Modelling fluctuations and optimal harvesting in perch populations

Yuri Tyutyunov a,c, Roger Arditi a, Bernard Büttiker b, Yuri Dombrovsky c and Erich Staub d

a Institute of Zoology and Animal Ecology, University of Lausanne, CH-1015 Lausanne, Switzerland, b Fauna Conservancy of Canton Vaud, Marquisat 1, CH-1025 Saint-Sulpice, Switzerland, c Research Institute of Mechanics & Applied Mathematics, Department of Mathematical Modelling in Ecology and Economics, Rostov State University, Stachki st. 200 /1, 344104, Rostov-on-Don, Russian Federation and d Swiss Federal Office for Environment, Forests and Landscapes, Halwylstrasse 4, CH-3003 Bern, Switzerland

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ABSTRACT


A mathematical model of perch (Perca fluviatilis L.) was elaborated, based on the data for ten Swiss lakes. The aim is management of a commercially exploited population. This required elucidation of dynamics of perch stocks and catches. Statistical data analysis demonstrated complicated population dynamics, including cycles of different periods and chaos. The model describes age and sex structure, nonlinear reproduction (including the effects of cannibalism and competition), individual growth, and harvesting, which depends on fishing effort and mesh size of nets. Bifurcation analysis of the model showed the presence of chaotic dynamics and, hence, high sensitivity to initial conditions. Sensitivity to model parameters was also investigated. Simulation analysis of the fishing process was done on the basis of data from Lake Constance. A multiobjective problem of harvest maximization combined with variance minimization was investigated. The isopleths of the annual harvest and of its dispersion were calculated. Pareto-effective strategies, accounting for trade-off between average harvest and its stability were evaluated. A recommendation was given for optimal mesh size and fishing effort. User-friendly software was developed for IBM PC compatible computers, which can be used to investigate a broad class of age-structured populations.

Correspondence to: Yuri Tyutyunov, Institute of Zoology and Animal Ecology, University of Lausanne, CH-1015 Lausanne, Switzerland.

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INTRODUCTION

Perch (*Perca fluviatilis* L.) is one of the most important species for commercial fisheries in Switzerland. Its yield amounts to 30% of the mean total catch of 3000 t per year. This species has a short reproductive cycle, a high birth rate and a tendency to be cannibalistic on younger individuals (Thorpe, 1977). Maximal individual life duration is 8 years.

The dynamics of catches and, apparently, the dynamics of the perch population itself are very complicated and may appear unpredictable. They are characterized by high fluctuations and show complicated dynamics. Maximal and minimal values differ by one or two orders of magnitude. A task of high practical and ecological significance is the estimation of population reaction to changes in fishing strategy. Since experiments with natural populations are extremely difficult, the only way to investigate the dynamics of the fish population is through mathematical modelling and experimentation on the computer image of the real system rather than working with the natural system.

The model should be based on specific field data and general knowledge of fish ecology. In Switzerland, the biology of perch is best known for Lake Constance for which all available data have been compiled by Staub et al. (1987) and Staub and Krämer (1991).

The questions we try to elucidate with help of the model are both scientific and practical. It is important to understand and to explain the nature of complicated annual fluctuations of perch stock and catches. These fluctuations may be explained by stochastic fluctuations of the natural environment (temperature, etc.), variations in fishing effort or internal population dynamics (competition, cannibalism). Since practical questions concern fishing regulations, we have had to use terms that are suitable for managers and fishermen such as gillnet mesh size, number of nets used, and seasonal fishing effort distribution. One important question is finding the optimal distribution of gillnet mesh sizes in order to maximize the mean annual harvest and to minimize its variability and the commercial risk for fishermen. Additionally, population persistence is an important problem for conservation ecology. Populations with strong fluctuations of abundance are vulnerable to negative, irregular environmental and anthropogenic influences, which may lead to an important depletion of population size or even to total extinction. Thus, ecological and practical questions are weaved together with natural population management.

To interpret the role of dynamic processes, we follow the conclusions of Fogarty et al. (1991). These authors examined the interactions between stabilizing mechanisms and sources of variability. They noted the important role of compensatory mechanisms (e.g. cannibalism, density-dependent...
growth coupled with size-dependent predation, intracohort competition for critical resources). On the other hand, high fecundity and high variance in mortality rates during the pre-recruitment phase increase variance in the catch time series. Interaction between environmental conditions and harvesting can also destabilize an exploited population.

In the perch population of Lake Constance, cannibalism is a natural compensatory mechanism. According to Staub et al. (1987), 1–8% of adults eat about 2.5 recruits (age class 0+) per day, between June and October. Strong selective removal of cannibals may lead to a reduction of this feedback regulation. Populations with little or no compensatory capacity are particularly vulnerable to overexploitation (Fogarty et al., 1991).

We also cannot neglect environmental factors altogether. The most important environmental parameter is temperature, which influences both fecundity of mature females and survival rates during the early life stages.

