspera* is meegenomen. Deze soort is daar recentelijk dominant geworden. Het model voorspelt inderdaad alternatieve evenwichten, maar laat zien dat de kans hierop sterk bepaald wordt door de grootte van het positieve effect van vegetatie op de helderheid en door de maximale groeisnelheid van de planten. Overeenkomstig met bestaande theorie, voorspelt Charisma verder dat ondiepe meren met een ‘plat’ diepteprofiel de sterkste hysterese hebben, en daarmee de grootste kans op alternatieve evenwichten. In meren met een geleidelijke dieptegradiënt, is de respons op veranderingen van de troebelheid sterk afhankelijk van de menging van het water tussen vegetatie en het open water. Bij een sterke horizontale menging verdwijnt de hysterese vrijwel geheel; bij weinig menging kunnen, volgens de modelberekeningen, ook lokaal alternatieve evenwichten bestaan. Verdere modelanalyse laat zien dat er vanuit een evolutionair oogpunt een optimale biomassa is die in voortplantingsorganen wordt gestoken. Te weinig investering verkleint de kans voor de planten om het volgend jaar weer dominant te worden, maar te veel energie in voortplantingsorganen benadeelt de fotosynthese. De werkelijke gemeten investering in overwinteringsorganen van schedefonteinkruid en *Chara aspera* komt verrassend goed overeen met het voorspelde optimum. Het model suggereert verder dat een korte periode met helder water gunstig is voor de overleving van de waterplanten. De optimale timing van de heldere periode voor stimulering van waterplanten is eind mei of in juni, hetgeen overeenkomt met de timing van de werkelijke helderwaterpiek in het voorjaar in veel meren.

In hoofdstuk 5 wordt een socio-economische dimensie van waterplantenontwikkeling geanalyseerd. Dichte waterplantenvelden kunnen recreanten hinderen en de waterstroming belemmeren. Daarom is het beheer van waterplanten in veel gevallen gericht op bestrijding. Als de overlast veroorzaakt wordt door exotische plaagsoorten, zal er doorgaans geen controverse zijn met natuurbeschermingsdoelen. In ondiepe meren echter kunnen de belangen van recreanten vaak op gespannen voet staan met natuurbescherming, omdat het bevorderen van inheemse waterplanten een belangrijk middel is bij het herstel van meren. Op het eerste gezicht kan deze controverse opgelost worden door het waterbeheer te richten op minder dichte waterplantenvelden. Het gepresenteerde grafische model laat echter zien dat zo'n compromis niet altijd de optimale economische oplossing is. Het model geeft aan dat de waarde van waterplanten voor de ecosysteemgebruikers bij zo'n middelgrote biomassa minimaal kan zijn. Geconcludeerd wordt dat het in die gevallen beter is om bepaalde delen van een meer in te richten voor recreatie en andere delen dicht begroeid te laten. Ook kan het dan nuttig zijn om het waterplantenbeheer op een andere soortensamenstelling te richten.

Hoofdstuk 6 gaat verder door op dit probleem. Op basis van het grafische model uit het voorgaande hoofdstuk kan worden geconcludeerd dat het soms in economisch opzicht gunstig is om het beheer wel te richten op een middelgrote vegetatiebiomassa. In dit hoofdstuk wordt echter gesuggereerd dat zo'n strategie in ecologisch opzicht niet altijd haalbaar is. Dit wordt gedemonstreerd door twee heel verschillende modellen te analyseren: een eenvoudig model dat eenvoudig te begrijpen is en het relatief complexe model Charisma. Als het ecosysteem geen alternatieve evenwichten heeft, kan theoretisch elke vegetatiebiomassa worden gerealiseerd. Bij een middelgrote biomassa zal de oogst wel maximaal zijn, en daardoor zullen ook de maaikosten groot zijn. Als het ecosysteem alternatieve evenwichten heeft, kan maaien riskant worden, omdat de vegetatie volledig kan verdwijnen onder een bepaalde in de praktijk onbekende biomassa. Ook kan zelfs een beetje maaien een negatief effect hebben op de veerkracht van de heldere fase met waterplanten, zodat het ecosysteem gevoeliger wordt voor andere verstoringen, zoals slecht weer of vogelvraat.

De laatste drie hoofdstukken gaan over het modelleren van vispopulaties met interacterende soorten. Het merendeel van de tot nu toe ontwikkelde individu-gebaseerde modellen heeft betrekking op vis. Dit is geen toeval, omdat in het bijzonder voor vissen de variatie in grootte van de individuen essentieel is, bijvoorbeeld voor predatie en kannibalisme. De meeste van de tot nu toe gepubliceerde modellen beschrijven echter een situatie met slechts één soort en laten de belangrijke interacties tussen soorten dus geheel buiten beschouwing.

