

Zeitschrift: Bulletin de la Société Vaudoise des Sciences Naturelles
Herausgeber: Société Vaudoise des Sciences Naturelles
Band: 82 (1992-1993)
Heft: 1

Artikel: Simulation of perch (*Perca fluviatilis* L.) : population dynamics in Lake Constance
Autor: Büttiker, Bernard / Staub, Erich
DOI: <https://doi.org/10.5169/seals-280166>

Nutzungsbedingungen

Die ETH-Bibliothek ist die Anbieterin der digitalisierten Zeitschriften auf E-Periodica. Sie besitzt keine Urheberrechte an den Zeitschriften und ist nicht verantwortlich für deren Inhalte. Die Rechte liegen in der Regel bei den Herausgebern beziehungsweise den externen Rechteinhabern. Das Veröffentlichen von Bildern in Print- und Online-Publikationen sowie auf Social Media-Kanälen oder Webseiten ist nur mit vorheriger Genehmigung der Rechteinhaber erlaubt. [Mehr erfahren](#)

Conditions d'utilisation

L'ETH Library est le fournisseur des revues numérisées. Elle ne détient aucun droit d'auteur sur les revues et n'est pas responsable de leur contenu. En règle générale, les droits sont détenus par les éditeurs ou les détenteurs de droits externes. La reproduction d'images dans des publications imprimées ou en ligne ainsi que sur des canaux de médias sociaux ou des sites web n'est autorisée qu'avec l'accord préalable des détenteurs des droits. [En savoir plus](#)

Terms of use

The ETH Library is the provider of the digitised journals. It does not own any copyrights to the journals and is not responsible for their content. The rights usually lie with the publishers or the external rights holders. Publishing images in print and online publications, as well as on social media channels or websites, is only permitted with the prior consent of the rights holders. [Find out more](#)

Download PDF: 14.04.2026

ETH-Bibliothek Zürich, E-Periodica, <https://www.e-periodica.ch>

Simulation of Perch (*Perca fluviatilis* L.) Population Dynamics in Lake Constance

BY

BERNARD BÜTTIKER¹ and ERICH STAUB²

Résumé.—BÜTTIKER B. et STAUB E., 1992. Simulation de la dynamique des populations de perches (*Perca fluviatilis* L.) dans le lac de Constance. *Bull. Soc. vaud. Sc. nat.* 82.1: 67-85.

La pêche de la perche constitue l'une des ressources piscicoles les plus intéressantes des grands lacs suisses. Dans ces lacs, les populations de perches se caractérisent par une mortalité naturelle et une croissance élevées. Nous avons développé un programme de simulation sur ordinateur, dans le but d'examiner l'influence des mesures de gestion sur le rendement piscicole. Les premiers résultats ont été obtenus pour les populations de perches du lac de Constance. Ils indiquent que la dimension minimale des mailles des filets, fixée actuellement à 32 mm, donne de bons rendements piscicoles et ne devrait pas être augmentée.

Abstract.—BÜTTIKER B. and STAUB E., 1992. Simulation of Perch (*Perca fluviatilis* L.) Population Dynamics in Lake Constance. *Bull. Soc. vaud. Sc. nat.* 82.1: 67-85.

The fishing of perch (*Perca fluviatilis* L.) is of major importance in the larger Swiss lakes. Perch populations in these lakes are characterized by high natural mortality and growth rates. To get a better understanding on how a perch population and its fishing yield are dependent upon management and fishing rules, a computer program for the simulation of perch populations was developed and tested. First results concerning the management of perch in Lake Constance are presented. They show that the minimum legal mesh size of 32 mm for gillnets is a good policy and should not be increased.

¹Conservation de la faune, chemin du Marquisat 1, CH-1025 St-Sulpice, Switzerland.

²Bundesamt für Umwelt, Wald und Landschaft, Hallwylstrasse 4, CH-3003 Berne, Switzerland

1. INTRODUCTION

Perch (*Perca fluviatilis* L.) is one of the most important fish species for commercial fisheries in Switzerland. As a consequence, the fishing effort for perch is high in all larger Swiss lakes. The yield amounts to about 30% of the mean total landings of 3,000 tons per year.

Important interannual fluctuations of the perch catch (2- to 10- fold in Lake Constance) and substantial differences in the legal mesh size for perch nets in different Swiss lakes, ranging from 23 mm in Lake Geneva to 34 mm in lower Lake Constance, raise the question of optimal fishing policy. For decision-making, a better understanding of the main factors governing perch population dynamics and a tool to compare the effect of different management alternatives are necessary.

Much information is available on the biology of perch in Lake Constance, especially from the partially published data of HARTMANN and KRÄMER. The data used in this study have been compiled in STAUB *et al.* (1987). We developed a computer program for the simulation of fish population dynamics and tested it with the biological data on Lake Constance perch.

The aim of this paper is to describe the concept of our model approach and the performance of the simulation program. Furthermore, our initial results provide advice for the future management of perch in Lake Constance.

2. MATERIAL AND METHODS

2.1. Description of the simulation program

The program was designed following the model of MENSHUTKIN and ZHAKOV (in THORPE 1977) and the "self-generating stock model" of TYLER and GALUCCI (1980; chap. 5.5). It is described by the simplified flow chart shown in Figure 1.

The program computes all important data on the fish population in bimonthly time steps (24 steps/year), separately for 7 age classes, and for both males and females. A run starts with 500,000 males and 500,000 females of the age class 1 in June. The main results of a run concern, for each age class, the number of surviving fish after mortality, the number and weight of fish caught, and the size distribution within the age classes. For the spawning time, it computes the number and biomass of the spawners and the number of eggs produced.

During each time interval, the perch population is subjected to the VON BERTALANFFY growth function, the exponential survival function and the BARANOV catch function (Table 1, Eq. 1 to 3).

The fish length in each age class and sex is normally distributed (Table 1, Eq. 4) among 11 length classes of equal width. Based on the observed data, the standard deviation, σ , is 6% of the mean length (STAUB *et al.*, 1987). The fish that fall outside of the 99% confidence limits (mean $\pm 2.6 \sigma$) of the length