STATISTICAL DATA ANALYSIS

Before using the model, a statistical analysis of available field data was performed to detect peculiarities of population dynamics.

The most reliable data are the time series of perch catches in main Swiss lakes (Table 1). Concerning Lake Constance we have additional information about the age-composition of the catches (J. Hartmann and A. Krämer, pers. commun., 1991) for the period 1971–1989, which enables us to estimate the total catch of a cohort during its lifetime. Besides, we use the temperature regime series on Lake Constance, expressed as the annual

<table>
<thead>
<tr>
<th>Lake</th>
<th>Min.</th>
<th>Max.</th>
<th>Mean</th>
<th>St. Dev.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constance</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Upper lake</td>
<td>20.00</td>
<td>890.00</td>
<td>366.68</td>
<td>219.26</td>
</tr>
<tr>
<td>Lower lake</td>
<td>18.47</td>
<td>365.38</td>
<td>76.79</td>
<td>75.96</td>
</tr>
<tr>
<td>Geneva</td>
<td>30.00</td>
<td>1007.00</td>
<td>399.44</td>
<td>299.87</td>
</tr>
<tr>
<td>Neuchatel</td>
<td>5.00</td>
<td>300.00</td>
<td>105.00</td>
<td>84.57</td>
</tr>
<tr>
<td>Biel</td>
<td>0.70</td>
<td>28.00</td>
<td>8.18</td>
<td>6.98</td>
</tr>
<tr>
<td>Morat</td>
<td>1.00</td>
<td>24.00</td>
<td>8.03</td>
<td>6.86</td>
</tr>
<tr>
<td>Zurich</td>
<td>10.00</td>
<td>80.00</td>
<td>39.18</td>
<td>22.49</td>
</tr>
<tr>
<td>Zug</td>
<td>1.50</td>
<td>45.00</td>
<td>14.31</td>
<td>10.06</td>
</tr>
<tr>
<td>Walenstadt</td>
<td>0.60</td>
<td>8.20</td>
<td>4.85</td>
<td>2.29</td>
</tr>
<tr>
<td>Lucerne</td>
<td>5.00</td>
<td>43.00</td>
<td>18.25</td>
<td>10.79</td>
</tr>
</tbody>
</table>
degree-days over 14 (Craig, 1987). To understand whether the main reason for such strong variability are external sources or internal properties, i.e., density-dependent reproduction and growth, we analyse the catch time series $C_t$ using several distinct approaches, each providing a different viewpoint of the temporal population dynamics.

As a first approach, we use the qualitative diagnostic techniques based on the autocorrelation function (ACF) and the partial autocorrelation function (PACF) (Kendall and Stuart, 1968; Box and Jenkins, 1970). The ACF is estimated by calculating the correlation coefficients $\rho_\tau$ between pairs of values $C_t$ and $C_{t-\tau}$ separated by the lag $\tau$ ($\tau = 1, 2, \ldots$).

The correlogram represents these correlation coefficients as a function of the lag. The ACF provides a concise description of temporal dynamics of the annual catch and is a good tool for recognizing the type of time series. For instance, ACFs of the well-known stochastic, first-order Markov process are characterized by an exponential decline to zero (Kendall and Stuart, 1968).

The PACF is the set of partial correlation coefficients between $C_t$ and $C_{t-\tau}$ ($\tau = 1, 2, \ldots$) under the assumption that the influence of intermediate points $C_{t-\tau+1}, \ldots, C_{t-1}$ have been removed. The PACF is also a particularly useful diagnostic tool for determining the order ($p$) of an autoregressive model of the form

$$C_t = a_0 + a_1 C_{t-1} + \ldots + a_p C_{t-p} + \epsilon_t, \quad \epsilon_t \in N(0, \sigma).$$

For example, the PACF of the first order Markov process has a single peak at lag 1 but all partial correlations with $\tau > 1$ are zero (compare with the ACF).

The PACF can help us understand the delayed density-dependent regulation in populations. Such regulation is typical for biological systems with pronounced age structure and density-dependent growth. In many cases, ACF and PACF analyses are useful when we have to deal with observed time series of population density or even of catch sizes.

Generally speaking, before we can calculate the ACF and the PACF, we have to be sure that the time series does not contain a trend and, if there is one, it should be removed from the data. We also do a log transformation of the data, which is a standard procedure when dealing with population dynamics data with large fluctuations.

The ACF and PACF of perch catch time series in ten Swiss lakes are presented in Fig. 1. In general, we did not obtain very significant correlation values. This means that irregular components prevail in the observed data. There are some significant correlations in ACFs and PACFs for the group consisting of Upper Lake Constance, Lakes Geneva, Biel, Zurich
and Lake Lucerne. Lower Lake Constance, Lake Walenstadt, Neuchatel and Lake Zug have no significant correlations, but for Lake Walenstadt and Lake Neuchatel there are relatively high peaks. ACFs on graphs for Lakes Morat, Zurich and Neuchatel are typical of strong oscillatory endogenous components. Lakes Morat and Neuchatel have a 3-year cycle for catches. Lake Zurich shows a 6-year cycle.

