Fisheries Research, 13 (1992) 95–117
Elsevier Science Publishers B.V., Amsterdam

A size- and age-structured simulation model for evaluating management strategies in a multispecies gill net fishery

Anthonie D. Buijse[a], Jos S. Pet[a], Wim L.T. van Densen[a], Marcel A.M. Machiels[a] and Rudy Rabbinge[b]

[a]*Department of Fish Culture and Fisheries, Agricultural University Wageningen, P.O. Box 338, 6700 AH Wageningen, Netherlands*

[b]*Department of Theoretical Production Ecology, Agricultural University Wageningen, P.O. Box 430, 6700 AK Wageningen, Netherlands*

(Accepted 27 August 1991)

ABSTRACT

Buijse, A.D., Pet, J.S., van Densen, W.L.T., Machiels, M.A.M. and Rabbinge, R., 1992. A size- and age-structured simulation model for evaluating management strategies in a multispecies gill net fishery. *Fish. Res.*, 13: 95–117.

A size- and age-structured simulation model is presented for evaluation of management strategies for a multispecies gill net fishery, using a commercial gill net fishery for pikeperch (*Stizostedion lucioperca*) and perch (*Perca fluviatilis*) as an example. The model takes size distributions within age groups into account. Growth for each sex is determined by length and temperature and dispersion in size distributions is controlled by the 'fractional boxcar train' method. The model is applied to evaluate the integrated short-term and long-term effects of management measures such as mesh size regulations, fishing effort limitations and combinations of both on the biomass, the size- and age-structure of the stock and of the yield. Changes in yield during the transitional period after a management measure has been implemented, can be quantified.

INTRODUCTION

In managing a fishery, the consequences of different management strategies have to be evaluated. Some consequences are easily deduced on the basis of classical fish stock assessment models as formulated by, for example, Beverton and Holt (1957) and Ricker (1958). In many cases these classical dynamic pool models are based on the concept of age-structured populations, and are simplified by assuming constant mortality and knife-edge recruitment to the fishery. More modern dynamic pool models include age-dependent mortality and gradual recruitment to the fishery (Pitcher and Hart, 1982; Jacobson and Taylor, 1985). Natural mortality is, however, more related to size than to age. For instance, predation, as the most important cause of natural mortality (Peterson and Wroblewski, 1984) is essentially size-selective (Dekker, 1983).

Fishing gears are also size-selective rather than age-selective, and considerable bias can be introduced by the assumption of knife-edge recruitment at a certain age to a fishery. This is particularly true for heavily exploited populations and for short-lived tropical species, where the selection range of the catching gear covers a large fraction of the size-distribution of the population. Although this problem can be overcome by applying empirical sigmoid selection curves in age-structured models as done for the Samar Sea multispecies trawl fishery (Silvestre and Soriano, 1988), an age- and size-structured model will show the consequences much more clearly (Sissenwine, 1977). Size-structured models are particularly suited for gill net fisheries, which exploit only a small proportion of population's size distribution.

Steady-state size-structured models have been used to evaluate management strategies for gill net fisheries on lake whitefish, *Coregonus clupeaformis* (Berkes and Gönenc, 1982), and on perch, *Perca fluviatilis* (Staub et al., 1987). Berkes and Gönenc (1982) note that their steady-state model is limited by not taking into account the progressive change in population structure due to the fishery-induced size-selective mortality. Dynamic age-structured models have been used to evaluate short-term as well as long-term effects (Hightower and Grossman, 1987), but dynamic size-structured models will probably provide a more realistic description.

In the present study a size- and age-structured dynamic pool model is described for scanning the effects of management alternatives for the multispecies gill net fishery on pikeperch, *Stizostedion lucioperca*, and perch in Lake IJssel ('IJsselmeer'), a 182 000 ha shallow eutrophic freshwater lake in the Netherlands. The stock of pikeperch is heavily exploited and, according to Willemsen (1977, 1983) and Van Densen et al. (1990), subject to growth-overfishing. Since large numbers of females are already caught at Age 2 when they are just maturing (Willemsen, 1983), there is even an imminent danger of recruitment overfishing. The perch stock, however, shows no signs of overexploitation. Since perch grow more slowly than pikeperch (Willemsen, 1977), fishermen foresee a permanent decrease in the perch catches if management measures, such as mesh size and effort regulations or a combination of both, are implemented to rationalise the exploitation of pikeperch. The model has been applied to investigate the integrated effects of a number of management options.

MATERIALS AND METHODS

Description of the Lake IJssel fishery

The mean yields of pikeperch and perch in the gill net fishery in the period 1980–1989 were 0.76 and 3.17 kg ha^{-1} amounting to 10.6% and 22.2% of the value of the total yield (Dfl 13 350 000) from Lake IJssel respectively. On average, the value per kilogram of pikeperch is twice the value of perch. The gill net fishing season lasts from 1 July until 15 March and the legal minimum mesh size of the gill nets is 101 mm stretched mesh. Legal minimum landing sizes of pikeperch and perch are 42 cm and 22 cm total length, respectively. Total mortalities were estimated at 81% for Age 2 pikeperch and at 67% for Age 4 perch in the beginning of the 1970s (Willemsen, 1977). Although the number of fishing companies has decreased by half over the last 20 years, the total fishing mortality increased because overall more gill nets were used (Dekker, 1991). Also, the fishermen switched from multifilament to monofilament gill nets, which are twice as efficient for perch and one and a half times for pikeperch (Schaap, 1987). A similar increase in efficiency was observed for *C. clupeaformis* in Lake Huron where catch comparisons showed that monofilament gill nets were 1.8 times as efficient as multifilament nets (Collins, 1979). There is no limitation on the number of gill nets allowed per fishing company, but the fishing effort has been restricted to some extent by a ban on gill net fishing during Saturdays and Sundays.

Model and parameters

Model structure

The general structure of the model is depicted in the relational diagram (Fig. 1). A list of symbols used is given in Table 1. The model includes two species, each of which consists of eight age groups, and is based on 100 size-classes (cm). Fish recruit to the stock at Age 1 (1 January). The initial size distribution of the Age 1 fish is described by a normal distribution. Growth rates are based on a Von Bertalanffy growth equation for each sex, which is modified to reflect inter-annual variations in the growth rate. The dispersion in the size distribution of an age group as it grows older is simulated by applying the 'fractional boxcar train' method (Goudriaan and Van Roermund, 1989). At 1 January, every age group switches to the next, the oldest one being removed from the model. Natural mortality is assumed to be length-dependent and decreases to a constant value for fish above a certain size. Fishing mortality is a function of the number of companies fishing with gill nets, the length of the fishing season and the mesh size of the gill nets. The model has been written in CSMP III (Continuous System Modelling Program: IBM, 1975) using a fixed time step of 1 day. This is a conservative choice taking into account that one quarter of the smallest time constant, being 25/4 days, is small enough to justify the assumption that the highest rate does not change materially over time (De Wit, 1982).