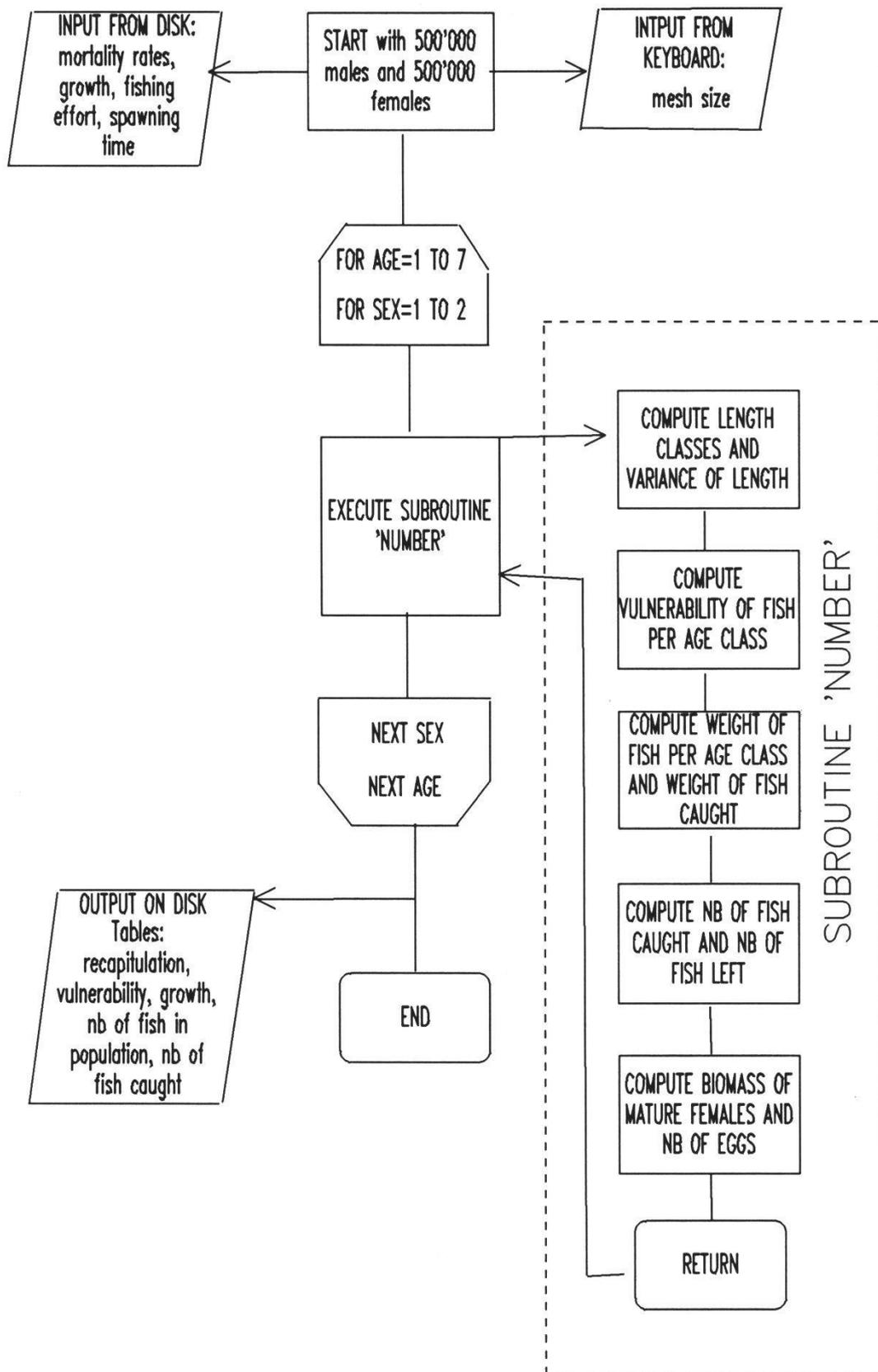


Figure 1.—Simplified flow chart of the simulation program.

Table 1.—Basic functions and values used in the simulation model (Compiled in STAUB *et al.* 1987). Numbers in brackets mean alternative growth or mortality coefficients used.

number	function	unit	values used in this study	
			males	females
1. VON BERTALANFFY growth function:				
	$L(t) = L_{\infty} (1 - \text{EXP}[-K(t-t_0)])$			
where	$L(t)$: fish length at time t	cm		
	L_{∞} : asymptotic length	cm	25.5	28.8
	K : growth coefficient	year ⁻¹	0.53 (0.43)	0.48 (0.39)
	t : time	year	1 to 7	1 to 7
	t_0 : correction for time	year	0.2857	0.3005
2. Exponential survival function:				
	$N(t+dt) = N(t) \text{VULN} \text{EXP}[-dt(M+E F)]$			
where	$N(t)$: number of fish at time t			
	dt : time step	1/24 year		
	VULN : vulnerability to fishing		0 to H_{ms} (see eq. (5))	0 to H_{ms}
	M : instantaneous rate of natural mortality	year ⁻¹	0.8 (0.5)	0.7 (0.4)
	E : fishing effort in time step		(see Table 2)	
	F : instantaneous rate of fishing mortality	year ⁻¹	1.5 (1.8)	2.1 (2.4)
3. BARANOV catch function:				
	$C = N \text{VULN} E F (M+E F) (1 - \text{EXP}[-dt(M+E F)])$			
where	C : number of fish caught in 1 time step (dt)			
	N : number of fish at time t			
4. normal distribution:				
	$Y = \text{EXP}[-0.5 ((X-\mu)/\sigma)^2 / (\sigma\sqrt{2\pi})]$			
where	μ : mean value			
	σ : standard deviation			
5. Amplitude of the selectivity function:				
	$H_{ms} = (L_{opt,ms} / L_{opt,b})^f$			
where	ms : mesh size	mm		
	$L_{opt,ms}$: optimal fish length for mesh size ms	cm	0.704 ms	
	$L_{opt,b}$: optimal fish length for reference mesh size b	cm		
	f : factor for cruising speed of fish		0.5	0.5
6. Number of eggs produced:				
	$NE = a L^b$			
where	NE : number of eggs produced per female			
	a : coefficient		2.85	
	b : coefficient		2.94	
	L : length of female	cm		
7. Length-weight function:				
	$W = a L^b$			
where	W : weight of one fish	g		
	a : coefficient		0.011	0.011
	b : coefficient		3.037	3.037

distribution are neglected. The fish are regrouped among the length classes after each time step, considering growth.

The perch are assumed to grow only from mid-June through the end of September. The VON BERTALANFFY growth function gives the length of the fish of each age class at the beginning and end of the growing season.

The selectivity functions of the gillnets (Fig. 2) have been computed using the method of HOLT (1963). The amplitude of each selectivity function depends on the cruising speed of the fish (RUDSTAM *et al.* 1984), which is proportional to fish size, and, therefore, increases with increasing mesh size. It is defined to be unity for 32 mm mesh size (the reference mesh size in this study), which is the minimum mesh size used for commercial perch fishery in Lake Constance. The amplitude of the selectivity function for all other mesh sizes is given by Eq. 5 in Table 1. Its exponent, $f=0.5$, falls within the range of different experimental (see RUDSTAM *et al.* 1984) and theoretical (BAINBRIDGE 1961) values. Its standard deviation is set to 40% of the mesh size.

The program is written in TURBO BASIC language.