In hoofdstuk 7 wordt het individu-gebaseerde model Piscator gepresenteerd. Dit model kan de ontwikkeling van visgemeenschappen met vele interacterende soorten beschrijven. De inherente complexiteit van visgemeenschappen en het grote aantal parameters van het model maakt het niet eenvoudig om het model te kalibreren. Een nieuwe kalibratie- en analysestrategie waarbij de complexiteit van het model stap voor stap wordt vergroot, wordt gepresenteerd. Verder wordt een speciale Monte-Carlo gevoeligheidsanalyse gebruikt om clusters van parameters te identificeren die een gelijksoortig effect op de modeluitkomsten hebben. Als voorbeeld wordt een analyse met het model een visserij-experiment in de Friese meren gegeven. De analyses geven onder meer aan dat warme zomers en piscivorie een erg dominante rol kunnen spelen in het reguleren van dynamiek in de gemeenschap. Verder blijkt dat effecten van een verandering in de visserij alleen kunnen worden begrepen als we weerseffecten en ecologische terugkoppelingen door predatie en concurrentie er bij betrekken. Tot slot worden modelberekeningen getoond die laten zien dat interacties in de beschouwde visgemeenschappen gemakkelijk kunnen leiden tot meerjarige populatiecycli en chaotische dynamiek; patronen die gewoonlijk alleen in sterk versimpelde ecologische modellen worden bestudeerd.

De laatste twee hoofdstukken geven meer voorbeelden van het gebruik van het vismodel Piscator. In hoofdstuk 8 wordt de ontwikkeling van de brasempopulatie geanalyseerd in drie verschillende meren met een verschillende exploitatie van de visgemeenschap: de Friese Meren (10.000 ha), het Veluwemeer (3400 ha) en het Volkerak-Zoommeer. Behalve directe effecten op de brasempopulatie worden ook indirecte effecten van visserij op de helderheid, de chlorofyl-a-concentratie, de waterplanten en de macrofauna geanalyseerd.

In het Veluwemeer is de brasempopulatie gedecimeerd (van 100 tot 20 kg ha^{-1}) nadat vijf jaar op brasem gevist was. Visserij zorgde voor een extra sterfte van ca. 38% per jaar van brasem groter dan 15 cm, terwijl de natuurlijke sterfte van volwassen brasem (groter dan 17 cm) 13% per jaar bedroeg. De instorting van de brasempopulatie werd gevolgd door het helder worden van het meer een snelle uitbreiding van de kranswiervelden en een explosieve groei van driehoeksmosselen (*Dreissena polymorpha*). In het Volkerak-Zoommeer, dat in 1987 is ontstaan na de afsluiting van de Oosterschelde, was de ontwikkeling van de brasempopulatie en de daaraan gerelateerde verschuiving in de rest van het ecosysteem tegenovergesteld aan die in het Veluwemeer. De onbeviste brasempopulatie begon vanaf 1988 te groeien en bereikte een biomassa van ongeveer 140 kg ha^{-1} in 1998. Het doorzicht van het meer verminderde van maximaal 3 m tot ca. 1 m. In dezelfde periode nam het chlorofyl-a niveau toe van 5 $\mu g\ l^{-1}$ naar 45 $\mu g\ l^{-1}$. De vegetatie kon zich in de beginperiode uitbreiden tot een bedekking van 20%, maar nam, toen het water troebeler werd, weer af tot 10%. De zegenvisserij in de Friese meren leek de brasempopulatie niet te beïnvloeden, ondanks de hoge vangsten van 40-50 kg ha^{-1} $jaar^{-1}$. De berekende natuurlijke sterfte van vis groter dan 15 cm was ongeveer 15% per jaar, terwijl de visserij daar 26%

aan toe voegde. De hoge verliezen werden gecompenseerd door goede reproductie en hoge groeisnelheden als gevolg van de hogere temperaturen in de periode van de visserij. Er was slechts een kleine afname in chlorofyl-a en een kleine afname van de helderheid.

In hoofdstuk 9 wordt de brasemdynamiek in het Veluwemeer verder geanalyseerd. De totale sterfte wordt berekend op grond van gegevens van de groei, voortplanting en de lengte-frequentieverdelingen. Daarbij is de sterfte onderverdeeld in natuurlijke sterfte en sterfte door visserij. Het model voorspelt dat de biomassa en de grootte van de vissen nauwelijks zou zijn veranderd zonder visserij. De visserij kon dus de biomassa-afname en de veranderingen in de lengte-frequentieverdelingen volledig verklaren. Er wordt beargumenteerd dat de snelle uitbreiding van kranswieren en de daarmee samenhangende verbetering van de helderheid, waarvan eerder werd verondersteld dat ze simpelweg het gevolg waren van afgenomen nutriëntenbelasting, waarschijnlijk nooit had plaatsgevonden zonder de brasemvisserij.