Note that practically all cases give some negative correlation values for lags longer than 1 year. This means that even for noncyclic time series there is strong delayed density-dependent regulation which produces chaotic (not random) behaviour. The exception of lag 3 may be interpreted as a natural delay between spawning and reaching a commercial (fishing) body length, because individuals of age 2+ are a majority in spawning and harvesting. Relatively low values of partial correlations with lag 3 are explained by the existence of positive (reproduction) and negative (intrapopulation competition and cannibalism) feedbacks. This implies that the model should include the age structure of the population.

The second approach we have used is Fourier analysis of the time series and computation of a process spectrum and a periodogram. This method gives the same information about the dynamics of observed values as the ACF does. Whether we prefer to think in terms of the spectrum or of the correlogram depends on personal preference (Hannan, 1977). We will not give results of Fourier analysis (periodograms and spectra) here, and simply say that in lakes Morat and Zurich, periodograms are typical of oscillatory regimes with strong peaks of periods 3 and 6 years respectively. Lake Neuchatel also shows a peak of 3-year periodicity, but in the background of other peaks. All other catch time series have complicated structures of spectra. The most chaotic behaviour was detected by this method for cases Lower Lake Constance, Lakes Biel and Zug.

The next step that we make in the correlation analysis is an estimation of the cross correlation function (CCF). It is simply the set of correlation coefficients between the pairs of different catch series separated by a lag \( \tau \) \((\tau = \ldots, -2, -1, 0, 1, 2, \ldots)\). Significant correlations are found between pairs of catch series for Lakes Biel, Morat and Neuchatel which have a 3-year cyclic component in catch dynamics. These lakes are neighbours and have approximately the same climatic conditions, they are connected by a river, and the fishing policy is similar (especially for the mesh size of nets (Staub et al., 1987)). The fact that the annual catch fluctuations of these three lakes are close in phase may be explained by these physical similarities.

In the final approach, we analyse the influence of the temperature regime on population dynamics. Using the data for Lake Constance (years 1971–1989), we have found that the correlation between the annual de-
gree-days and the total catch of the cohort born in that year is 0.4 for both parts of the lake (Lower and Upper lakes). This is not enough to establish linear dependence, but it suggests that temperature might be significant.

The main conclusions are: the perch population dynamics are complicated and different in different lakes. Some are clearly cyclic (Biel, Morat, Neuchatel, Zurich), some vary in an apparently chaotic way. Such kind of dynamics with switching between cycles of different periods and with chaos is typical of nonlinearly regulated systems (May, 1976). External factors are essential but not prevailing in this determination of dynamics. The character of dynamics leads us to concentrate on the internal mechanisms including age structure and nonlinear reproduction.

THE MODEL

For constructing the simulation model, we have taken as a basis the cohort model of Büttiker and Staub (1992) and have combined it with population dynamics modelling (Dombrovsky et al., 1986).

The model combines a Leslie (1945) model for discrete age structure with nonlinear reproduction and a linear continuous model for intrayear dynamics. The state variables are population abundance and individual weight. The details of the model depend on the aims and interests and, if necessary, we can take into account sex, age and spatial structure of the population system. The central part of the model are the processes of reproduction, mortality, growth and harvesting. These are operators, i.e., functions that transform the system state vector in time. Lastly, there are environmental and external factors such as temperature and fishing strategy, which influence the above processes. We can introduce temperature-dependent growth and survival rates of larvae into the simulation model. Temperature time series can be computed according to an introduced distribution function (randomly or periodically). Regarding the investigation of asymptotic properties of the mathematical model, it is more interesting to examine the deterministic system with fixed values of environmental factors. This practice may be important for separating external and internal sources of variability.

Following Büttiker and Staub (1992), we divide the population into seven age classes. Since growth characteristics of perch are sex dependent, we have distinguished between the two sexual subgroups. Hence, the model contains 14 state variables: \( N_{r}^{m}, N_{r}^{f} \) are the abundances of classes aged \( r \) (\( r = 1,2,\ldots,7 \)), respectively for males and females. The total abundance is \( N_{r} = N_{r}^{m} + N_{r}^{f} \).

The model runs with a half-month time step \( \Delta t \) (24 steps per year).
Population dynamics

The within-year dynamics of population abundance is described by the simple exponential survival function

\[ N_f(t + \Delta t) = N_f(t) \exp\{- (M_f + F_f(t)) \Delta t\}, \]  

(2)

where \( M_f \) and \( F_f(t) \) are natural and fishing mortality rates (\( f \) stands for female). This operator integrates the transformation induced by the mortality processes and calculates a new population state.

