

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

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Abstract

Unraveling the mechanisms that drive dynamics of multi-species fish communities is notoriously difficult. Not only are the interactions between fish populations complex, but 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 limited in their capacity to describe the 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 demonstrates 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 high bream catches (40–50 kg ha⁻¹ per year), 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 3 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. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Individual-based model; Fish; Fisheries management; Multi-species; Sensitivity analysis

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1. 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, though in the 1970s several multi-species models were published based on a model of Andersen and Ursin (1977). 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 (DeAngelis et al., 1991; Rose et al., 1993; Dong and DeAngelis, 1998), are focussed on a certain life stage (Madenjian, 1991; Cowan et al., 1993) or focus on spatial processes (Anneville et al., 1998; Huse and Giske, 1998) or the effect of fisheries on a population (Martinez-Garmendia, 1998; Beard and Essington, 2000). We are aware of only few other individual based models dealing with multi-year interactions between two (Rose et al., 1996b; Clark and Rose, 1997a,b) or more (McDermot and Rose, 2000) fish species. In this paper, we present Piscator, an individual-based model designed to simulate interacting fish species. The model includes effects of fishery and piscivorous birds on the populations.

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 with this problem. It is a step-wise 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 to 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.

2. Model description

2.1. 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 model and the user manual is available on the internet (<http://www.dow.wau.nl/aew/piscator>).

The basic components of the model are fish species, fisheries (fykes, gill nets and seine nets) piscivorous birds, zooplankton and zoobenthos (Fig. 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 individ-

ual-based fashion. To model the large numbers of individuals in an efficient way, we use the concept of ‘super-individuals’ (Scheffer et al., 1995). 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 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.

2.2. Fish

2.2.1. Reproduction

On 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 (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 fol-

lowing ten to 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):

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

where T_t is the water temperature (in °C), n is the number of days between 1st March 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.

2.2.2. Growth

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

$$L = a_1 W^{b_1} \quad (2)$$

where a_1 and b_1 are parameters. We used values that were determined for Tjeukemeer (Mooij et al., 1994).

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

$$W_t = W_{t-1} p C_{\max} A - R_{\text{tot}} \quad (3)$$

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).

$$R_{\text{tot}} = \frac{R_{\max}}{1 + 2(1 - p)} \quad (4)$$

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 ($\text{Act}(T)$):

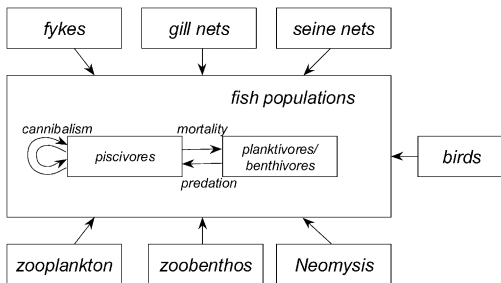


Fig. 1. Overview of the components of the model PISCATOR.

Table 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	gd ⁻¹
b_cons	Exponent in consumption eq.	–
b_resp	Exponent in respiration eq.	–
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 eq.	°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	Halfsaturation of the length dep. background mortality	cm
MaxAge	Maximum year class	year
MaxLength	Maximum length above which scenescense mortality takes place	cm
MaxLength2	Absolute maximum length of the fishes	cm
PBackgrMort	Power of the length dependent background mortality	–

Table 1 (Continued)

Parameter	Description	Unit
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 (S.D./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	year
MinMaturityWeight	Minimal weight of spawning fish	g
NSuperInd	Number of super-individuals per year class	–
SpawnDuration	Duration of spawning period	d
SpawnWeightLoss	Weight loss during spawn	fraction
YoYHEggs	Halfsaturation 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

$$R_{\max} = a_r W^{b_r} Q_{10}^{(T-20)/10} \text{Act}(T) \quad (5)$$

in which a_r is a constant and b_r the exponent of the weight (W in 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:

$$\text{Act} = 0.5 + (2 - 0.5) \frac{T^3}{T^3 + H_T^3} \quad (6)$$

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):

$$\left(\frac{dW}{dt}\right)_{\max} = (G_{\text{mean}} + T_1(T - T_0))W^{b_c} \quad (7)$$

in which G_{mean} (g d^{-1}) is the average growth of 1 g fish at the mean temperature ($T_0 = 17.5^\circ\text{C}$ in The Netherlands), T_1 is a first order temperature effect ($\text{d}^{-1}^\circ\text{C}$) and b_c is an exponent of $\approx 2/3$. 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. (3), with $p = 1$).