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Omdat individu-gebaseerde modellen nog niet zo lang worden gebruikt in de ecologie, heb ik erg veel gehad aan de adviezen van de Nederlandse pioniers op dit gebied: Hans Baveco en Wolf Mooij. Al waren onze computertalen niet uitwisselbaar, de ideeën waren dat gelukkig wel! Het ontwikkelen van het vissenmodel is in het begin ook begeleid door een groepje (vis)deskundigen: Willem Dekker, Peter Mous, Tom Buijse, Wim van Densen, Mennobart van Eerden and Wolf Mooij. Hartelijk dank voor jullie adviezen; ik heb daar veel aan gehad. Ook stagiaire Edith Adriaanse leverde een bijdrage door haar analyse van de voedselkeuze van vissen. Daarnaast bedank ik de andere medewerkers van RIZA-WSE voor de fijne werksfeer en de goede collegialiteit. Dankzij de vele opdrachten en samenwerkingsverbanden voel ik me nog altijd een beetje 'RIZA-nees'.

I thank Irmgard Blindow and Anders Hargeby for the nice modeling workshop some years ago. Though it seemed not easy to change a *Chara aspera* into a *C. tomentosa*, we learned a lot from the differences between Sweden and the Netherlands. Thank you for your contribution. Other international cooperation was with Hans Schutten and Tony Davy in Norwich and with Dietmar Straile and Susanne Wolfer in Konstanz. Thank you for your enthusiasm for the model Charisma and for your hospitality during the workshops. Allesandra Gragnani helped me to understand the difference between the transcritical and the fold bifurcation. Thank you for your patience and for teaching me the basics of bifurcation analysis.

De modelanalyses en het schrijven van het proefschrift is voor het grootste deel tijdens mijn huidige baan in Wageningen uitgevoerd, deels gefinancierd door het RIZA. Hoewel de tijden onstuimig waren (twee reorganisaties in drie jaar), vond ik het uitzonderlijk dat de werksfeer ondanks alle slechte berichten altijd heel goed bleef; ik dank alle collega's daarvoor. In deze periode hebben de studenten Femke van den Berg, Tijs Haeyen en Sybrand Landman bijdragen geleverd, doordat ze voor hun afstudeervak kritisch met Charisma hebben gewerkt. De laatste fase van het maken van het proefschrift was wat hectischer omdat er ineens een deadline voor het afronden van het manuscript bleek te zijn. Het was daarom een goed idee om een weekje een riante bungalow te huren om ongestoord aan één van de laatste hoofdstukken te kunnen werken. Bart Koelmans en Jeroen de Klein, bedankt voor het regelen vooraf en de gezelligheid tijdens ons verblijf. Het heeft er sterk toe bijgedragen dat de deadline uiteindelijk werd gehaald.

Verder leverde Bart Koelmans, Caroline Moermond, Michiel Hootsmans en Jan Vermaat een bijdrage door commentaar op manuscripten te geven. Voor de laatste twee hoofdstukken zijn monitoringsgegevens van het Veluwemeer en Volkerakmeer gebruikt die verzameld waren door Witteveen & Bos en AquaTerra door o.a. Jouke Kampen, Marcel Klinge, Joost Backx. De Friese meren zijn jarenlang bemonsterd door onder meer Koos Swart en Bauke Vink. Hartelijk dank voor het gebruik van die waardevolle gegevens. Verder leverden Hans Baveco, John Clayton, Don DeAngelis, Ekko van Ierland, Marie-Louise Meijer, Wolf Mooij en Kenny Rose bijdragen.

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Curriculum vitae

Egbert Hendrik van Nes werd op 6 februari 1961 te Oosterbeek geboren. In 1979 behaalde hij het VWO diploma aan de Thorbecke Scholengemeenschap te Arnhem. Daarna begon hij met zijn studie Milieuhygiëne aan de Wageningen Universiteit (toen nog Landbouw Universiteit geheten). Als doctoraalonderwerpen koos hij: een macrofauna-onderzoek in genormaliseerde beken bij de vakgroep Natuurbeheer en een modelstudie naar nitrificatie en denitrificatie in waterbodems bij de vakgroep Waterzuivering. Dit laatste onderzoek werd toegepast op Deense beken tijdens een stage bij het NERI te Silkeborg, Denemarken. De studie werd in 1986 afgesloten (met lof), waarna hij één jaar werkte bij de toenmalige Vakgroep Natuurbeheer aan de stikstofhuishouding in Brabantse beken. Daarna werd hij aangesteld als projectmedewerker bij het RIZA te Dordrecht (1987-1991) en deed onderzoek naar de natuurontwikkelingen in het verzoetende Volkerak-Zoommeer. Aansluitend werkte hij bij het RIZA in Lelystad achtereenvolgens aan de ontwikkeling van een informatiesysteem voor de gegevens van meren, gevolgd door de ontwikkeling individu-gebaseerde modellen, een project waarbij de basis werd gelegd voor dit proefschrift. In 1998 keerde hij terug naar de Wageningen Universiteit. Vanaf die tijd is hij werkzaam bij de leerstoelgroep Aquatische Ecologie en Waterkwaliteitsbeheer.