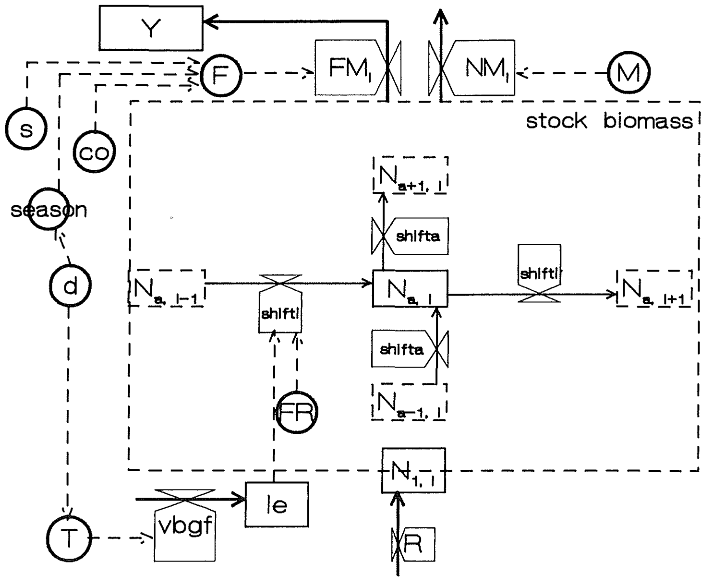

Fig. 1. Relational diagram of the size- and age-structured model (notations are according to the conventions introduced by Forrester). State variables or the contents of integrals are presented by rectangles, the rates of changes by valves and auxiliary variables by circles. The flow of material is presented by solid arrows and the flow of information by dotted arrows (De Wit and Goudriaan, 1978). Abbreviations are explained in Table 1.

Parameter estimates

Parameters are based on data collected on pikeperch and perch in Lake IJssel in the period 1966–1989. Certain parameters for pikeperch, which could not be derived from the stock of Lake IJssel because little fishery-independent data could be collected due to the high exploitation rate there, are based on data from the pikeperch stock in Tjeukemeer, a 2000 ha shallow eutrophic lake in the northern part of the Netherlands. This stock has a slightly faster growth rate than the one in Lake IJssel (W.L.T. van Densen, unpublished data, 1987).

Recruitment

Recruitment as number of Age 1 fish at the beginning of the year is held constant. Although the inter-annual variation in recruitment has been shown to be large, especially for perch (Willemsen, 1977; Van Densen et al. 1990), relative yield estimates per age group are insensitive to year-to-year variation in recruitment, as long as growth and mortality are density-independent. Therefore, to evaluate the effect of possible management strategies, only the ratio of recruitment in the two species is required. Since 1966, bottom trawl surveys in autumn have been carried out to estimate the year-class strength of pikeperch and perch, indexed as the number of Age 0 per standard haul.

TABLE 1

List of abbreviations used in the relational diagram

Parameter variable or abbreviation	Description
a	age-class (years)
co	companies (numbers)
d	day number of the year
F	fishing mortality rate (day^{-1})
FM	fishing mortality (numbers day^{-1})
FR	fraction to control dispersion
l	length-class (cm)
le	fish length in an unexploited population (cm)
M	natural mortality rate (day^{-1})
N	number of fish (arbitrary units)
NM	natural mortality (number day^{-1})
R	recruitment (arbitrary units year^{-1})
S	selectivity of gill net
season	open or closed (1/0)
shifta	transfer of all fish to next age-class at 1 January
shiftl	transfer of fraction FR of total number to next length-class
T	temperature (°C)
vbgf	growth according to Von Bertalanffy (cm day^{-1})
Y	yield (kg)

During the period 1966–1987 the average ratio in recruitment of pikeperch and perch was 1 : 8. This ratio is used (in arbitrary units) in the model.

Growth

In the model the daily growth in length is assumed to be dependent on length and on temperature and is specific to sex. Growth is formulated according to the Von Bertalanffy growth function

$$\frac{\partial L}{\partial t} = k_d(L_\infty - L_{t-1}) \qquad (1)$$

where L_{t-1} is the total length (cm), t is the time (days), k_d is the temperature-dependent daily growth constant (day^{-1}), and L_∞ is the theoretical length at infinite age (cm). Lengths at Age 1 serve as a starting value for L_{t-1}.

The resulting mean lengths-at-age and standard deviations of male and female perch and pikeperch are given in Table 2. Pikeperch grow faster than perch and females faster than males. Parameter estimates are based on information on mean length at successive ages. For pikeperch, Willemsen (1983) estimated potential growth ("theoretical growth in unexploited situation") for the Lake IJssel stock. The differences in growth rate between sexes are based on data from Tjeukemeer. For perch no data on potential growth were

TABLE 2

Mean total length, L (cm), and standard deviations, s (cm), at age (years) for populations of male and female pikeperch and perch in Lake IJssel in the case without exploitation. Lengths at age were calculated using the Von Bertalanffy growth parameters L_{∞}, k and t_0

	Age (years)								L_{∞} (cm)	k (year^{-1})	t_0 (years)
	1	2	3	4	5	6	7	8			
Pikeperch ♂									81.2	0.26	0.21
L	15.0	30.1	41.8	50.8	57.7	63.1	67.2	70.4			
s	1.7	2.6	2.6	2.6	2.6	2.6	2.6	2.6			
Pikeperch ♀									94.4	0.21	0.20
L	14.8	30.1	42.4	52.4	60.5	67.0	72.2	76.5			
s	1.7	2.6	2.6	2.6	2.6	2.6	2.6	2.6			
Perch ♂									42.7	0.19	0.05
L	7.1	13.2	18.3	22.5	26.0	28.9	31.3	33.3			
s	0.6	1.3	2.0	2.5	2.9	3.2	3.4	3.7			
Perch ♀									54.2	0.14	0.04
L	6.8	13.0	18.4	23.1	27.1	30.7	33.7	36.4			
s	0.6	1.3	2.0	2.5	3.0	3.4	3.7	4.0			

available. Growth parameters for perch are based on back-calculations with the aid of opercula (Le Cren, 1947) of Age 1 to Age 5 perch, which were caught during bottom trawl surveys in Lake IJssel in 1987 (Pet, 1988).

Pikeperch and perch grow if the water temperature is above 14°C (Le Cren 1958; Willemsen 1978). The average daily water temperatures in Lake IJssel from 1971 to 1986 show that this minimum temperature for growth was exceeded from 15 May until 29 September (Fig. 2). Therefore, growth is made a function of water temperature and in this way the Von Bertalanffy growth function is seasonalised. The growth rate k is assumed to be linearly related to the water temperature above 14°C. This seems reasonable because water temperature in Lake IJssel never exceeded 21 °C, which is well below the temperature for the physiological optimum of pikeperch (27.3°C) or perch (25.4°C) (Hokanson, 1977). For convenience, a fifth-order polynomial is fitted through the annual cycle of temperature, and daily temperatures in the model are calculated with this polynomial. From the sum of degree-days above 14°C (453°C days) divided by the number of days per year (365 days), which equals 1.24°C, the daily growth constant k_d was calculated according to

$$k_d = \frac{(T_d - 14)}{1.24} \frac{k}{365} \tag{2}$$

where d is the day number (1–365), T_d is the water temperature (°C), and k is the yearly growth constant (year^{-1}).