Food limitation is described as a Holling type 2 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 fish. Larger fish also needs more food, but this additional need is roughly proportional with $W^{2/3}$ (Eq. (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):

$$p = \frac{C_r}{C_{\text{max}}} = \frac{\text{TotFB}}{\text{TotFB} + H/L} S \quad (8)$$

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:

$$S_i = \min\left(\frac{\text{MaxLen}_i^{\text{pow}}}{\text{MaxLen}_i^{\text{pow}} + L^{\text{pow}}}, \frac{L^{\text{pow}}}{L^{\text{pow}} + \text{MinLen}_i^{\text{pow}}}\right) \quad (9)$$

We used a large power of these Hill function (default $\text{pow} = 8$) 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}).

$$\text{TotFB} = \sum_{j=0}^n \sum_{i=0}^{N_j} W_i \text{Sel}_{ij} \quad (10)$$

in which n is the number of species (j) of the food category and N_j , the 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:

$$\text{Sel}_{ij} = f\left(\frac{L_{ij}}{L_k}\right) S_j \quad (11)$$

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 until 0, which is reached at 1 1/3 of the maximum limit. The limits of each species are based on field observations in Lake Tjeukemeer (Lammens and Mooij, unpublished results).

2.2.3. Mortality

If the respiration is larger than the growth, the fish loses weight, but the length is not re-

duced. If the expected weight on the basis of their length is lower than a certain fraction (we take 0.7 on the basis of Ivlev (1961)), starvation mortality takes place (Rose et al., 1996a). 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.

2.3. 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:

$$c_t = N \sum_{j=0}^n \sum_{i=0}^{N_j} W_i e_{ij} \quad (12)$$

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:

$$L_{opt} = \frac{\text{Mesh}}{LM_i} \quad (13)$$

‘Mesh’ is the mesh size of the gill nets in centimeters, 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 S.D. of 0.1. Fish are vulnerable of being caught in gill nets in a narrow range of lengths (L_i in cm):

$$e_{ij} = e_{\max, j} \exp\left(-0.5 \frac{(L_i/L_{opt})^2}{0.1^2}\right) \quad (14)$$

$e_{\max, j}$ 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:

$$e_{ij} = f(L_{ij}) e_{\max, j} \quad (15)$$

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 to 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:

if $L_i LM_{ij} > \text{Mesh}$ then

$$e_{ij} = e_{\max, j}$$

else

$$e_{ij} = 0 \quad (16)$$

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

2.4. 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_i in kg d⁻¹) are external variables. The consumption (B in kg ha⁻¹ d⁻¹) of the birds is calculated as follows:

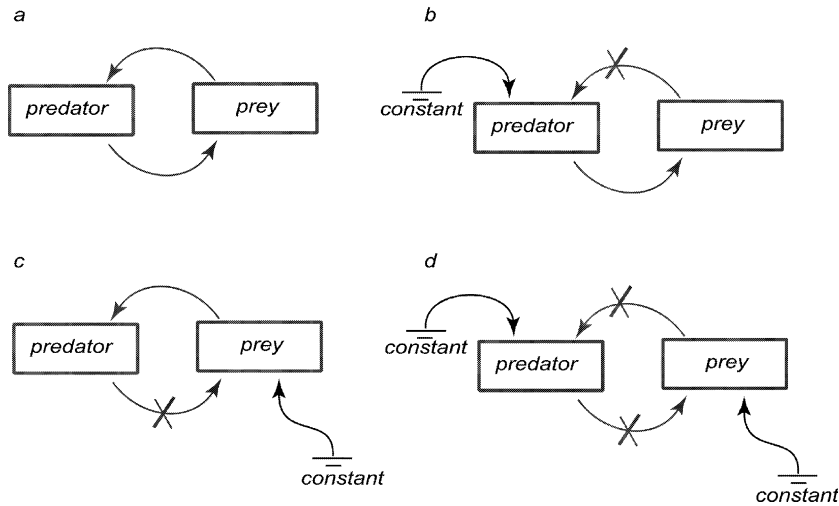


Fig. 2. Three modes of simplifications in the predator–prey relationships in the model. (a) The full feedback loop between predator and prey ('dependent growth/dependent mortality mode'); (b) the food dependent consumption of the predator is replaced by a fixed consumption ('fixed growth mode'); (c) the mortality of the prey caused by predation is replaced by a fixed mortality ('fixed mortality mode'); and (d) the predator is completely independent of the prey biomass and vice versa ('fixed growth/fixed mortality mode').