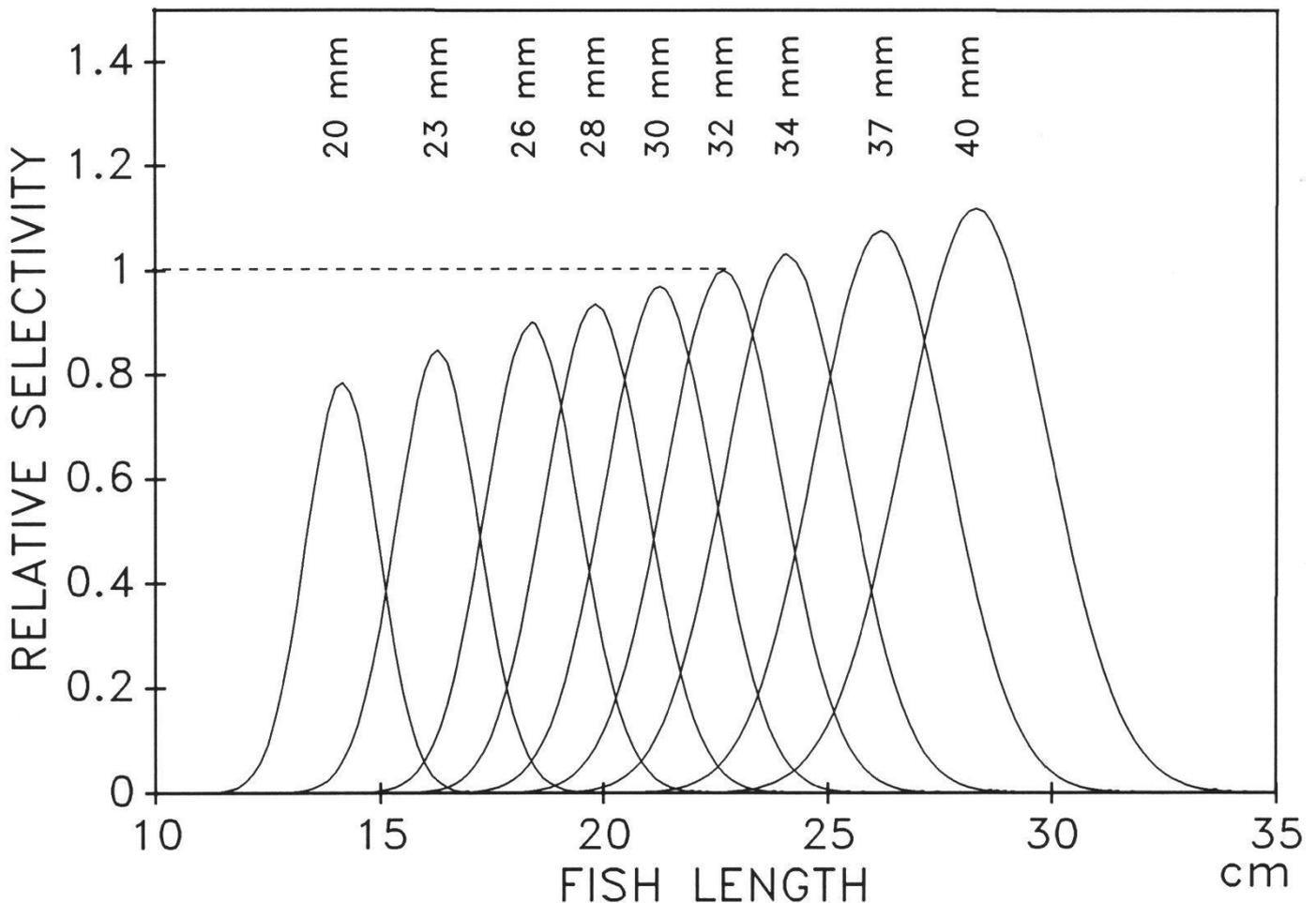


Figure 2.—Gillnet selectivity curves for perch in Lake Constance in relation to the total fish length. The mesh sizes are given above each corresponding curve. The reference mesh size is 32 mm, and its amplitude is 1.

2.2. *The relative amount of fish vulnerable to the fishing gear*

The relative amount of fish vulnerable to the fishing gear, *VULN* (see Table 1), is the product of the length distribution of the fish and the selectivity function of the fishing gear.

Figure 3, A and C, show the distribution of *VULN* for female perch of the age classes 3+ and 5+, each in the first half of June. The resulting values range from 0 (fish too small or too large to be caught) to a maximum value equal to the amplitude of the selectivity function. This maximum value is reached if the optimum of the fish length distribution corresponds to the optimum of the selectivity function.

2.3. *Input data for the simulation*

All mesh size values given in this paper correspond to the local knot to knot measuring method using 1 kg weight for stretching the net. They must be reduced by 7 % if they are compared to unstretched mesh sizes.

The input data for the program are given in Tables 1 and 2. These fundamental data are saved in a file read in each run. The mesh size of the gillnets used and, optionally, the level of fishing effort are entered in each run interactively.

The simulations have been run assuming two strategies:

- fishing with unique mesh sizes (20, 23, 26, 28, 30, 32, 34, 37 and 40 mm);

- fishing with a lower mesh size limit from 20 through 40 mm (as for unique mesh size) and an upper mesh size limit of 44 mm, which corresponds to the upper mesh size normally used in Lake Constance. If mesh size ranges are used, the program works with a selectivity function composed of a selectivity function for the smaller mesh size and a separate one for the 44 mm mesh size. The amplitude is equal to the amplitude of the selectivity function of the smaller mesh size. The composed selectivity curve for a lower mesh size of 32 mm and the vulnerability of 3+ and 5+ female perch are shown in Figure 3, B and D.

As fishermen seldom adapt the mesh sizes of their nets to fish growth, the simulation with unique mesh sizes seems reasonable. The strategy with composed mesh sizes could, nevertheless, be closer to reality: in spite of the fact that fishermen do not use larger meshed nets to catch big perch, these fish are actually caught in the coarser nets intended for other fish species. Therefore, unless otherwise specified, the mesh sizes used in this work stand for the lower mesh size limit with an upper mesh size limit of 44 mm.

2.4. *Data on observed population structure and water temperature*

Catch survey data collected by HARTMANN (unpublished data) from 1976 to 1981 and by local Swiss fishery administrations (KRÄMER, unpublished data) from 1982 to 1990 were used. These data include length, weight, age, and sex

of perch collected monthly with 32 mm gillnets (legal gear for commercial fishery). Information on total monthly perch catch are also available.

Water temperature is measured daily at the outflow of Lake Constance (FEDERAL OFFICE OF ENVIRONMENT, FORESTRY AND LANDSCAPE 1975 and following).

Table 2.—Input data used for the simulation

a) annual variation of relative fishing efforts E
(annual mean=1; values of 0.00 signify total protection)

month	1st half	2d half	month	1st half	2d half
January	0.93	0.93	July	1.56	1.56
February	0.93	0.93	August	1.56	1.56
March	0.93	0.93	September	1.56	1.56
April	0.93	0.93	October	1.17	1.17
Mai	0.00	0.93	November	0.93	0.00
June	0.93	1.17	December	0.00	0.93

b) percent of mature females per age class

age	% mature
1+	50
2+	100
3+ and older	100

c) life-cycle

date of hatching
(= begin of biological year) : 1st June
date of spawning period : mid May
begin of growth period : second half of June
end of growth period : second half of September