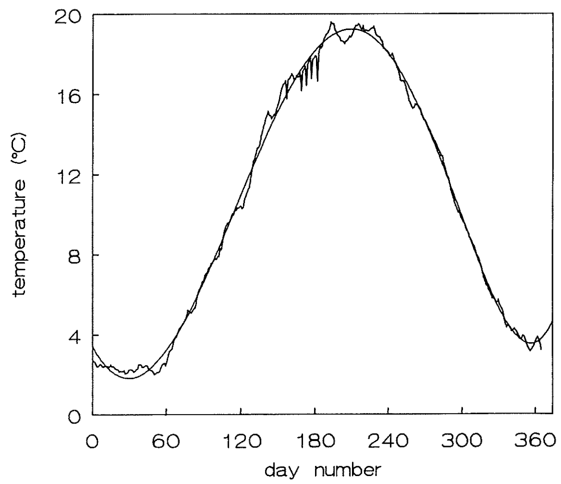

Fig. 2. Mean daily water temperature in Lake IJssel in the period 1971–1986. A fifth-order polynomial function is fitted to the data: T (°C)$=3.39-1.11\times10^{-1}\times d+2.04\times10^{-3}\times d^2-2.94\times10^{-6}\times d^3-2.18\times10^{-8}\times d^4+4.62\times10^{-11}\times d^5$; where d is the day number, $n=365$, $r=0.998$.

Size structure per age group

The initial length–frequency distribution of the recruiting age group was described by a normal distribution function according to which the fish were distributed among length-classes. Recruitment was split into males and females, assuming an initial sex ratio of 1 : 1. Thus, the initial length–frequency distribution for each species and sex is given by equation

$$N(L)=\frac{1}{2}\frac{R}{s_1(2\pi)^{1/2}}\,\mathrm{e}^{-(L-L_1)^2/2s_1^2}\,W \qquad (3)$$

where $N(L)$ is the calculated initial frequency in length-class L, L is the mid-length of length-class (cm), R is the recruitment (arbitrary units), s_1 is the standard deviation at Age 1 (cm), L_1 is the mean length at Age 1 (cm), and W is the width of the length-class (cm). The number 2 in the denominator accounts for the sex ratio.

The standard deviations of the mean lengths-at-age indicate an increasing divergence in the length–frequency distribution with age (Table 2). This divergence can be simulated with the 'fractional boxcar train' method, by which dispersion in a length–frequency distribution of an age group is controlled. The method is based on a fractional, repeated shift of the number of fish in a length-class: a fraction FR of the frequency in a length-class is transferred to the next length-class as soon as the increase in length, based on the summation of the daily growth according to eqn. (1), equals a proportion FR of the width of the length-class. FR is a function of the mean length and the standard deviation of the consecutive age groups

$$FR = 1 - \left(\frac{s_{a+1}^2 - s_a^2}{L_{a+1} - L_a} \right) \tag{4}$$

where L is the mean total length of an age group, calculated with eqn. (1) (cm), s is the standard deviation of the size distribution of an age group (cm), and a is the age (years). After transfer, the summation function of daily growth is reset to zero.

Length–weight relationship
An allometric function is used to describe the relation between body length L (cm) and body weight W (g) of pikeperch and perch. For pikeperch $W = 0.00425 \times L^{3.2}$ and for perch $W = 0.0104 \times L^{3.13}$ is used.

Size at maturity
Data on the size at maturity are needed for the calculation of the spawning stock biomass. The range for which the fraction of mature females increases from 0 to 1 is 40–50 cm for pikeperch and 14–23 cm for perch. A simple linear relationship is assumed between the fraction of mature females per length-class and fish length.

Natural mortality
Natural mortality has been estimated for Age 0 and 1 pikeperch and Age 0–2 perch based on the numerical abundance of pikeperch and perch age groups in bottom trawl surveys in Lake IJssel. Daily instantaneous natural mortality rate M_d (day^{-1}) is described as a function of the body length L (cm): $M_d = 0.0047 \times e^{-0.079L}$ and $0.0049\ e^{-0.087L}$ for pikeperch smaller than 27 cm and perch smaller than 25 cm respectively. The natural mortality rate for larger fish is assumed to be constant (0.2 year^{-1} = 0.00055 day^{-1}).

Fishing mortality
The daily instantaneous fishing mortality rate (F_d) per length-class is assumed to be a function of the mean daily fishing mortality for the length-class optimally caught in a gill net (F_{op}) and the selectivity (S) per length-class, which is a fraction (0–1) of F_{op} (see eqn. 5). Within a year, the fishing mortality also varies due to the number of companies fishing with gill nets, which is zero if the season is closed (Fig. 3).

$$F_{d,i}(L) = F_{op} S_i(L) \frac{C_d}{C_m} \tag{5}$$

where $F_{d,i}$ is the fishing mortality per length-class per day (day^{-1}), F_{op} is the

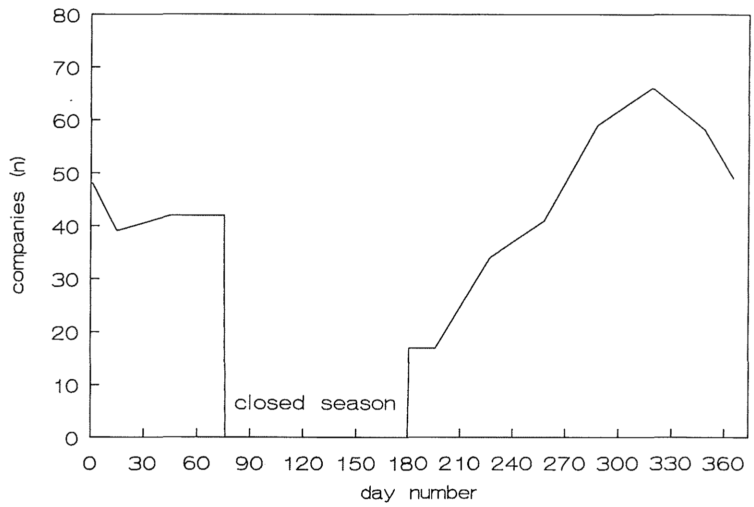

Fig. 3. Intra-seasonal variation in the number of companies fishing with gill nets based on monthly averages over the period 1969–1982 which were linearly interpolated between the middle of two months (Anonymous 1969–1982). The gill net season is closed from 15 March to 1 July.

mean daily fishing mortality during the open season for the length-class optimally caught in a gill net (day^{-1}), d is the day number, i is the ith distinct mesh size used in the gill net fishery (1–n), S_i is the selectivity per length-class of a gill net with a certain mesh size (0–1), L is the total length (cm), C_d is the number of companies fishing with gill nets on a given day, and C_m= mean number of companies fishing with gill nets during the open season.

F_{op} varies proportionally with fishing effort and was used to simulate year-to-year variations in fishing effort. Total yearly instantaneous fishing mortality rate (F_y) per age group is the summation of daily fishing mortalities of all length-classes of an age group

$$F_y(A) = \sum_{d=1}^{365} \sum_{L=1}^{100} \sum_{i=1}^{n} F_{d,i}(L) \qquad (6)$$

where A is the age group (years), F_y is the fishing mortality per age group per year ($year^{-1}$), and n is the number of distinct mesh sizes used in the gill net fishery.

In this way it is possible to simulate the outcome of gill net fisheries with varying combinations of mesh sizes and fishing effort per mesh size.