If $\text{TotFB}_t < \text{FB}_{\text{crit}}$ then

$$B = N_t C_t \quad (17)$$

else if $\text{TotFB}_t < \text{FB}_{\text{min}}$ then

$$B = N_t C_t \frac{\text{TotFB}_t - \text{FB}_{\text{crit}}}{\text{FB}_{\text{min}} - \text{FB}_{\text{crit}}} \quad (18)$$

else

$$B = 0 \quad (19)$$

TotFB_t is the 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.

2.5. 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):

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

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

2.6. 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 (Gagnani 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. 2). This is carried out by replacing mortality caused by pre-

dation by a predator independent mortality and making food consumption of fish independent of food availability. This is implemented as follows:

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

$$m_f = \left(m_{f,\text{adult}} + (m_{f,\text{young}} - m_{f,\text{adult}}) \frac{h^p}{h^p + L^p} \right) \times Q_{10}^{(T-20)/10} \quad (21)$$

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 in understanding the causation on the model.

3. 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 is 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 to 1995 (Lammens et al., 1990; Lammens, 1999b) and is dominated by bream, which represents $\approx 70\%$ 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 until 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 commercially 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 a 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 reduced (Lammens, 1999b).

3.1. 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 (ten to 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 (RIZA, unpublished data). The initial size and structure of the populations were in accordance with the field situation at the start of the monitoring.

3.2. 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).

$$s_{i,j,t} = \frac{\partial M_{j,t}}{\partial p_i} \frac{\Delta p_i}{M_{j,t}} \quad (22)$$

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

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

$$s_{\text{tot},i} = \sqrt{\left(\sum_{j,t} (s_{i,j,t})^2\right)} \quad (23)$$

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 carried out 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.

4. Results

4.1. 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 $\pm 10\%$, using a uniform distribu-

tion. 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 4 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. 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. 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) of smelt (Fig. 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 cannot 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 param-

eters. 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. 4c).

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. 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 that 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. 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).

4.2. *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 5 years (from 1985 to 1990) without fishing. The next 5 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).