At spawning time \( t_s \) (first half of May in Lake Constance), the model calculates the number of eggs produced by the reproductive part of the population according to the allometric formula

\[ E(\tau) = a_p(L_f^\tau)^{b_p}, \]  

(3)

where \( E(\tau) \) is the number of eggs produced by one mature female of age class \( \tau = 1, 2, \ldots, 7 \); \( L_f^\tau \) is the age-specific body length of females (cm); \( a_p = 2.85 \) and \( b_p = 2.94 \) are empirical parameters of individual productivity (Staub et al., 1987).

The total number of eggs produced in the current year, \( NE \), is

\[ NE = \sum_{\tau=1}^{7} m_\tau N_f(t_s)E(\tau), \]  

(4)

where \( m_\tau \) is the proportion of mature females in age class \( \tau \).

Being cannibalistic, perch should obey the well-known Ricker (1954) relationship between parental investment and recruitment. The field data agree with this hypothesis (Staub and Krämer, 1991). The abundance of the next generation, \( N_1(T + 1) \) (age group 1) at the beginning of the next biological year \( t_b \) (corresponding with hatching of the fry, 1 June (Staub et al., 1987)) is computed with a formula which is similar to the reproduction model of Ricker (1954):

\[ N_1(t_b + \Delta t) = \alpha NE \exp\{- \beta \sum_{\tau=2}^{7} N_\tau(t_b)\}, \]  

(5)

where \( \alpha \) is the survival coefficient; \( \beta \) is the competition and cannibalism activity parameter. The sex ratio in the fry is assumed to be 1:1.

To determine the parameter \( \beta \) (0.2349 \cdot 10^{-6}), we used the cannibalism-recruitment correspondence curve of Staub and Krämer (1991). This was done by linearization of Eq. (5) and estimation of coefficients by linear regression.

Once a year (at the moment called “beginning of the biological year”, i.e. 1 June), the model renumbers the age classes and calculates recruitment according to Eq. (5).
Growth

Individuals of each age class and each sex are assumed to grow at a constant rate from mid-June to the end of September, and are assumed to stop growing for the remainder of the year. The von Bertalanffy (Beverton and Holt, 1957) growth function (6) gives the body length at the beginning and the end of the growing season:

\[ L(\tau) = L_\infty \left[ 1 - \exp\left\{ -K_g (\tau - \tau_0) \right\} \right], \]  
\[ (6) \]

where \( L_\infty \) is the asymptotic body length; \( \tau \) is the age; \( K_g \) is the growth coefficient; \( \tau_0 \) is the age correction. Values are given in Table 2.

To determine the weight \( W(\tau) \), we use the following length–weight empirical allometry (Staub et al., 1987):

\[ W(\tau) = a_w L(\tau)^{b_w}; \]  
\[ (7) \]

where \( a_w = 1.1 \cdot 10^{-5} \); \( b_w = 3.037 \) with \( W(\tau) \) in kg and \( L(\tau) \) in cm.

Equations (6) and (7) are applied to each age class and each sex. It is further assumed that length is normally distributed with a standard deviation of 6% of the mean length (Ammann et al., 1976; Staub et al., 1987):

\[ F_f(L) = \frac{1}{\sqrt{2\pi} \sigma_{L_f}} \exp\left\{ -\frac{(L - L_{f\tau})^2}{2\sigma_{L_f}^2} \right\}, \]  
\[ (8) \]

where \( F_f(L) \) is the length frequency of females aged \( \tau \) and \( \sigma_{L_f} = 0.06L_{f\tau} \). The formula for males is analogous.

Harvesting

The abundance and composition of the harvest depend both on the abundances of the different age and sex classes and on the characteristics of the gear applied. In Lake Constance, the main kind of fishing gear used are gillnets, which are selective in the sizes of fish they capture. The main character of gillnets that determined capture efficiency is mesh size.

In the model, arbitrary distribution of nets \( r_\mu \in [0,1] \) for each mesh size \( \mu \) from 11 to 50 mm can be selected. The sum of all \( r_\mu \) is 1. Each mesh size \( \mu \) is characterized by a selectivity function \( S_\mu(L) \), the probability of catching fish of body length \( L \). Following Holt (1963), \( S_\mu(L) \) is taken as a normal distribution:

\[ S_\mu(L) = \frac{1}{\sqrt{2\pi} \sigma_\mu} \exp\left\{ -\frac{(L - L_\mu)^2}{2\sigma_\mu^2} \right\}, \]  
\[ (9) \]

where \( \sigma_\mu = 0.04L_\mu \) is the standard deviation; \( L_\mu \) is the most vulnerable body length. Expression (9) and parameter values conform to various experimental data (e.g. Rudstam et al., 1984; Büttiker and Staub, 1992).
The global selectivity function $S(L)$ is defined as

$$S(L) = \sum_{\mu} r_{\mu} S_{\mu}(L)$$

(10)

and it is easily seen that $S(L)$ is also a probability distribution function:

$$\int_{-\infty}^{\infty} S(L) \, dL = 1.$$  

(11)

The fishing vulnerability (Fig. 2) of age class $\tau$ is the integral of the product of the fish length distribution (8) and the selectivity function (10) (f stands for "females"):

$$\text{Vuln}_\tau^f = \int_{-\infty}^{\infty} F_\tau^f(L) S(L) \, dL.$$  

(12)