Gill net selectivity

The selectivity of gill nets for pikeperch is based on data from Van Densen (1987), who calculated a length-dependent selection curve according to the method of Holt (1963). This selection curve was transformed into a selection curve as a function of the maximum girth/mesh perimeter ratio, because this gives a more realistic description. The selectivity of gill nets for perch is based on studies made by McCombie and Berst (1969) on yellow perch, *Perca flavescens*, which has a very similar morphology to perch (Thorpe, 1977). The maximum girth G (cm) is related to the total length L (cm) of the fish, for pikeperch, by $G=0.58\,L-3.51$ and for perch, by $G=0.81\,L-2.26$. The selectivity S is described as a normal distribution function of the maximum girth of the fish and the mesh size of the gill net and varies between 0 and 1

$$S_i(L)=e^{-(G(L)/2m-OP)^2/2s_{op}^2} \tag{7}$$

where S_i is the selectivity per length-class, L is the total length (cm), G is the maximum girth (cm), m is the mesh size (cm stretched mesh), OP is the ratio of maximum girth/mesh perimeter ($=2\,m$) for the optimum of the selection curve, and s_{op} is the standard deviation of the selection curve.

For pikeperch, $OP=1.22$ and $s_{op}=0.15$, and for perch a normal distribution was fitted through the data of McCombie and Berst (1969) resulting in $OP=1.20$ and $s_{op}=0.12$. The resulting selection curves for the two species in 101 mm and in 140 mm stretched mesh gill nets are presented in Fig. 4. These selectivity curves broaden with increasing mesh size.

Calibration of the fishing mortality

The gill net fishery on pikeperch and perch in Lake IJssel in the period 1974–1983 was used as a reference point for evaluating management strategies. The fishermen mostly used gill nets with 101 mm stretched mesh. The

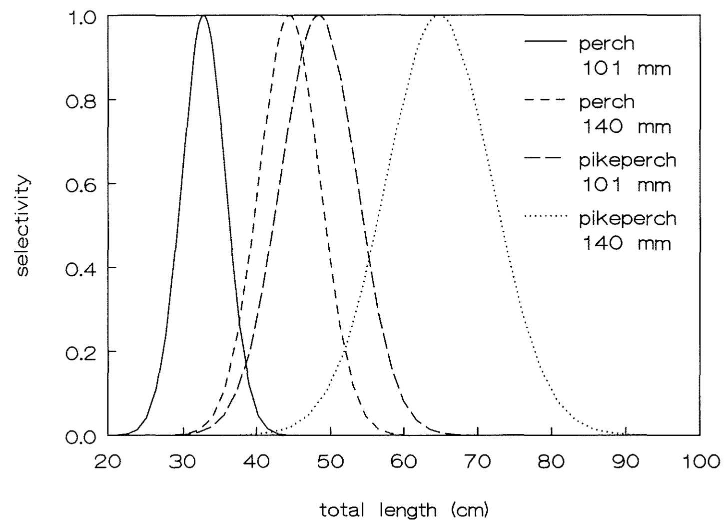

Fig. 4. Selectivity of 101 and 140 mm (stretched mesh) gill nets for pikeperch and perch (see text).

estimated yearly instantaneous fishing mortality rate F_y was 1.27 year^{-1} (72%) for Age 3 pikeperch, based on cohort analysis of catches of the year-classes 1971–1980 in the period 1974–1983. For Age 5 perch fishing mortality was 1.05 year^{-1} (65%) for the year-classes 1969–1978 in the same period (A.D. Buijse, unpublished data, 1991). F_{op} was calibrated to simulate these yearly fishing mortalities for both species.

RESULTS

Validation

The model has been used to calculate and evaluate effects of various management measures on the yield and stock of pikeperch and perch. At first a comparison was made between model outcome and observations made on the pikeperch and perch yield and stock.

The length–frequency distribution of the simulated yield and the length–frequency distribution of the actual yield as observed at the fish auction during the 10 year reference period are presented in Fig. 5. The choice of the parameters in the simulation model for the gill net selectivity and the exploitation rate, as based on cohort analysis, yielded a length–frequency distribution for perch similar to the one observed at the fish auction. For pikeperch, the simulated length frequency is bimodal with modes for Age 2 and Age 3 fish. The observed frequency distribution was unimodal, probably due to the

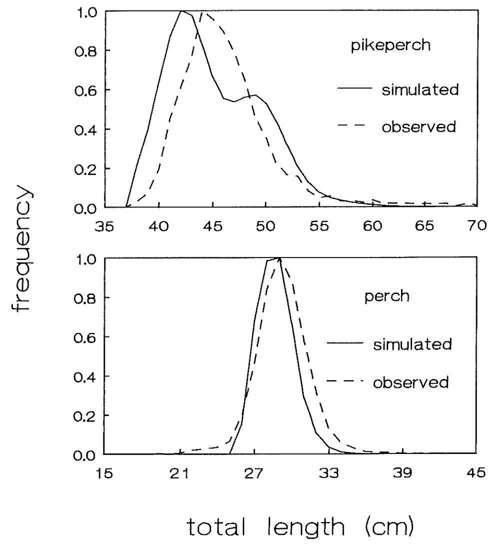

Fig. 5. Observed (the mean during the reference period 1974–1983) and simulated length–frequency distributions of pikeperch and perch catches in 101 mm stretched mesh gill nets.

effect of year-to-year differences in growth, which 'flattened out' the bimodal pattern. The model predicts a considerable proportion of the catch to be below the legal minimum landing size (42 cm), which suggests that discarding occurs on a relatively large scale.

The gill net selectivity appears to have had a most pronounced size-selective impact on the population structure of perch. The mean length-at-age observed in the catch was always larger than the mean length observed in the stock (Fig. 6). Thus, the gill net fishery appears to selectively exploit the larger perch in every age group. Simulated mean lengths-at-age were always higher for the unexploited (Table 2) than for the exploited population (Table 3). The selective impact of the gill nets is also illustrated by the decrease of the standard deviation in the exploited situation. Apparent growth of the observed and simulated exploited stock almost ceased after Age 4 due to the size-selective removal of larger perch (Fig. 6). The observed mean lengths were, however, about 3 cm larger than the simulated ones. This might indicate that the growth parameters used for perch underestimate potential growth.

Pikeperch quickly grow through the selection range of 101 mm gill nets. The Age 2 fish are exploited on the right-hand (larger) side of their size distribution, while Age 4 and older fish were selectively exploited on the left-hand (smaller) side (Tables 2 and 3). Mean lengths in the simulated ex-

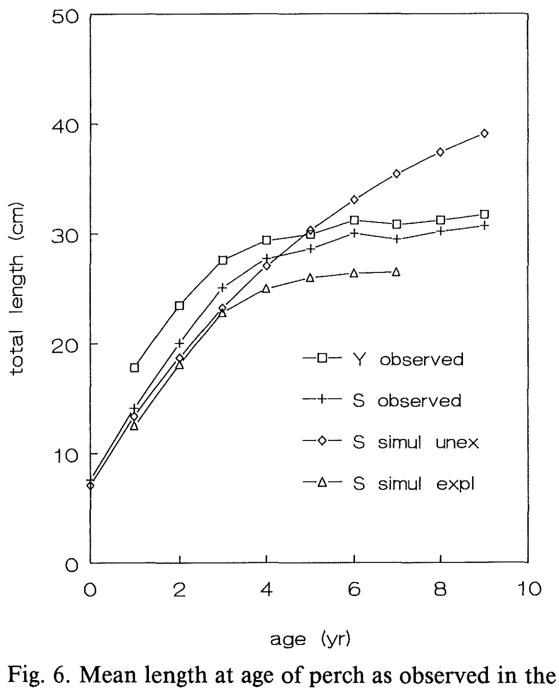

Fig. 6. Mean length at age of perch as observed in the stock (S) and yield (Y) in Lake IJssel over the period 1970–1988 and as simulated in an unexploited and in an exploited stock.