Dendrogram using Average linkage

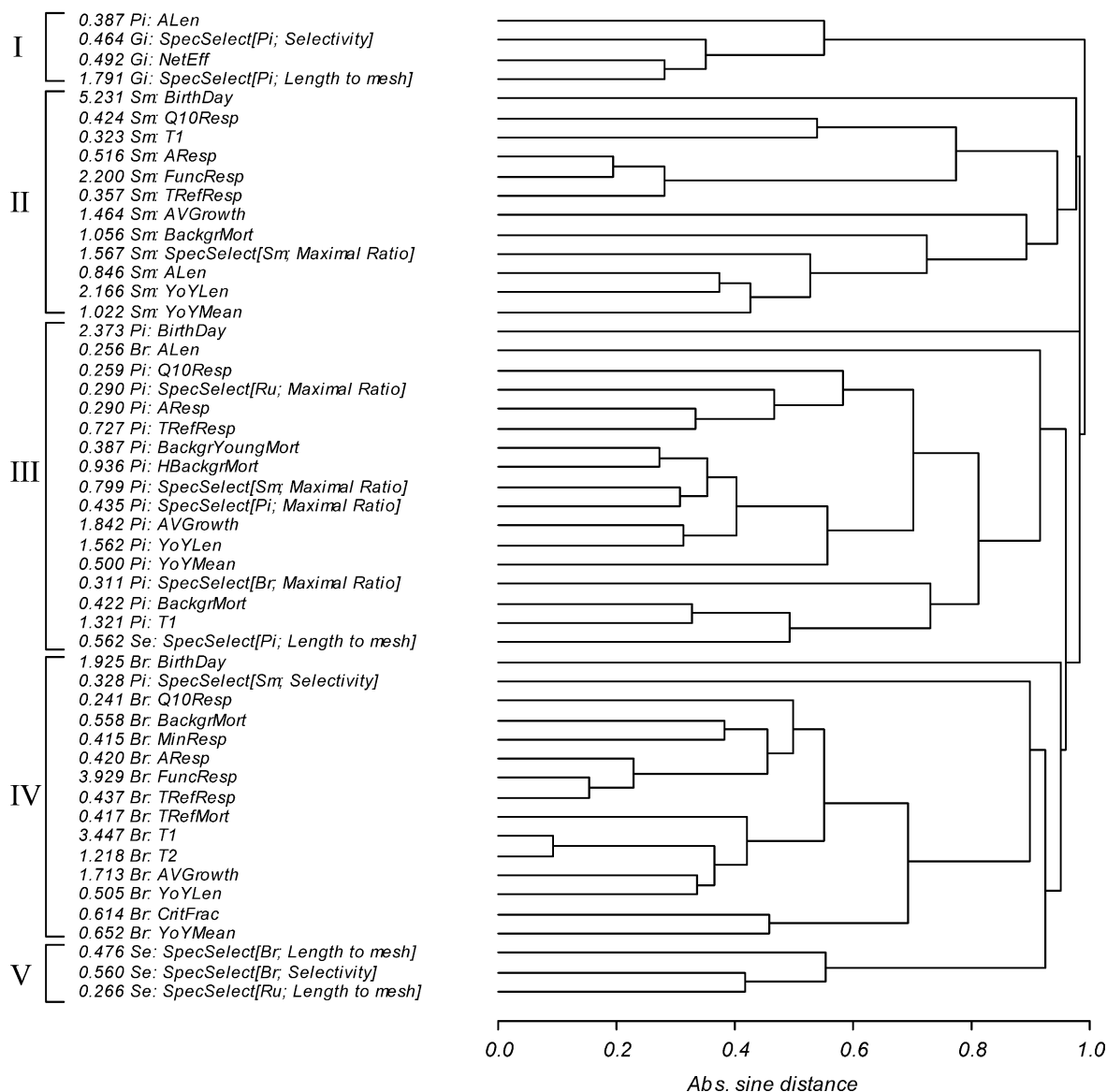


Fig. 3. Cluster analysis of parameters on the basis of their sensitivity indices. Parameters with the same or opposite effect on the model results (biomass, numbers on 3 days per year) are grouped together. The value before each parameter is the length of the vector of the sensitivity coefficients (Klepper, 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 1.