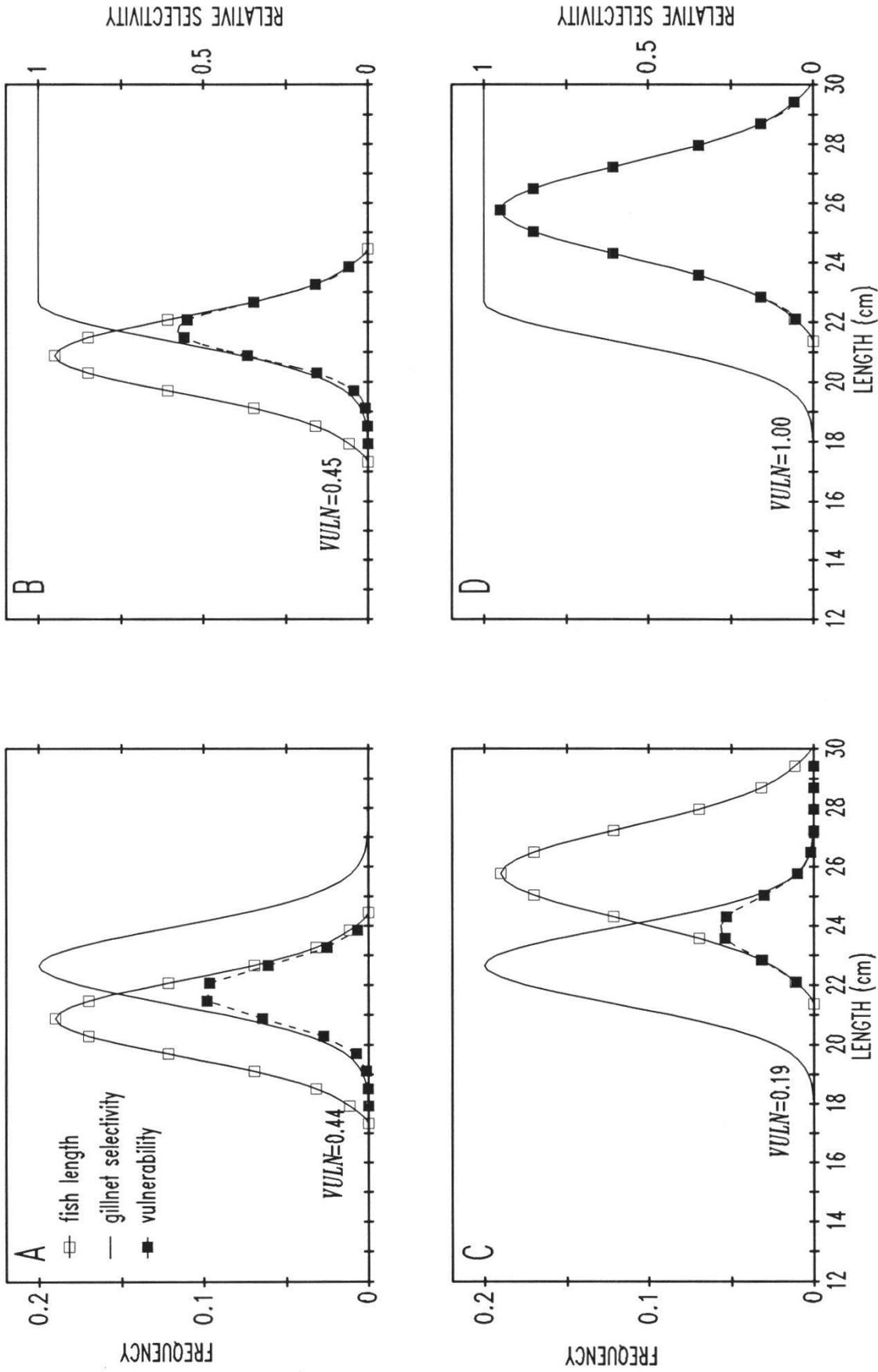


Figure 3.—The vulnerability of perch to fishing with gillnets. The relative fish length frequency distribution of the 3+ (A & B) and 5+ (C & D) female perch, each in the first half of June, the selectivity curves for single 32 mm gillnets (A & C) and the combined selectivity curves for 32 to 44 mm gillnets (B & D), and the relative vulnerability (product of the length frequency distribution and selectivity), are shown. *VULN*: total vulnerability = sum of the vulnerabilities of each 1 cm length class.

3. RESULTS

3.1. How do yield and egg production respond to the mesh size of the gillnets used in commercial fishery ?

The total catch and egg production for one cohort, followed through the seven-year period and caught with nets of different mesh sizes, was simulated with 3 different basic assumptions: a) standard settings for natural mortality and fishing with a range of mesh sizes; b) reduced natural mortality (alternative values in Table 1) and fishing with a range of mesh sizes; and c) standard settings and fishing with only one mesh size. The results are shown in Figure 4.

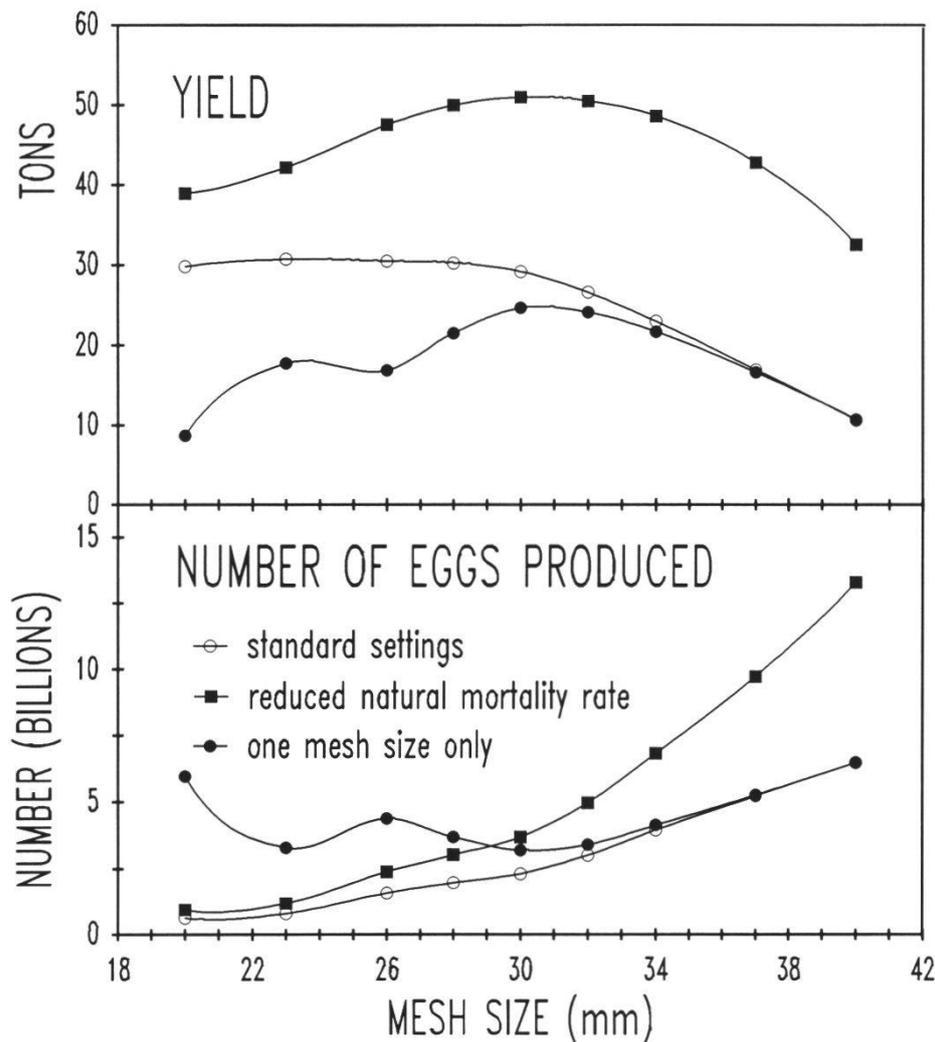


Figure 4.—Simulated annual yield and egg production for 1 million 1-year-old perch, plotted in relation to the lower mesh size limit of gillnets. Standard settings: standard natural and fishing mortality rates (see Table 1) and combined selectivity function (with 44 mm upper mesh size). Reduced natural mortality rate : see alternative values for M in Table 1. One mesh size only: standard natural and fishing mortality rates and selectivity function for single mesh sizes.

For assumption a), yield is not strongly dependent on minimum mesh size up to about 30 mm, and decreases for larger mesh sizes. For assumption b), the yield reaches a maximum value at about 30 mm mesh size. These results suggest that the simulated yield is extremely sensitive to the values assumed for the natural mortality rate. For the rather unrealistic assumption c), the yield also reaches a maximum value for about 30 mm mesh size.

The egg numbers increases with increasing mesh size (more surviving females), except under assumption c). In this case, several maxima appear below 30 mm mesh size. This can be explained by the survival of females larger than selectivity range.

Figure 5 shows that the proportion of females caught (66%) is higher than for males. This is a consequence of more rapid female growth rates, as well as the fact that males are exposed for a longer time to a higher natural mortality. This simulated sex ratio in the simulated catch agrees well with the sex ratio observed in the real catch (a mean of 61 % females for the cohorts 1980 to 1987).

For a simulated exploitation using 32 mm nets, the age classes 2+, 3+ and 4+ are nearly exclusively represented in the catch (Fig. 5). This also agrees with the occurrence of age classes in the observed catch (STAUB and KRÄMER 1991).