A property of normal functions permits calculating the integral (12) directly:

$$\text{Vuln}_\tau^f = \sum_{\mu} \frac{r_{\mu}}{\sqrt{2\pi}(\sigma_{\mu}^2 + \sigma_{L_{\tau}}^2)} \exp\left\{-0.5\left(L_{\mu}^f - L_{\tau}^f\right)^2/\left(\sigma_{\mu}^2 + \sigma_{L_{\tau}}^2\right)\right\}.$$  

(13)

The model also includes a relative seasonal fishing effort $H(t)$, i.e. a time distribution of annual fishing intensity, with $\int H(t) \, dt = 1$ over 1 year. For example, a protection period at spawning time, or a reduction of fishing effort during the winter season can be simulated. As a result, the instantaneous rate of fishing mortality is finally

$$F_{\tau}^f(t) = H(t) \text{Vuln}_\tau^f \varphi_f,$$  

(14)

where $\varphi_f$ is the total annual fishing effort for females. Analogous formulas are used for males.

The Baranov (1918) catch function

$$C_{\tau}^f(t) = \frac{N_{\tau}^f(t) F_{\tau}^f(t)}{M^f + F_{\tau}^f(t)} \left\{1 - \exp\left(-(M^f + F_{\tau}^f(t)) \Delta t\right)\right\}$$  

(15)

computes the number of fish aged $\tau$ which were caught during the finite time interval $(t, t + \Delta t)$. Then, the body length distribution can be used to determine the weight of the catch $B_{\tau}^f(t)$.

It is essential that the external parameters of mesh size distribution $r_{\mu}$ and of fishing effort $H(t)$ can be manipulated in order to explore reactions to different fishing policies.

QUALITATIVE ANALYSIS OF THE MODEL

We are dealing with a rather complicated model which includes nonlinear processes in perch population dynamics. Before using this model for
Fig. 1. Correlogram and partial correlogram of time-series of catches in ten Swiss lakes. Data were log-transformed and linear trends were removed from the time series.
TABLE 2
Parameter values fixed for bifurcation analysis of the model

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>$L_o$ asymptotic body length (cm)</td>
<td>25.5 males</td>
<td>Hartmann and Knöpfler (1986)</td>
</tr>
<tr>
<td></td>
<td>28.8 females</td>
<td></td>
</tr>
<tr>
<td>$K_g$ growth coefficients (year$^{-1}$)</td>
<td>0.534 males</td>
<td>Staub et al. (1987)</td>
</tr>
<tr>
<td></td>
<td>0.479 females</td>
<td></td>
</tr>
<tr>
<td>$\tau_0$ correction for time (year)</td>
<td>0.286 males</td>
<td>id.</td>
</tr>
<tr>
<td></td>
<td>0.301 females</td>
<td>id.</td>
</tr>
<tr>
<td>$M$ natural mortality rate (year$^{-1}$)</td>
<td>0.8 males</td>
<td>id.</td>
</tr>
<tr>
<td></td>
<td>0.7 females</td>
<td>id.</td>
</tr>
<tr>
<td>$\varphi$ fishing effort</td>
<td>1.5 both sexes</td>
<td>id.</td>
</tr>
<tr>
<td></td>
<td>2.1</td>
<td></td>
</tr>
<tr>
<td>$t_b$ beginning of biological year (month)</td>
<td>6</td>
<td>Büttiker and Staub (1992)</td>
</tr>
<tr>
<td>$t_g$ beginning of growth (month)</td>
<td>6.5</td>
<td>id.</td>
</tr>
<tr>
<td>$t_e$ end of growth (month)</td>
<td>9.0</td>
<td>id.</td>
</tr>
<tr>
<td>$t_s$ spawning time (month)</td>
<td>5.5</td>
<td>id.</td>
</tr>
<tr>
<td>$\alpha$ survival coefficient of eggs and larvae</td>
<td>0.029</td>
<td>id.</td>
</tr>
<tr>
<td>$\beta$ cannibalism and competition parameter</td>
<td>0.2349$\cdot$10$^{-6}$</td>
<td>Staub et al. (1987)</td>
</tr>
</tbody>
</table>

![Vulnerability of Age groups](image)

Fig. 2. Fishing vulnerability of the age class 2 at the beginning of September is the integral area under the curve of the product of the selectivity function (with 28- and 32-mm mesh sizes) and the fish body length distribution.
fishing management, we have to know its properties and compare them with reality.

A characteristic feature of nonlinear systems is that varying a parameter can induce *qualitative* changes in the dynamics. These changes are called bifurcations, and the parameter values at which changes occur are bifurcation values. If the bifurcation parameter is near a bifurcation value, then even a very small change can lead to a new regime of the system. For example, it can undergo a transition from an equilibrium to chaos or to a new equilibrium with a very low level of population density. It is easy to understand that such an event might be catastrophic for the population. As far as exploited populations are concerned, bifurcations in abundance dynamics occur very often because of overexploitation or because of critical environmental pollution levels followed by a subsequent increase in natural mortality. The fact that, after such overexploitation, the collapse of the population takes place suddenly and without forewarnings is well known.