TABLE 3

Simulated mean length, L (cm), and standard deviations, s (cm), at age (years) of male and female pikeperch and perch in a population, which has been exploited with 101 mm gill nets during the reference period (see text for further explanation)

	Age (years)						
	2	3	4	5	6	7	8
Pikeperch ♂							
L	29.9	40.3	49.0	57.0	63.5	67.6	70.6
s	2.6	2.5	2.7	2.7	2.5	2.5	2.5
Pikeperch ♀							
L	29.8	40.9	51.0	59.8	67.0	72.0	76.0
s	2.6	2.5	2.7	2.6	2.5	2.5	2.5
Perch ♂							
L	12.6	18.2	22.7	24.8	25.8	26.2	26.3
s	1.3	2.0	2.3	2.1	1.8	1.6	1.5
Perch ♀							
L	12.4	18.0	22.9	25.2	26.2	26.6	26.7
s	1.2	2.0	2.3	2.0	1.7	1.5	1.3

TABLE 4

Effects of management options in respect of mesh size (MS), effort (f) and length of season, on the yield (Y), stock biomass (SB) and spawning stock biomass (SSB) of pikeperch and perch. Y, SB and SSB of both species are given as percentages of the initial pikeperch SB; values between brackets are percentages of the initial Y and SSB for each species separately (see text for further explanation)

Management option	MS (mm)	f (%)	Open season	Y	SB	SSB
Pikeperch						
Initial situation	101	100	1 July–15 March	58	100	19
1	120	100	1 July–15 March	76(132)	127	18(93)
2	101	25	1 July–15 March	35(61)	343	130(672)
3	101	100	1 October–15 March	55(96)	143	35(183)
	101	25		29(50)		
4			1 July–15 March		136	22(112)
	140	100		49(84)		
Perch						
Initial situation	101	100	1 July–15 March	74	152	43
1	120	100	1 July–15 March	87(119)	268	90(210)
2	101	25	1 July–15 March	81(110)	202	63(145)
3	101	100	1 October–15 March	77(105)	173	45(104)
	101	25		80(109)		
4			1 July–15 March		199	61(141)
	140	100		2(1)		

ploited and unexploited stocks did not differ by more than 1.8 cm. Observations of mean length-at-age in the stock were not available and a comparison between observed and simulated growth could therefore not be made.

The observed yields over the period 1974–1983 were 2.35 kg ha^{-1} and 3.42 kg ha^{-1} for pikeperch and perch, respectively. In the present version, the model does not provide yield in terms of kg ha^{-1}, because recruitment indices are in arbitrary units. However, the ratio between the pikeperch and perch yields can be compared, which for the reference period resulted in a somewhat lower ratio (1.28) than observed (1.46) (Table 4).

Management options for the Lake IJssel gill net fishery

The model was applied to evaluate the effects of four possible management strategies which were considered to represent realistic management options. In Fig. 7 the effects of the different management measures on the yield of pikeperch and perch are shown on a yearly basis during a transitional period until stabilisation. Detailed information on the size and age composition of the yield after stabilisation is given in Fig. 8 and Fig. 9, respectively.

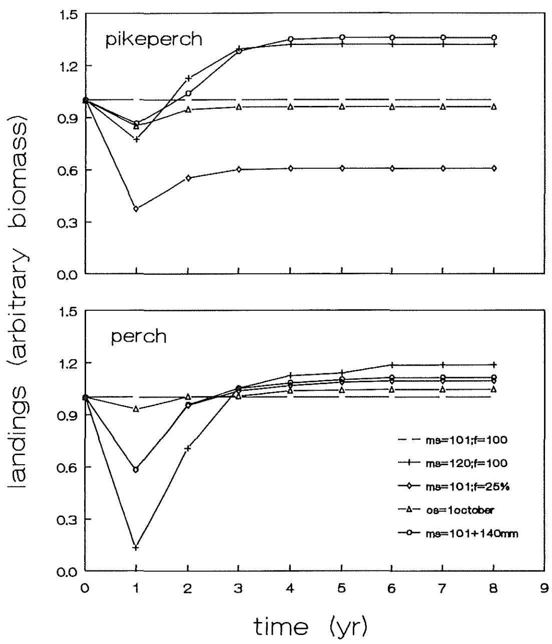

Fig. 7. Development in the yield of pikeperch and perch, relative to the initial situation (ms = 101 mm; f = 100%), in the first 8 years after implementation of four different management options (see also text). ms is the mesh size (mm stretched mesh); f is the relative fishing effort (%); os is the opening of the fishing season.

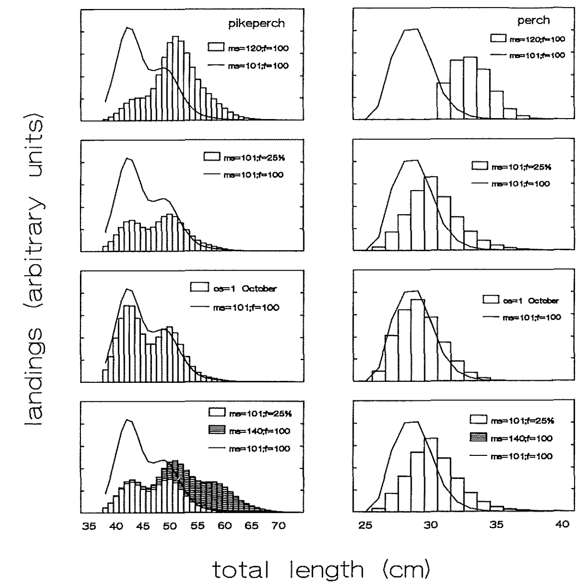

Fig. 8. Length–frequency distributions of the yield of pikeperch and perch. Line indicates the situation during the reference period; bars indicate the length composition after implementation of management measures. ms is the mesh size (mm stretched mesh); f is the relative fishing effort (%); os is the opening of the season.

Since recruitment in the model reflects the observed ratio between the two species, and reference exploitation rates were taken over the same period, changes in the yield and the stock of both species can be compared simultaneously after implementation of a management measure. Consequently, yield and (spawning) stock of both species are given as percentage of the stock biomass of pikeperch under the exploitation rate during the reference period (Table 4).

Option 1. Increase of legal minimum mesh size from 101 to 120 mm

The yield of pikeperch increases, after a reduction of 23% in the first season, to a 32% higher yield after three to four seasons (Fig. 7). The pikeperch stock increases by 25%, whereas the spawning stock decreases slightly (Table 4). An increase in mesh size to 120 mm results in large reductions of 87% and 29% of the perch yield during the first two seasons, but the yield stabilises after 6 years at a 20% higher level. The perch stock increases by 76% and the spawning stock by 110%. Due to the increase in mesh size, the size- and age-structure of the yield changes (Fig. 8 and 9). The number of age groups in the yield stays the same, but the fish are about 1 year older.