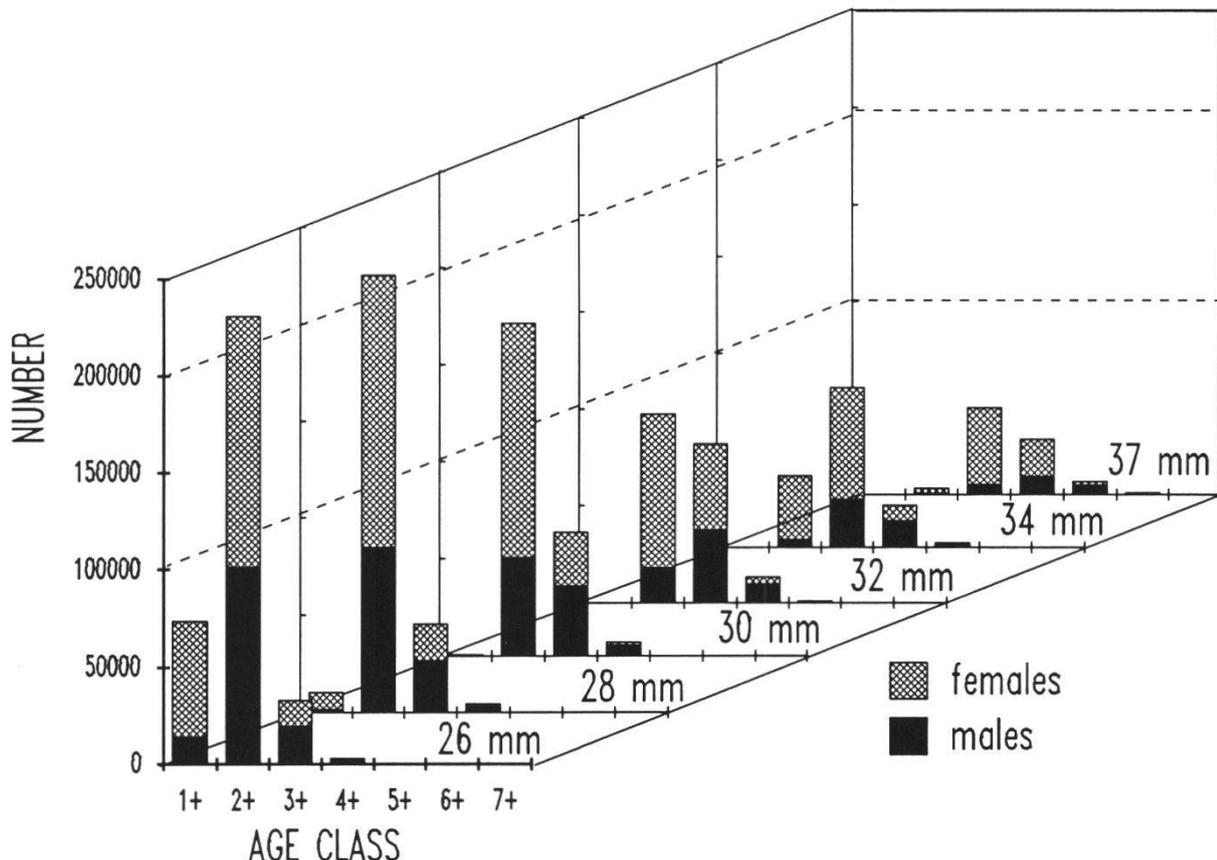


Figure 5.—Number of perch caught per age class (assuming a start with 500,000 1-year-old females and 500,000 1-year-old males) versus lower mesh size limit, assuming composed selectivity functions with an upper mesh size limit of 44 mm.

3.2. Simulation of catch curves

The catch curves for males and females (i.e. the virtual number of fish in a cohort) are represented in the left part of Figure 6 A, for a simulation run based on 32 mm mesh size, and standard settings for natural and fishing mortality. The virtual population of perch decreases about 100 times after an exploitation period of 2.5 to 3 years. A decrease of the same magnitude was observed in Lake Constance for strong cohorts, for example the cohorts 1973 and 1976 (Fig. 6, B). For the weaker cohorts 1980 and 1983 (Fig. 6, C), the correspondence with the simulated catch curves is not as good. This might be a consequence of density-dependent growth rates and different fishing effort in years with a low yield. Methodological problems in estimating the virtual population, such as underestimation of weak cohorts in the presence of a strong one, is another possible explanation.

The similarity of the shape and of the steepness of the simulated and the observed catch curves suggests that the model is a good representation of the actual dynamics of fish populations in Lake Constance.

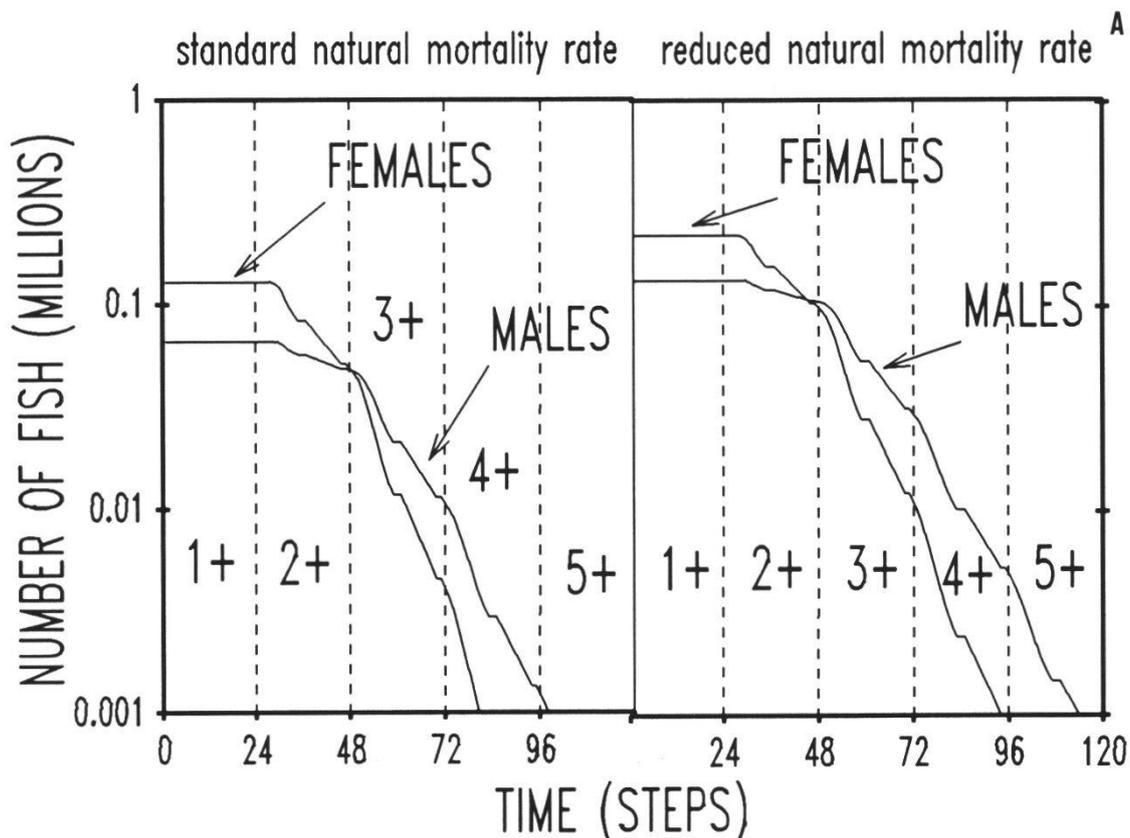


Figure 6.-A: simulated catch curves (virtual population), for fishing with composed mesh sizes, with a 32 mm lower mesh size limit and a 44 mm upper mesh size limit. Twenty-four time steps represent one year. Vertical dashed lines: 1st of June. Left: standard mortality rates. Right: reduced instantaneous rate of natural mortality.