There are many parameters in the model. Some are fixed to values found in the literature or obtained from field data (e.g., parameters of the growth function). The remaining parameters form a multidimensional space, each point of which is characterized by a certain type of system behaviour. Some of these parameters can lead to bifurcations: the survival coefficient $\alpha$, the cannibalism parameter $\beta$, the natural mortality rates $M^m$, $M^f$ and the fishing efforts $\varphi^m$, $\varphi^f$. In order to understand the set of typical behaviours of the model, we make a bifurcation analysis.

All parameters are fixed to the values of Table 2. Then, in turn, the value of one parameter only is varied in rather wide limits. First is the survival coefficient $\alpha$. Bifurcation diagrams (Fig. 3a) for the total annual catch show a rich spectrum of dynamics ($\alpha \in [0.002; 0.03]$). Each value of the parameter (horizontal axis) corresponds to 300 annual values of the state variable (vertical axis) after the stationary regime was attained. Arrows on Fig. 3b show the direction of map evolution with increase of the bifurcation parameter. The bifurcations generated by coefficient $\alpha$ follow a pattern which is typical of one-dimensional maps, from equilibrium to chaos through a succession of period doublings. In such one-dimensional systems, Sharkovskii (1964) has shown that the sequence in which periods alternate is

$1 \leftarrow 2 \leftarrow 2^2 \leftarrow 2^3 \leftarrow \ldots \leftarrow 2^{35} \leftarrow 2^{33} \leftarrow \ldots \leftarrow 2 \cdot 5 \leftarrow 2 \cdot 3 \leftarrow \ldots \leftarrow 7 \leftarrow 5 \leftarrow 3,$

where arrows mean that if there exists an orbit of period $k$, then it is also true that the map has all orbits to the left of $k$. This means that the existence of a 3-point cycle implies that there must exist cycles of all other periods. Our model is not one-dimensional: there are seven age groups and
Fig. 3. Bifurcation diagram (a) and iterative map (b) of annual catch (t). Full spectrum of dynamics generated by the survival coefficient $\alpha \in [0.002, 0.03]$ with mesh sizes of 28 mm and 32 mm.
two sexes. The fact that it has Sharkovskii's properties suggests that it could be possible to use a one-dimensional map to model population abundance and catch. Models of such type are well known: for example, the classical Ricker model and the logistic map actually give the same bifurcation patterns in response to the reproduction coefficient (Lauwerier, 1986).

However, in our case the bifurcation diagram for natural mortality \( M \) is more complicated. Figure 4a shows that the chaotic orbits are followed by a 5-point cycle. Then, after new chaotic regimes with high amplitude (here an increase of natural mortality increases the annual amplitude of catch), a 3-point cycle follows. After doublings of 2-point cycles, the model finally comes to an equilibrium. Note that on the second bifurcation from the 3-point cycle to the chaotic orbit, there is a sudden and strong decrease of the annual catch.

The fishing effort \( \varphi \) gives a rather similar diagram (Fig. 4b). The differences are that, in the beginning, an increase of fishing intensity leads to an increase of stock and catch amplitudes and, eventually, through doublings of 3-point cycles, the model abruptly comes to a very low level of population abundance and catch. This result is a demonstration of the effect of overfishing. It is important to remember that each bifurcation diagram we obtain is a simple section of the complex high dimensional space of model parameters. These diagrams help understand the real picture and help find the adequate parameter values for modelling a concrete population. Bifurcation diagrams are also very useful for assessing parameter sensitivity of the mathematical model.

It was also found that the types of dynamics and 1-year maps depend essentially on net mesh sizes. Thus, if nets of mesh size 28 mm are used, the annual catch has a higher amplitude than using a mesh size of 32 mm. Harvesting of all age groups of the population (taking equal proportions of nets from 28 to 42 mm) shows similar bifurcation diagrams and 1-year maps for catch as for stock. This is not true in the general case: time series for catch and for stock are different from one another. This is one of the reasons of the difficulty of reconstructing population abundance dynamics from observed values of commercial catches.

In a rather wide range of the parameter \( \beta \) (cannibalism and intrapopulation competition), from \( 0.32 \cdot 10^{-7} \) to \( 0.32 \cdot 10^{-5} \), we have not found bifurcations. Increasing this parameter leads to exponential reduction of the average population weight and catches. Therefore, it is possible to use the parameter \( \beta \) for model calibration in order to apply it to a concrete lake.