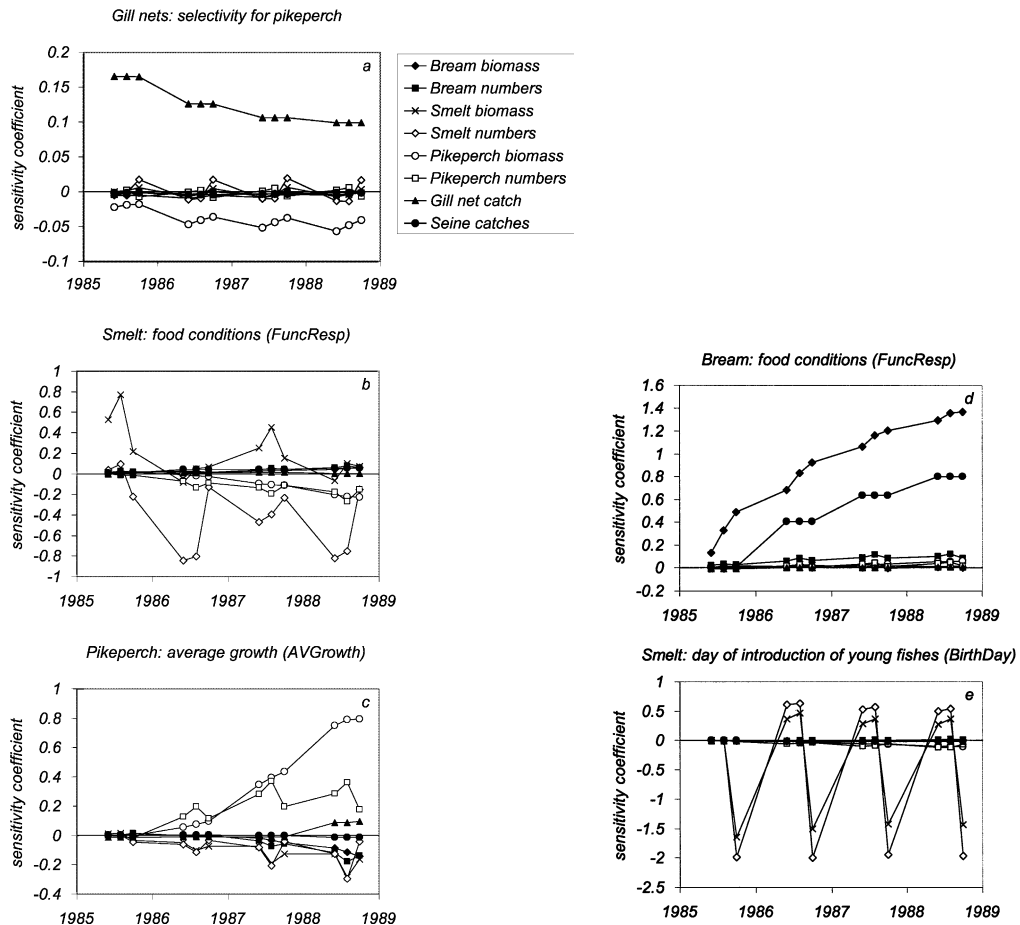


Fig. 4. Time course of the relative effect (expressed as sensitivity coefficient) of variation in parameters on various model variables (lines) for simulations starting in 1985. The panels (a–e) show effects of representative parameters selected from each the five clusters marked in Fig. 3, respectively.

(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. 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 (Fig. 6) had a reasonable fit with estimated catches (Lammens et

al., in press). Also, the simulated size distributions were realistic (Fig. 7).

Fig. 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. 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. 6b), the main causes of mortality are background mortality, seine fishery and predation by pikeperch. Smelt is hardly affected by fishery (Fig. 6c), apart from the background mor-

tality, 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. 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 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. 7c, d). If we simulate fishing with both kinds of nets combined (Fig. 7a, b), this year class of both species

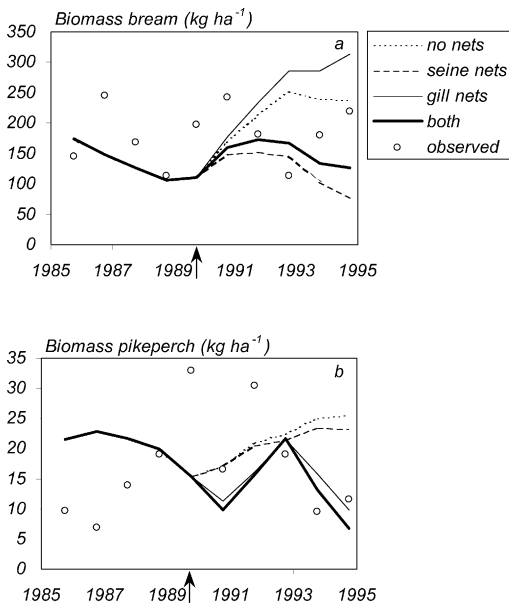


Fig. 5. Simulated biomass on 1 November of pikeperch (a) and bream (b) calculated with four scenarios. The arrows indicate the start of the fishery experiment.

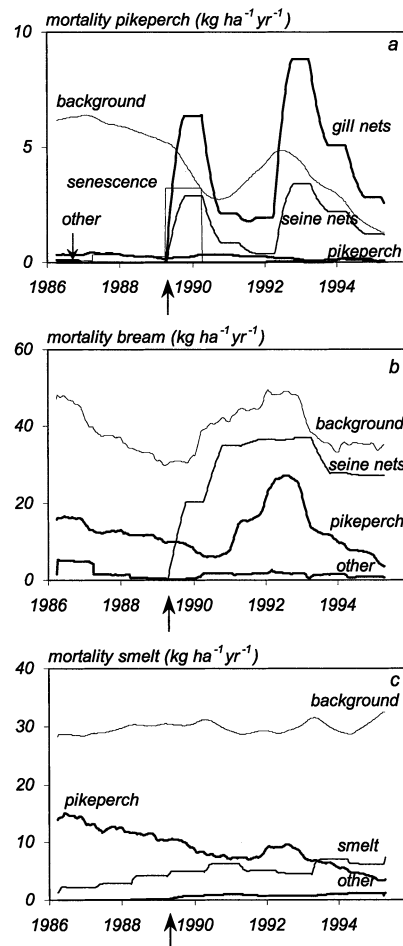


Fig. 6. The causes of mortality of bream (a), pikeperch (b) and smelt (c) in the Frisian lakes. The mortality values are shown as moving averages with an averaging window of 1 year. Seine nets and gill nets were introduced in October 1989 (indicated with an arrow).