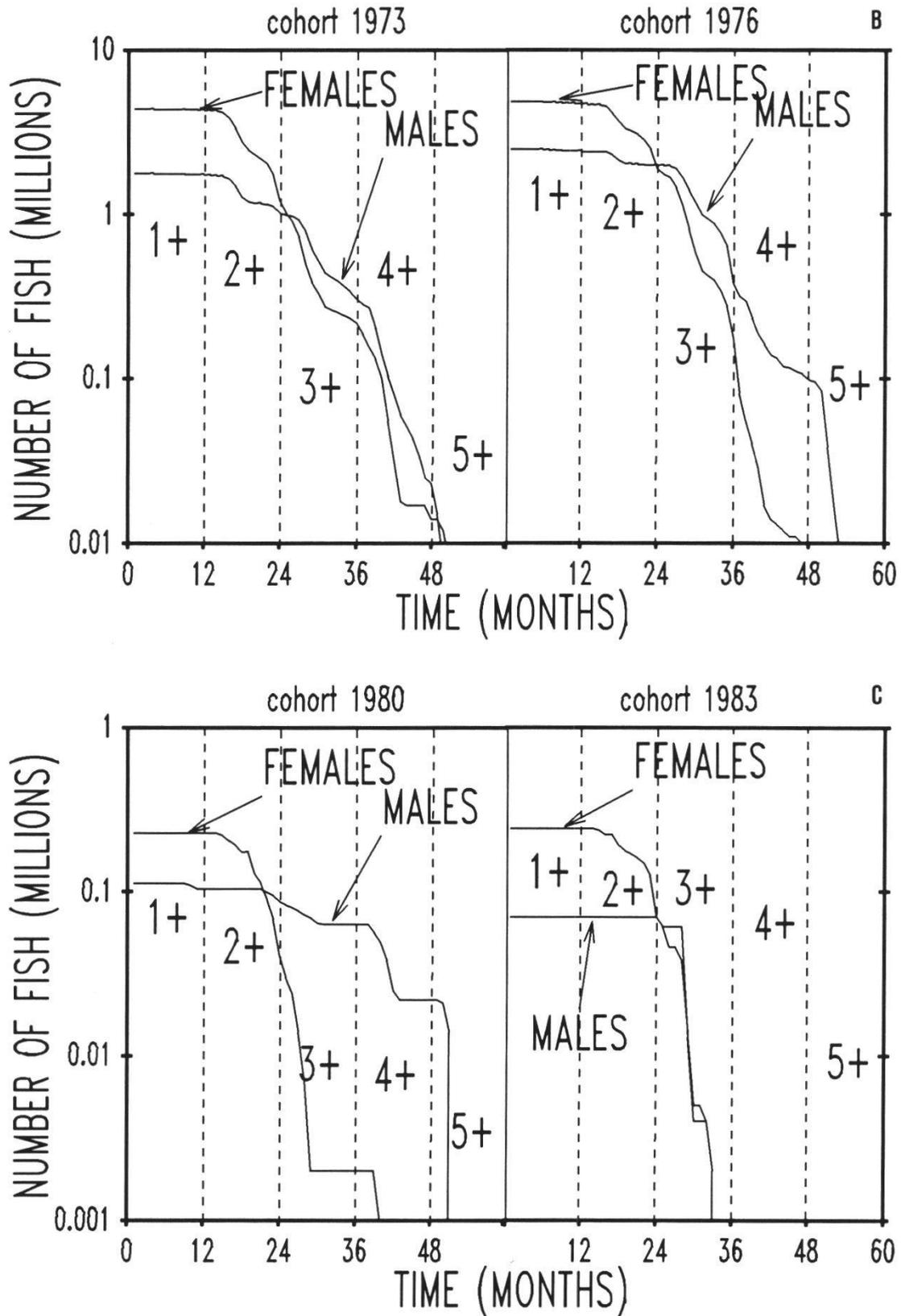


Figure 6.-B and C: observed catch curves for Lake Constance perch. B: examples of strong cohorts (more than 2 million individuals caught); C: examples of weaker cohorts (less than 2 million individuals caught). Vertical dashed lines: 1st of June.

3.3. Simulation of annual and monthly yields

Table 3 lists the simulated annual catch data for the cohorts from 1970 through 1988 (yield from January to December). As the simulation starts with 1 million 1-year-old fish, these data have been corrected by multiplying by the quotient

$$Q = \text{observed VCS} / \text{simulated VCS}$$

where *VCS* is the virtual cohort strength (number of fish of one cohort caught during its whole life span). The totals of the columns give the simulated annual yield for all cohorts present, which is shown in Figure 7 together with the observed yield. We proceeded the same way with the monthly simulated and observed catch data for the years 1982 to 1984 (inlet of Fig. 7).

The observed and simulated yield curves are similar for periods with low to average yields. However, for very high yields, an important discrepancy is observed, because the very strong cohorts (like the one born in 1982) are caught later than weaker cohorts, probably as a consequence of a density-dependent reduction of growth. As no data on density-dependent growth of perch in Lake Constance are available, we reduced the growth coefficient, *K*, by 20 % for the cohort born in 1982 (alternative values in Table 1). However, even with this reduced growth rate, the correspondence between the yield curves was unsatisfactory for the years 1985 and 1986.

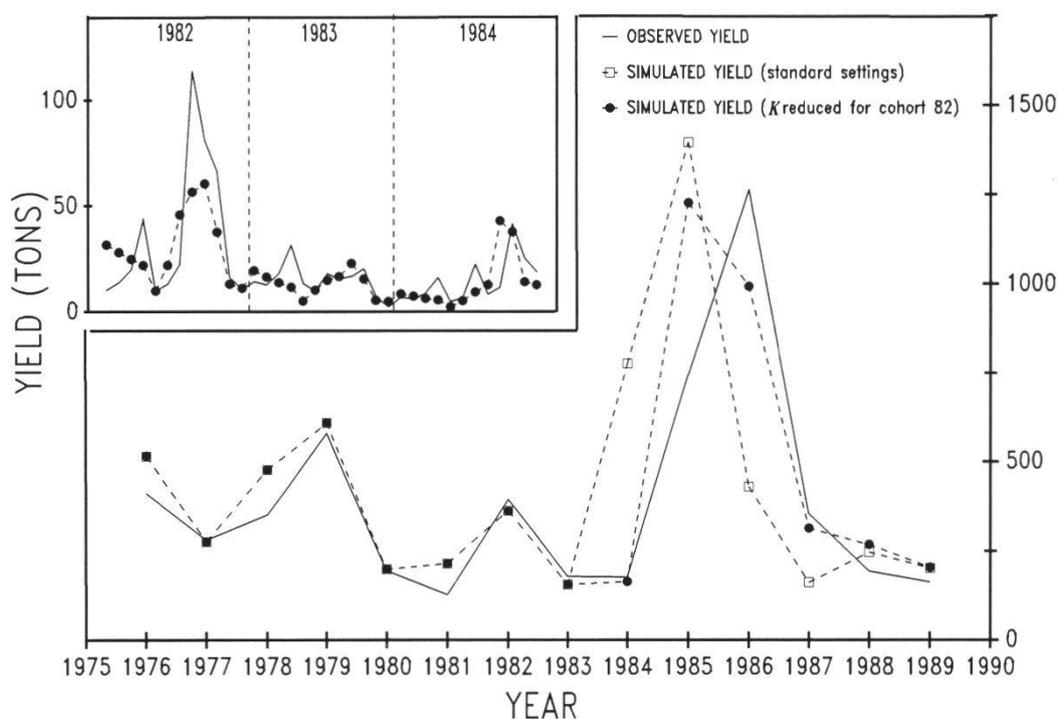


Figure 7.—Simulated and observed annual yields of Lake Constance perch. The standard settings concern the values of growth parameters and mortality rates *M* and *F* (*M*, *F* and *K*: see Table 1).

The inlet shows the detail of monthly yields for the years 1982, 1983 and 1984 .

Table 3.—Simulated catch data for the years 1975 to 1988, in tons. The catch for the cohort borne in 1982 has been corrected for reduced growth rate (alternative value for K , eq. 1 in Table 1).