All comments above are related to the deterministic model with constant parameter values. It is also possible to add noise to the system. Let the survival coefficient be equal to \( \alpha = \alpha' + \xi_\alpha \), where \( \alpha' \) is the average value
and $\xi_\alpha$ is a stochastic value evenly distributed in the interval $[-\sigma \cdot \alpha'; \sigma \cdot \alpha']$, $(0 \leq \sigma < 1)$. This means that survival of eggs and larvae is affected by a stationary stochastic process. Simulation results show that small values

![Fig. 4. Bifurcation diagrams in response (a) to natural mortality rate $M \in [0.2; 3.0]$; and (b) in response to fishing effort $\varphi \in [0; 40.0]$. Mesh sizes are from 28 to 32 mm.](image)
of $\sigma (<30\%$ of $\alpha')$ do not change the qualitative model dynamics very much. Actually, they give the same dynamics as in the deterministic case. The greater dispersion of $\alpha$ increases very much the catch fluctuation amplitude and moves the upper beam of the 1-year map (Fig. 3b) to the vertical axis of the graph. Such arrangement of the map seems to be characteristic for Lower Lake Constance, Lakes Morat, Neuchatel and Zug (Fig. 5).

This analysis has some important consequences for the application of the simulation model. First, the chaotic behaviour detected both in the mathematical model and in the field data actually means that attempts to compare the observed time series with the trajectories of the model dynamics are useless. The reason is extremely high sensitivity of chaotic trajectories to initial conditions. Model trajectories with even slightly different initial conditions diverge very soon and only the general character of trajectories has some similarity.

However, the model can be helpful for qualitative analysis and estimation of average values. For instance, in order to evaluate the qualitative behaviour of a population in some lake, one should not compare the time-series but the phase maps of the real and modelled systems. To represent such maps, one only needs to plot the serial data $N(t)$ on a graph with $N(t + 1)$ versus $N(t)$. A 1-year map of the stationary process is not sensitive to initial conditions; it is an invariant representation of the system's dynamics. The iterative presentation (1-year maps) of the commercial perch catches in ten Swiss lakes is depicted on Fig. 5. Some of them display a definite order and determinism in their chaotic behaviour. It also seems that density-dependent mechanisms are more important than stochastic environmental factors in the chaotic dynamics of these natural populations of perch. We can compare them with model maps. Thus, we can use a collation of 1-year maps of catch, spectra, ACFs and PACFs computed for observed data and for model output. This will be a more reliable approach than just looking at the time series graph.

SIMULATION RESULTS

Simulation experiments were performed in order to explore population reactions to different fishing strategies. To decide which strategy is good and which is bad, one must first set a criterion for their evaluation. However, the problem of natural resource exploitation is multicriterial. The minimal list of criteria to be considered is (a) maximization of total harvest; (b) minimization of catch variance; (c) population conservation.

Unfortunately, these criteria are often conflicting. Apparently, the first and the last ones are such: the higher the exploitation rate, the higher the
population extinction risk. Later, we will also see that maximization of average catch is hardly compatible with minimization of catch variance, which is very important for industry and trade. Quantitative evaluation of

Fig. 5. Iterative presentation (1-year maps) of perch commercial catches in ten Swiss lakes.
Fig. 6. Isopleths of the average annual catch (logarithmic scale) for fishing effort and mesh size.

criterion (c) is the most difficult. This task is discussed in detail by Soulé (1987). This author introduced the concept of minimal viable population, which is the lower limit of population abundance ensuring stable reproduction. The simplest consequence in our case is that the fishing strategy should maintain population variations within their natural range.

We shall consider the constant effort policy, and a fishing strategy will be characterized with two parameters: the fishing effort and the mesh size. The first one is determined by fishing intensity, i.e. numbers of nets applied, and we shall measure it by the fishing effort $\varphi$ in Eq. (14).

Calculations of the average annual catch (logarithmic values) under fishing mortalities from 1 to 30 and mesh sizes from 11 to 50 mm over 60-year runs are presented on Fig. 6. As stated above, the model can simulate every combination of multiple mesh sizes. Not to overcomplicate the situation, we restrict the investigation to the case of a single mesh size. The curves on Fig. 6 are isocatches, i.e. curves of parameter combinations giving the same average annual catch. The figure shows that both very large and very small mesh sizes give low catches. However the reasons are different: while a large mesh net has simply low fishing efficiency, usage of small mesh nets depletes the population. It could seem that relatively small mesh sizes of 20–23 mm are the most efficient, substantially more than the
current strategy of 32-mm mesh. However, it turns out a small mesh strategy has great disadvantages.

Firstly, the catch consists in smaller fish. Figure 7a contains some other essential information. Here, the standard dispersion of the catch is presented. We can see, secondly, that a mesh of 20–23 mm is also characterized by the highest deviation. This implies high fluctuations of both stock and catches, which are undesirable according to criteria (b) and (c). Figure 7b contains some additional information on catch stability. Here, the minimal (guaranteed) catches are depicted. One can see that the highest values (ca. 5.26) occur with moderate mesh sizes around 32 mm.