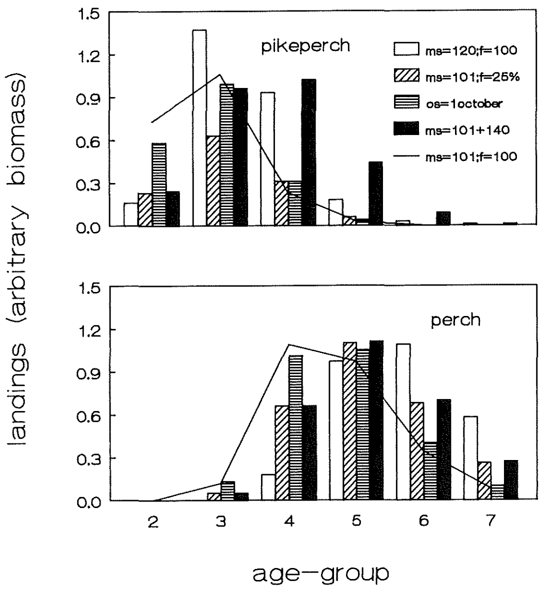

Fig. 9. Age-frequency distributions of the yield of pikeperch and perch. Line indicates the situation during the reference period; bars indicate the age composition after implementation of management measures. ms is the mesh size (mm stretched mesh); f is the relative fishing effort (%); os is the opening of the season.

Option 2. Reduction of fishing effort by 75%

A 75% reduction in the number of gill nets has a negative effect on the total yield of pikeperch. After two to three seasons with a 50–60% lower yield, the yield stabilises at about 60% of the former level (Fig. 7). The pikeperch stock increases by more than 200% and the spawning stock by more than 500%. For perch, the yield stabilises after a decline of 42% during the first year, at a 10% higher level after 4–6 years. The perch stock and spawning stock increase by 33% and 50%, respectively. For both species the yield is more evenly distributed over the age groups than in the original situation (Fig. 9).

Option 3. Extension of the closed season to 1 October

Fishing effort can also be reduced by extending the period in which the fishery is closed, e.g. less fishing days during the week or a shortening of the open season. However, it should be noted that fishermen might respond by setting more nets so that the effect of the measure is lost. A postponement of the start of the fishing season from 1 July to 1 October has been suggested in order to utilise fully the growing season and to reduce, at least temporarily, the fishing effort. In the simulation the numbers of companies fishing during the remainder of the year was as given in Fig. 4.

Shortening of the open season has the most pronounced effect on the (spawning) stock biomass of pikeperch; the yield of both species remain close to the former level. For pikeperch the portion of Age 2 fish in the yield decreases while that of Age 4 fish increases. The pikeperch stock and spawning stock increase by 43% and 83%, respectively. The increase in biomass of perch is much less.

Option 4. 101 and 140 mm gill nets with 75% effort reduction of 101 mm nets

Management of a multispecies fishery will always try to find a compromise between the optimum exploitation rates for the most important individual species, depending on species-related differences in growth and mortality rates. In Lake IJssel, the choice of a minimum mesh size of 101 mm is based on the length at maturity of pikeperch. Short-term losses are large for perch when mesh size is increased, whereas a reduction in fishing effort might result in a permanent lower yield of pikeperch as illustrated by Option 2. Therefore, a compromise was sought by allowing a certain number of 101 mm gill nets in order to catch the perch, but to keep this number low in order not to overex-

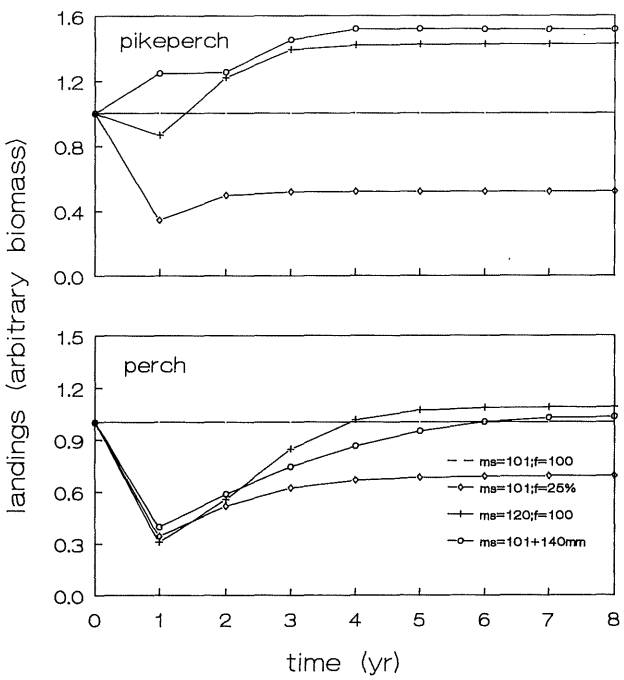

Fig. 10. Development in the yield of pikeperch and perch, relative to the initial situation (ms = 101 mm; f = 100%) and not accounting for size-selective processes, in the first 8 years after implementation of three different management options (see also text). ms is the mesh size (mm stretched mesh); f is the relative fishing effort (%).

ploit the pikeperch stock. In addition a number of 140 mm gill nets is allowed in order to catch the surviving pikeperch, which have spawned several times.

In this model, the effect of using gill nets with different mesh sizes simultaneously can easily be evaluated. The option comprises a 75% effort reduction for 101 mm gill nets, and the introduction of 140 mm gill nets with an effort equal to the effort practised with 101 mm gill nets during the reference period. The yield of pikeperch in the 101 mm gill nets is comparable to the catch after implementing Option 2 (Table 4). The additional yield in the 140 mm gill nets results in a higher total yield after 2 years. Furthermore, the decline in the yield of pikeperch after 1 year is only 14%. After 4–5 years the yield stabilises at 34% above the reference level. The stock and spawning stock are raised by 36% and 12%, respectively. The age composition of the yield shifts to a dominance of Age 3 and 4 instead of Age 2 and 3 fish (Fig. 9). In general, the yield has a more diverse age composition than is the case with other management measures. As perch is seldom caught in 140 mm gill nets, its yield and stock size are comparable with those after implementation of Option 2.

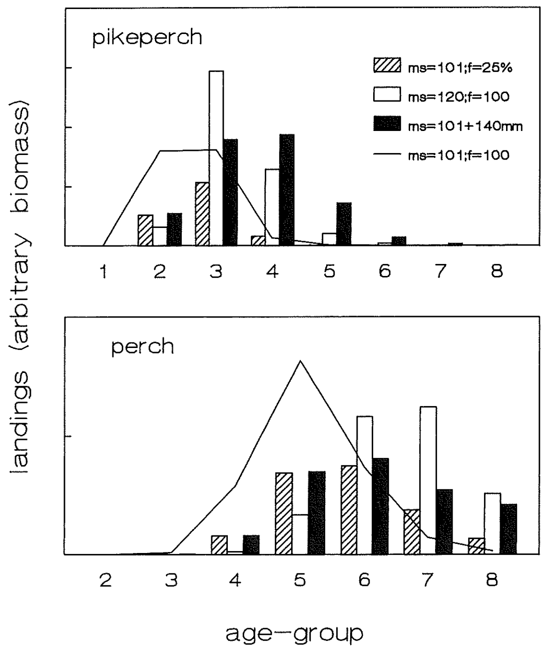

Fig. 11. Age-frequency distributions of the yield of pikeperch and perch, not accounting for size-selective processes. Line indicates the situation during the reference period; bars indicate the age composition after implementation of management measures. ms is the mesh size (mm stretched mesh); f is the relative fishing effort (%).