VCS : observed virtual cohort strength (million fish).

cohort	VCS	year of catch													
		1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989
1970	2.71	0.8	0.1	-	-	-	-	-	-	-	-	-	-	-	-
1971	5.61	16.1	1.7	0.2	-	-	-	-	-	-	-	-	-	-	-
1972	0.83	18.3	2.4	0.3	<0.1	-	-	-	-	-	-	-	-	-	-
1973	6.17	455.4	136.3	17.7	1.9	0.2	-	-	-	-	-	-	-	-	-
1974	0.66	24.9	48.7	14.6	1.9	0.2	<0.1	-	-	-	-	-	-	-	-
1975	2.27	<0.1	85.7	167.5	50.2	6.5	0.7	0.1	-	-	-	-	-	-	-
1976	7.34	-	<0.1	277.3	541.7	162.2	21.0	2.3	0.2	-	-	-	-	-	-
1977	0.33	-	-	<0.1	12.5	24.4	7.3	0.9	0.1	<0.1	-	-	-	-	-
1978	0.14	-	-	-	<0.1	5.3	10.3	3.1	0.4	<0.1	<0.1	-	-	-	-
1979	4.64	-	-	-	-	<0.1	175.3	342.5	102.5	13.3	1.4	0.1	-	-	-
1980	0.34	-	-	-	-	-	<0.1	12.8	25.1	7.5	1.0	0.1	<0.1	-	-
1981	0.72	-	-	-	-	-	-	<0.1	27.2	53.1	15.9	2.1	0.2	<0.1	-
1982	18.58	-	-	-	-	-	-	-	<0.1	89.9	1203.1	973.7	204.5	26.6	2.9
1983	0.15	-	-	-	-	-	-	-	-	<0.1	5.7	11.1	3.3	0.4	<0.1
1984	0.15	-	-	-	-	-	-	-	-	-	<0.1	5.7	11.1	3.3	0.4
1985	2.49	-	-	-	-	-	-	-	-	-	-	<0.1	94.1	183.8	55.0
1986	1.41	-	-	-	-	-	-	-	-	-	-	-	<0.1	53.3	104.1
1987	1.1	-	-	-	-	-	-	-	-	-	-	-	-	<0.1	41.6
1988	7.3	-	-	-	-	-	-	-	-	-	-	-	-	-	<0.1
TOTAL CATCH		515.5	275.0	477.5	608.2	198.7	214.7	361.7	155.5	163.8	1227.1	992.8	313.2	267.4	204.0

3.4. How can fluctuations in yield be explained?

Cohort strength or recruitment do not necessarily depend directly on the parental stock present in the lake. Proceeding the same way as for the total catch (see section 3.3. and Table 3), we estimated, from the simulated results, the number of eggs produced each year and the total biomass of adult perch in the first half of June of the same year. The observed VCS (virtual cohort strength = total numbers of fish of each cohort actually caught) were divided by these simulated egg numbers to obtain a value related to the survival of the population of one cohort, from the eggs to the exploited fish. This value is named "survival" for simplification. A multiple regression was computed with the natural logarithm of survival as dependent variable, and with the natural logarithm of the biomass of adult perch and the water temperature, given in degree-days over 14°C (from June to October), as independent variables (multiple $R^2 = 0.83$). The regression was forced through the origin, because the constant term (-0.55) is not significant ($P=0.84$), while the regression coefficients are highly significant ($P<0.001$). This relation is shown in Figure 8.

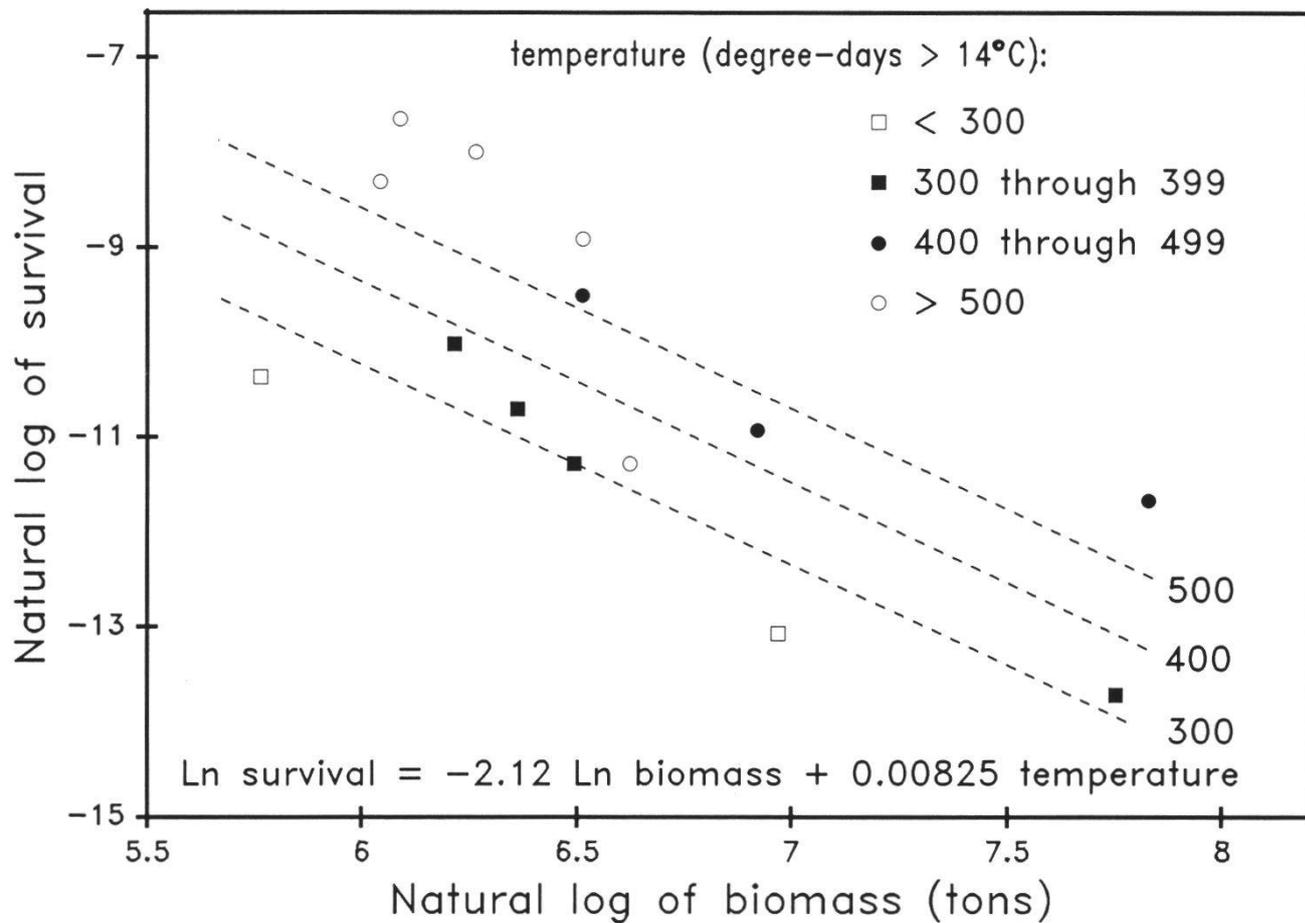


Figure 8.—Relation of the natural log of survival vs. natural log of biomass of Lake Constance perch and water temperature (cohorts 1976 through 1989). For the definition of “survival” see text in section 3.4. The lines show the limits between temperature ranges for 300, 400 and 500 degree-days over 14°C.

4. DISCUSSION

4.1. Mortality rates

The mortality rates were amongst the most difficult basic parameters to estimate (STAUB *et al.* 1987).

LANG (1987) found total annual mortality rates for adult female perch in Lake Geneva ranging from 73.1 to 82.1% (corresponding to an instantaneous rate of mortality ranging from 1.3 to 1.7), based on two different methods. These values are lower than the basic values for mortality rates used in this study (Table 1). CRAIG (1982, in CRAIG 1987) estimated that instantaneous rates of total mortality for perch in Lake Windermere, which are considered to be equal to rates of natural mortality, because the population is nearly unexploited, ranged from 0.1 to 1.2. These values are closely related to the

coefficient K of the VON BERTALANFFY growth function (Eq. 1 in Table 1). For a K of about 0.5 (as in Lake Constance), the estimated value is about 0.8. This value is equal to the instantaneous rate of natural mortality we used in this study. In their simulation model for perch and pikeperch in Lake Ijssel (Netherlands), BUIJSE *et al.* (1992) used length-dependent annual rates of natural mortality M : for perch smaller than 25 cm, this rate was assumed to be $M=1.79 \text{ EXP}(-0.087 L)$, where L is the total fish length; for larger perch, M was assumed to be constant ($M=0.2$)

KRÄMER (pers. communication) tagged about 17,000 young perch in Lake Constance. However, none of these tags could be recovered. This gives a further indication that the rate of natural mortality must be very high.