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. 7f), whereas pikeperch is removed by the gill nets only if the individuals become large enough (Fig. 7g).

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. (in press) proposed two hypotheses for this development. Firstly, in 1989, just before the experiment, the

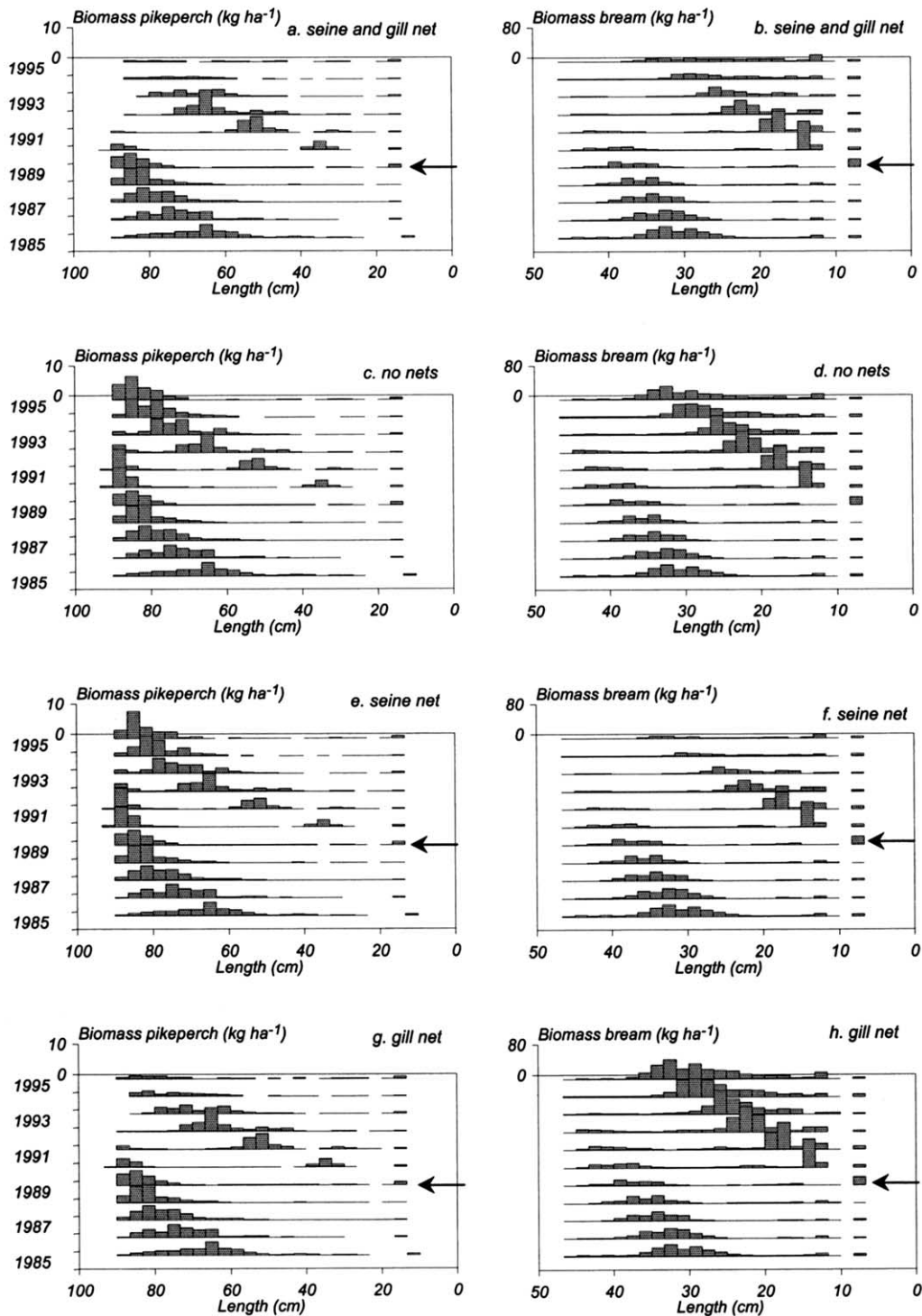


Fig. 7. The development of the pikeperch (a, c, e, g) and bream (b, d, f, g) population before and after the fishery (from 1991 on) with the four fishery scenarios. (a, b) Seine and gill net fishery in the winter period; (c, d) no fishery; (e, f) with seine fishery in winter; and (g, h) gill nets in the winter. The arrows indicate the start of the fishery experiment.

reproduction of both species was very high. Secondly, the mean water temperature from 1990 to 1992 was relatively high (Lammens et al., in press). 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 the main cause of the good development of the strong bream year class (Fig. 8).

5. Discussion

We agree with McDermot and Rose (2000) that considering multispecies interactions may improve predictions of fish population dynamics and may help to explain unanticipated responses in nature. However, multi-species models are notoriously complex to understand and Piscator and similar models are no exceptions. 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 multivari-

ate analysis of the sensitivity matrix not only detected the most important parameters, it also gave insight in the functioning of the model. In particular, the visual inspection of the sensitivity coefficients (Fig. 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, such as 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. (8))

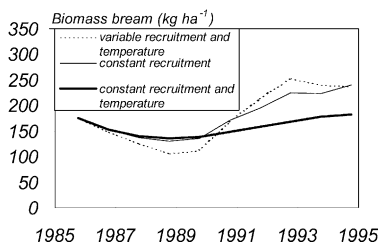


Fig. 8. The effect of the observed annual variation in recruitment and temperature on the development of the bream biomass without fishery.