To combine these different criteria, we made another presentation of the same data on the plane of criteria (Fig. 8). Each point on this figure represents a fishing strategy with some mesh size and some fishing effort. The coordinates of a point are the average catch and its standard deviation (both are in logarithmic scale) based on the same simulation runs as Figs. 6 and 7. According to criteria (a) and (b) we are trying to maximize the catch and to minimize its variance. For the majority of depicted strategies it is possible to improve both criteria by modifying the fishing parameters. However, some cannot be improved. The problem of multi-criteria optimization was first investigated by V. Pareto. He introduced the definition of an efficient strategy as one which cannot be improved for one criterion without worsening for another one. Walters (1986) applied this approach to fishery. In our case the set of fishing strategies, for which average harvest cannot be increased without also decreasing deviation, forms the lower frontier of the possible strategies. This set depicted on Fig. 8 is called the Pareto frontier. The most inefficient strategies are on the opposite side.

One can see that the current strategy which is characterized by a mesh size of 32 mm and a fishing effort of value 2 is close to efficiency whereas the discussed one with 28-mm nets (that was experimentally introduced for 2 years in Lake Constance) is closer to the inefficient set. The average catch is hardly different with the two strategies (it is barely higher with 28 mm) while the standard deviation of the 32-mm strategy is much lower than of the 28-mm one (Fig. 7a). Analysing Figs. 6–8, we notice that a strategy with the same mesh size but with a higher fishing intensity (\( \varphi = 4 \) to 5) should provide higher catches with a lower deviation. Even the minimal catch would be slightly higher with more intensive fishing. So, according to the model results, the fishing intensity (i.e. the number of 32-mm nets) could be increased with no harm.

Using the model, we made a detailed comparison between 28-mm and 32-mm mesh size strategies with the current fishing intensity (\( \varphi = 2 \)). The results are summarized in Table 3 and one can be satisfied that the 32-mm strategy generates a regime with a lower variance. The increased age of the
Fig. 7. Standard deviation of the catch (a) and minimal guaranteed catch (b) isopleths for fishing effort and mesh size (logarithmic scales).
Fig. 8. Possible combinations of average catch and standard deviation of catches. Each point represents a fishing strategy with some mesh size and some fishing intensity. Best possible trade-off between criteria forms the Pareto frontier.

catch is not only caused by increased mesh size per se but also by the change in population age structure. Besides, we have simulated the transition process. Switching from 28- to 32-mm mesh sizes, the fluctuations become noticeably lower (Table 3).

DISCUSSION

Our opinion is that the complicated and sometimes chaotic fluctuations of perch population abundance in Swiss lakes are a manifestation of

<p>| Table 3 |</p>
<table>
<thead>
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<th>Comparison of 28-mm and 32-mm mesh size strategies</th>
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<tr>
<td>Range of annual catch (t)</td>
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<td>Range of perch stock (t)</td>
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<td>Average age of harvested perch (years)</td>
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nonlinear relations in the reproduction function and strong negative feedbacks such as cannibalism and competition. Furthermore, in exploited populations, such behaviour in the catch time series means that managers are quite far from the optimal harvesting regime and that there is a way to improve the exploitation policy.

To recommend any changes in natural population management, based on a mathematical model, is a rather risky enterprise. Even if a model is valid for some combination of external parameters, one never knows whether it will still be valid if the environment changes. Some new factors may become significant in a new situation and the behaviour of the population may change. Thus, it is not very reliable to recommend changes of the fishing strategy on the basis of model forecasts.

However, our conclusions concerning the different mesh sizes are better

![Catch variation](image)

Fig. 9. Catch variation (ratio of standard deviation to average catch) versus mesh size. Simulated values (circles) and observed values (squares) from Staub et al. (1987). Both graphs show strong decrease of variation with mesh size increase. The higher variations of observed data can be explained with observation errors and with environmental stochasticity.
founded. Operating within the span of 28- to 32-mm mesh size, we only follow the real strategy. Switching from 28- to 32-mm gillnets produces a small decrease in catch for a few years only during the transition period. The essential advantage of the 32-mm strategy is a lower variance of catches and of the population itself.

An additional confirmation of this conclusion is given by the comparison of simulated catch variations with those calculated by Staub et al. (1987) on the basis of observed catches for 11 Swiss lakes with different mesh sizes (Fig. 9). It is evident that both relationships show a strong decrease of variation with growing mesh size. The higher variations of observed data can be explained by observation errors and by environmental stochasticity.

A conclusion which is less reliable concerns fishing intensity. According to the model, if one doubles the fishing effort the average catch increases and the variance decreases. According to the model, we would take the risk of recommending permission to increase fishing intensity in Lake Constance. However, the model does not take into consideration economic factors, particularly, fishing expenses. It is not sure whether fishermen will really be interested to increase their activity. This suggests a possible field for modelling.

Another direction for model development is working out in detail the description of perch ecology: age-specific mortality, growth, subpopulation structure, and, most of all, the reproduction process. This requires estimation of eggs and larval dynamics and probably marking experiments.

REFERENCES