The simulated catch curves in the right part of Figure 6 A are based on reduced natural mortality rates. The steepness of the graphic based on standard mortality rates (left part of Fig. 6, A) is in better agreement with the graphics based on observed data (Fig. 6, B and C).

The facts discussed in this chapter and the good agreement of our simulated results with the observed data lead us to the conclusion that the standard mortality rates we first assumed (Table 1) are realistic. However, the curves for simulated catch (Fig. 7) show that the global results of the simulation are not very sensitive to differing mortality rates. They are, in fact, much more influenced by fish growth rates.

4.2. Actual number of fish

At the end of October 1983, a hydroacoustic survey was carried out on Lake Constance. The estimated standing stock of all fish species was about 600 million fish (HARTMANN 1988). At the time of this survey, the very strong cohort born in 1982 (age class 1+) was dominant in the lake. This cohort gave later landings of about 18 million perch. The virtual stock of older perch at that time was about 1 million. This corresponds to a total stock of about 5 million perch. The simulated stock for the first half of November is 731,766 perch of age class 1+, which is rounded off to 750,000 in the calculations that follow.

Starting with 1 million 1-year-old perch, the simulation results in a total catch of 195,000 individuals, if fishing is based on gear with 32 mm mesh size (left part of Fig. 6, A). After conversion of this number to the real number of perch caught in the lake, the number of 1-year-old individuals belonging to the 1982 cohort can be estimated to be $750,000 \cdot 18,000,000/195,000 =$ about 69 million fish. The total number of older perch (born in the years before 1982) left in the lake at end of October 1982 is estimated to be about 5 million individuals. The total number of perch present in the lake in the first half of November 1983 is, therefore, estimated to be about 74 million. This number is not in contradiction with the 600 million total stock of all fish species estimated by the hydroacoustic method.

4.3. Sources of inaccuracy and improvement of the simulation program

By its nature, a simulation program cannot give the absolutely true image of reality. It is important to be aware of its limits. The most important sources of inaccuracy are as follows:

- the use of fishing gear other than gillnets is neglected. In Lake Constance, the main fishing effort comes from these nets; for the analysis of other lakes, fishing with bow-nets and recreational fishery may have to be introduced in the model;

- growth parameters have been computed from age-length data of exploited perch in Lake Constance. The growth rates could be underestimated because of LEE's phenomenon (RICKER 1969);

- growth and mortality parameters could possibly undergo annual variations, depending on cohort strength and climatic conditions. The data available for Lake Constance were insufficient to detect such differences;

- the gillnet selectivity functions used in this study have been computed by the simple model of HOLT (1963), in which normal selectivity curves are assumed. In many cases however, selectivity functions are not normal (HAMLEY 1975). HARTMANN and QUOSS (1986) compared selectivity functions computed for Lake Constance perch using the methods of HOLT and ISHIDA (HAMLEY 1975). The optimal lengths computed by the method of ISHIDA were 4% shorter than the optimal lengths computed by the method of HOLT. The available data for Lake Constance perch (STAUB *et al.* 1987) do not allow computation of the real shape of the gillnet selectivity functions. In the context of general management problems, this inaccuracy is negligible in comparison with unpredictable factors such as the behaviour of fishermen (e. g. numbers of nets actually used), net quality (e. g. elasticity and hanging factor of the mesh, which strongly influence selectivity) or differences in the behaviour and activity of fish belonging to different age classes. A higher degree of complexity of the computer model would only mask the inaccuracy of the basic data used for the investigations;

- as shown in Figure 3, the fish in one age class are not equally vulnerable to fishing, depending on their length. In fact, this selective fishing should result in a deformation of the length frequency distribution of the fish in one age class. The program does not take in account this fact: after each time step, the remaining fish are normally distributed again.

This study shows that our simulation program may already lead to realistic and useful results for managing perch populations. It could easily be adapted for simulation of other fish species. Nevertheless, we have decided to improve it. In its final version (prepared by Dr. Yury TYUTYUNOV, Univ. of Lausanne), the program will be able to simulate the populations of fish for an unlimited number of years, under variable conditions of exploitation and environment. Such a dynamic program should be able to compute recruitment in function of the stock of adult fish and water temperature. For Lake Constance, such a function could be based on the data shown in section 3.4. and Figure 8.

The possibility of fishing simultaneously with both gillnets and other types of gear will also be introduced into the simulation program. Finally, functions for density-dependent mortality and growth parameters would probably improve the results of the simulations.

5. CONCLUSIONS CONCERNING THE MANAGEMENT OF PERCH IN LAKE CONSTANCE

The results obtained in this study lead to the following conclusions concerning the management of perch populations in Lake Constance:

—an increase in minimum mesh size would lead to a reduction in yield. A slight reduction of the mesh size to 30 mm would possibly increase yield without endangering the reproductive capacity of the population. However, since the influence of the mesh size on year class fluctuations is not known at present, mesh size should not be changed in the near future;

—even assuming a low rate of natural mortality, the optimal mesh size limit would be close to the present legal mesh size. Thus an increase of the mesh size cannot increase the yield.

6. ACKNOWLEDGEMENT

We thank Dr. Hartmann, Dr. Krämer and Dr. Rühle for the permission to use their unpublished data for this work, and Mrs. Ann Arquit for her helpful criticism of this manuscript.

7. REFERENCES

- BAINBRIDGE R., 1961. Problems of fish locomotion. *Symp. zool Soc. London* 5: 13-32.
- 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 gillnet fishery. *Fischeries Research* 13: 95-117.
- CRAIG J.F., 1987. The biology of perch and related fish. Chap. 3: Growth, mortality and longevity. London & Sidney (CROOM HELM): 45-65.
- FEDERAL OFFICE OF ENVIRONMENT, FORESTRY AND LANDSCAPE, 1975 ff. *Annuaire hydrologique de la Suisse*. Berne: Dep. fédéral de l'intérieur.
- HAMLEY J.M., 1975. Review of gillnet selectivity. *J. Fish. Res. Board Can.* 32:1943-1969.
- HARTMANN J. 1988. Zur Berechnung der Sterblichkeitsraten beim Barsch des Bodensees. *Oesterr. Fischerei* 41:14-21.
- HARTMANN J. and QUOSS H., 1986. Selektivität von Kiemennetzen im Bodensee. *Oesterreichs Fischerei* 39:337-340.
- HOLT S.J., 1963. A method for determining gear selectivity and its application. *ICNAF Spec. Publ.* 5: 106-115.
- LANG C., 1987. Mortality of perch, *Perca fluviatilis* L., estimated from the size and abundance of egg strands. *J. Fish Biol.* 31:715-720.

- STAUB E., BÜTTIKER B. and KRÄMER A., 1987. Grundlagen für Modell-simulationen zur Bewirtschaftung des Barsches (*Perca fluviatilis* L.) im Bodensee. Federal Office of Environmental Protection, Bern. Schriftenreihe Fischerei 46, 40 p.
- STAUB E. and KRÄMER 1991. Grossversuch mit 28 mm-Netzen zur Befischung der wachstumsverzögerten Barschkohorte 1988. SVA/IBK, internal paper, 27 p.
- RICKER W.E., 1969. Effect of size-selective mortality and sampling bias on estimates of growth, mortality, production and yield. *J. Fish. Res. Bd. Canada* 26: 479-541.
- RUDSTAM L. G., MAGNUSON J. J. and TONN W. M., 1984. Size selectivity of passive fishing gear: a correction for encounter probability applied to gill nets. *Can. J. Fish. Aquat. Sci.* 41:1252-1255.
- THORPE J., 1977. Synopsis of biological data on the perch *Perca fluviatilis* Linnaeus, 1758 and *Perca flavescens* Mitchill, 1814. *FAO Fish. Synop.* 113:1-138.
- TYLER A. V. and GALLUCI V. F., 1980. Dynamics of fished stocks. In: R. T. LACKEY and L. A. NIELSEN (eds): Fisheries management. Oxford (Blackwell): 111-147.

Manuscrit reçu le 25 mars 1992