and the parameters defining the ontogenetic food switches (Eq. (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 first sight surprising observation that it was possible to remove 40–50 kg ha⁻¹ per year of 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 et al. (in press)), IJsselmeer (Lammens, 1999a), Lake Veluwe (Lammens et al., in press, Lammens et al., submitted) and Lake Volkerak (Lammens et al., in press)). 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.

Other individual-based fish models have also been used mainly to generate or substantiate hypotheses about certain mechanisms. Examples are the reason of density-dependence in larval stages (Cowan et al., 2000), the effect of predative interactions (McDermot and Rose, 2000), the effects of angling on the size distribution of a species

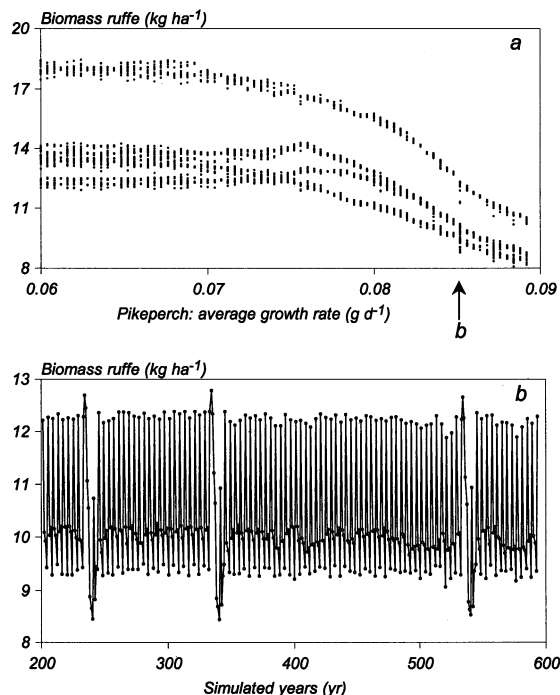


Fig. 9. Example of more complex behavior of the model based on unpublished results of the fish community in Lake IJsselmeer. (a) Dots represent the biomass of ruffe in October of 50 subsequent years, with various settings of the growth rate of pikeperch. The picture was created by increasing this parameter in small steps. Dynamics for each new parameter setting were left to stabilize for 50 simulation years before plotting the next 50 years. The growth and mortality of all species were dependent on predation and food biomass, and temperature and 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 ≈ 12 years.

(Beard and Essington, 2000) and difference in the effect of interspecific competition for different species (Clark and Rose, 1997b).

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 formula-

tion 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. 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 assist fishery biologists in making management decisions.

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