Size- versus age-structured models

The results of our size-structured model were compared with an age-structured version of the same model. In the age-structured version, all fish of the same age have the same length, which corresponds with the calculations based on the Von Bertalanffy growth parameters (Table 2). The size-structure within age groups is therefore not modified by the fishery. The gill net selectivity was estimated by using mean length-at-age in eqn. (7).

Especially for perch, large differences in the total yield and the age composition of the yield are found between the size-structured (Figs. 7 and 9) and age-structured versions of the model (Figs. 10 and 11): the decline after increasing the minimum legal mesh size to 120 mm was smaller for the age-structured version; a considerable amount of perch is landed by 140 mm gill nets; the age-structured model predicts a permanent reduction in the yield of perch if only the effort of 101 mm gill nets is reduced. Dominant age groups in the yield of perch were about 1 year older in the age-structured than in the size-structured version. In the age-structured version, the ultimate gain of pikeperch when the Options 1 and 4 were applied was slightly higher and the ultimate loss in the case of Option 2 was slightly more, than in the size-structured model. Also, for both species the importance of the dominant age group in the yield is more pronounced in the age-structured version of the model. All these differences are the consequence of not taking into account the size-selective impact of fishing gear.

DISCUSSION

A size- and age-structured dynamic pool model has been developed to integrate existing knowledge on the population dynamics of pikeperch and perch in Lake IJssel. The differentiation into size categories was deliberately chosen, because interactions between gears and species are more directly related to size than to age.

The 'fractional boxcar train method', introduced to control growth dispersion within an age group, clearly allows an evaluation of the size-selective impact of gill nets on a fish stock, which has been considered an important limitation of other existing models for gill net fisheries (Berkes and Gönenc, 1982). Calculations with other types of models, which were based on individuals (10 000 $\pm$ 2000 recruits) and characterised by specific values of L_∞ and k taken randomly from assumed normal distributions (Hampton and Majkowski, 1987), appear to be much more time-consuming than our model (which used eight age groups divided over 100 size-classes).

The present version of our model has a number of limitations. First, uncertainty exists with respect to the potential growth and natural mortality of pikeperch and perch in unexploited situations. Willemsen (1983) stated that his estimate for the potential growth of pikeperch is conservative. For perch there are, to date, no estimates of potential growth. The opercula which were used to calculate the growth were taken from the perch population in Lake IJssel. Age 4 and Age 5 perch had already been exploited by the gill net fishery there, so their size distributions were probably altered by size-selective removal of the larger specimens. Although Willemsen (1977) describes faster growth of perch in Lake IJssel, which is more in line with the observed growth, we preferred to use our own data, because they contained information on sexual differences in growth rate. Estimates of natural mortality for the currently exploited age groups are tentative. For perch, natural mortality varied largely from year to year and a well-founded choice for Age 3 and older could not be made (Born, 1991). Hence a constant value of $M=0.2$ year^{-1} for larger fish, as assumed in many other situations, was chosen.

Second, it is known that some fishermen use gill nets with mesh sizes larger than the legal minimum in order to catch large pikeperch. Calculations were made under the assumption that in the case of a minimum legal mesh size, either 101 or 120 mm gill nets were used. This has probably resulted in unrealistic underestimations of the yield and a too high (spawning) stock biomass in the case of fisheries with 101 mm gill nets only.

Third, the model is density-independent and therefore acts just as a refined Beverton and Holt yield-per-recruit model. Up to now, stock-recruitment relationships have not been quantified, but inter- and intra-specific interactions in respect of recruitment might alter the results of simulations significantly. Although, the food web structure is known, estimates of energy fluxes are uncertain (Buijse et al., 1991). Once quantified, density-dependent processes will be incorporated into the model as has been done for, for example, walleye, *Stizostedion vitreum* (Jensen, 1989).

Fourth, recruitment was held constant in the present version of the model. Variation in recruitment will not influence the consequences of management measures in terms of maximum yield, as long as density-dependent processes for the two stocks are not incorporated in the model. Variation in recruitment has, however, a direct effect on the stability of the yield. Therefore management strategies should in future be evaluated on the basis of maximum yield as well as stability in the yield.

So far the model could only be validated by comparing the size and age structure of the simulated and of the observed yield and stock. Although there is a high degree of similarity, there appear to be marked differences, which might be resolved by specific data collections. In particular, discard practices appear to be an important issue.

Simulation of the different management strategies indicate that all options have a positive influence on the spawning stock size of both species, with the exception of pikeperch in the case where the legal minimum mesh size is increased to 120 mm. A substantial permanent reduction of the yield was observed only for pikeperch when the fishing effort with 101 mm gill nets is reduced by 75% and no other mesh size is allowed, because pikeperch quickly grew through the selection curve. Considering the losses during the transitional period and the gain thereafter, the combination of a reduced number of 101 mm gill nets with the addition of 140 mm gill nets, seems to be the most profitable management strategy.

Due to the model being size-structured, it appears to be very suitable for analysing the impact of gill net fisheries on the size- and age-structure of the fish stocks. Many different methods have been suggested for calculation of the gill net selectivity (Hamley, 1975). The model is readily capable of evaluating the effect of different approaches to selection curves, like unimodal curves with constant efficiency (Holt, 1963) or bimodal curves with increasing efficiency for larger mesh sizes (Hamley and Regier, 1973).

ACKNOWLEDGEMENTS

We are grateful to Marco Faasse, Tom van de Akker and Gon van Laar for their contributions to the development of the model; Henk Oudelaar (Ministry of Agriculture, Nature Conservation and Fisheries, Department of Coastal and Inland Fisheries and Cultures) for supplying bottom trawl survey data on the fish stocks in Lake IJssel; Leo Schaap (Netherlands Institute for Fisheries Research) for supplying data on size and age distribution of pikeperch and perch in the commercial yield from the gill net fishery; Prof. Dr. Niels Daan, Willem Dekker and Prof. Dr. Bram Huisman for critically reviewing the manuscript.

REFERENCES

Anonymous, 1969–1982. Visserij, voorlichtingsblad voor de Nederlandse visserij (Fishery, Information Journal for the Dutch Fishery). Ministry of Agriculture and Fisheries. Vols. 22–35 (in Dutch).

Berkes, F. and Gönenc, T., 1982. A mathematical model on the exploitation of northern lake whitefish with gill nets. North Am. J. Fish. Manage., 2: 176–183.

Beverton, R.J.H. and Holt, S.J., 1957. On the dynamics of exploited fish populations. Fish. Invest. Minist. Agric. Fish. Food (G.B.) Ser. II Mar. Fish. 19. 533 pp.

Born, A.F., 1991. Schattingen van de aantallen en de mortaliteit van baars (*Perca fluviatilis*) in het IJssel- en Markermeer in de periode 1969–1987 (Estimations of numbers and mortalities of perch (*Perca fluviatilis*) in the IJssel- and Markermeer in the period 1969–1987). Department of Fish Culture and Fisheries, Agricultural University Wageningen. M.Sc. thesis no. 1337. 53 pp. (in Dutch).

Buijse, A.D., Van Eerden, M.R., Dekker, W. and Van Densen, W.L.T., 1991. A trophic model for IJsselmeer (The Netherlands), a shallow eutrophic lake. In: V. Christensen and D. Pauly (Editors), Trophic Models of Aquatic Ecosystems. ICLARM Conference Proceedings, No. 26.

Collins, J.J., 1979. Relative efficiency of multifilament and monofilament nylon gill net towards lake whitefish (*Coregonus clupeaformis*) in Lake Huron. J. Fish. Res. Board Can., 36: 1180–1185.

Dekker, W., 1983. An application of the Andersen consumption model in estimating prey size preference in North Sea cod. ICES CM 1983/G:63, 16 pp.

Dekker, W., 1991. Assessment of the historical downfall of the IJsselmeer fisheries using anonymous inquiries for effort data. In: I.G. Cowx (Editor), Catch Effort Sampling Strategies and Their Application in Freshwater Fisheries Management. Fishing News Books, Blackwell Scientific Publications, Oxford, pp. 233–240.

De Wit, C.T., 1982. Coordination of models. In: F.W.T. Penning de Vries and H.H. van Laar (Editors), Simulation of plant growth and crop production. Pudoc, Wageningen, pp. 26–31.

De Wit, C.T. and Goudriaan, J., 1978. Simulation of ecological processes. Pudoc, Wageningen, 175 pp.

Goudriaan, J. and Van Roermund, H.J.W., 1989. Modelling of ageing, development, delays and dispersion. In: R. Rabbinge, S.A. Ward and H.H. van Laar (Editors), Simulation and Systems Management in Crop Protection. Pudoc, Wageningen, pp. 47–79.

Hamley, J.M., 1975. Review of gillnet selectivity. J. Fish. Res. Board Can., 32: 1943–1969.

Hamley, J.M. and Regier, H.A., 1973. Direct estimates of gillnet selectivity to walleye (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can., 30: 817–830.

Hampton, J. and Majkowski, J., 1987. A simulation model for generating catch length–frequency data. In: D. Pauly and G.R. Morgan (Editors), Length-based Methods in Fisheries Research. ICLARM Conference Proceedings 13. ICLARM, Manila, Philippines, pp. 193–202.

Hightower, J.E. and Grossman, G.D., 1987. Optimal policies for rehabilitation of overexploited fish stocks using a deterministic model. Can. J. Fish. Aquat. Sci., 44: 803–810.

Hokanson, K.E.F., 1977. Temperature requirements of some percids and adaptations to the seasonal temperature cycle. J. Fish. Res. Board Can., 34: 1524–1550.

Holt, S.J., 1963. A method for determining gear selectivity and its application. ICNAF Spec. Publ., 5: 106–115.

IBM, 1975. Continuous System Modeling Program III. Program reference manual SH19-7001-2. Techn. Publ. Dept., White Plains, USA.

Jacobson, P.C. and Taylor, W.W., 1985. Simulation of harvest strategies for a fluctuating population of lake whitefish. North Am. J. Fish. Manage., 5: 537–546.

Jensen, A.L., 1989. Simulation of the potential for life history components to regulate walleye population size. Ecol. Modelling, 45: 27–41.

Le Cren, E.D., 1947. The determination of the age and growth of the perch (*Perca fluviatilis*) from the opercular bone. J. Anim. Ecol., 16: 188–204.

Le Cren, E.D., 1958. Observations on the growth of perch (*Perca fluviatilis* L.) over twenty-two years, with special reference to the effects of temperature and changes in population density. J. Anim. Ecol., 27: 287–334.

McCombie, A.M. and Berst, A.H., 1969. Some effects of shape and structure of fish on selectivity of gillnets. J. Fish. Res. Board Can., 26: 2681–2689.

Pet, J.S., 1988. An interactive size- and age-structured simulation model for the gillnet fishery on pikeperch and perch in Lake IJssel. M.Sc.Thesis Agricultural University Wageningen. Department of Fish Culture and Fisheries (Rep. No. 1276) and Department of Theoretical Production Ecology, 126 pp.

Peterson, I. and Wroblewski, J.S., 1984. Mortality rates of fishes in the pelagic ecosystem. Can. J. Fish. Aquat. Sci., 41: 1117–1120.

Pitcher, T.J. and Hart, P.J.B., 1982. Fisheries ecology. Croom Helm, London, 414 pp.

Ricker, W.E., 1958. Handbook of computations for biological statistics of fish populations. Bull. Fish. Res. Board Can., 119: 300 pp.

Schaap, L.A., 1987. Vergelijking van de vangsten in mono- en multifilament staande netten in het IJsselmeer (Comparison of catches in mono- and multifilament gill nets in Lake IJssel). Netherlands Institute for Fishery Research, IJmuiden, Report BV 87-03, 12 pp. (in Dutch).

Silvestre, G.T. and Soriano, M.L., 1988. Effect of incorporating sigmoid selection on optimum mesh size estimation for the Samar Sea multispecies trawl fishery. In: S. Venema, J. Möller-Christensen and D. Pauly (Editors), Contributions to Tropical Fisheries Biology: Papers presented by the participants of FAO/DANIDA Follow-up training courses. FAO Fish. Rep. No. 389, pp. 482–492.

Sissenwine, M.P., 1977. A compartmentalized simulation model of the southern New England yellowtail flounder, *Limanda ferruginea*, fishery. Fish. Bull., 75: 465–482.

Staub, E., Büttiker, B. and Krämer, A., 1987. Grundlagen für Modellsimulationen zur Bewirtschaftung des Barsches (*Perca fluviatilis* L.) im Bodensee. Bundesamt für Umweltschutz, Bern. Schriftenreihe Fisherei, Nr. 46, 40 pp.

Thorpe, J.E., 1977. Morphology, physiology, behavior, and ecology of *Perca fluviatilis* L. and *P. flavescens* Mitchill. J. Fish. Res. Board Can., 34: 1504–1514.

Van Densen, W.L.T., 1987. Gillnet selectivity to pikeperch, *Stizostedion lucioperca* (L.), and perch, *Perca fluviatilis* L., caught mainly wedged. Aquacult. Fish. Manage., 18: 95–106.

Van Densen, W.L.T., Cazemier, W.G., Dekker, W. and Oudelaar, H.G.J., 1990. Management of the fish stocks in Lake IJssel, the Netherlands. In: W.L.T. van Densen, B. Steinmetz, R.H. Hughes (Editors), Management of Freshwater Fisheries, Proceedings of a symposium organized by the European Inland Fisheries Advisory Commission, Göteborg, Sweden, 31 May–3 June 1988. Pudoc, Wageningen, pp. 313–327.

Willemsen, J., 1977. Population dynamics of percids in Lake IJssel and some smaller lakes in the Netherlands. J. Fish. Res. Board Can., 34: 1710–1719.

Willemsen, J., 1978. Influence of temperature on feeding, growth and mortality of pikeperch and perch. Verh. Int. Ver. Limnol., 20: 2127–2133.

Willemsen, J., 1983. Biology and management of pikeperch. Proc. 3rd. Br. Freshwater Fish. Conf., pp. 115–125.