Extinction risk assessment and optimal harvesting of anchovy and sprat in the Azov Sea

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Summary

1. We explored harvested fish populations in which an extinction risk exists as a consequence of a notable drop in abundance. An adequate formulation of the optimal harvesting problem must account for several criteria. Economic maximization should be balanced against minimization of extinction risk. In addition, environmental stochasticity should be taken into consideration to obtain a realistic description of the population dynamics.

2. The approach to multicriteria optimization of the harvesting policy is illustrated by models of two commercially harvested planktophagous fish found in the Azov Sea in Russia. A stochastic simulation model for the community of competing anchovy *Engraulis encrasicholus* and sprat *Clupeonella delicatula* was developed and investigated. The parameters of the model were estimated on the basis of time series of population abundance and environmental factors that influence reproduction.

3. The model was used to assess numerically the extinction risk of this exploited community. A Pareto approach was used to treat the optimization problem with two criteria: maximizing the total catch and minimizing the extinction probability. No single solution exists but a set of Pareto-optimal fishing strategies was defined, i.e. a set of trade-off solutions. These various solutions can easily be compared by fishery managers and experts before making final decisions.

4. It was found that the harvesting strategy that is currently applied is quite efficient since it is very close to the Pareto-optimal set of solutions. Our recommendation is that these two populations should be considered as a community. Specifically, by increasing the harvest of endemic sprat and decreasing the harvest of the less productive migratory anchovy, fishermen will obtain a higher total harvest with only a slightly higher extinction risk.

Key-words: fishing, population, quasi-extinction, simulation model, stochasticity.

Journal of Applied Ecology (1999) **36**, 297–306

Introduction

A situation in which an endangered population is also harvested is not rare. Indeed, harvesting, aggravated by habitat deterioration, has been a main cause of extinction in the recent past and still takes place in many developing countries. Mathematical modelling can address this problem. It can help to provide a

rational exploitation strategy without conducting unacceptable experiments on the real populations. Specific features of appropriate mathematical models must be stochasticity and multicriteriality. A probabilistic approach is typical of the extinction risk evaluation of endangered populations (e.g. Ginzburg *et al.* 1982; Soulé 1987; Burgman, Ferson & Akçakaya 1992; Whittle & Horwood 1995) while optimal harvesting problems usually imply an economic criterion (e.g. Beverton & Holt 1957; Horwood & Whittle 1986; Getz & Haight 1989; Arditi & Dacorogna 1992). Since in most realistic cases any harvest will increase the extinction risk, these two criteria – the harvest value

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and the extinction probability – are unlikely to be curtailed to one. Thus, a trade-off problem arises. Additionally, environmental variability along with possible chaotic dynamics due to non-linear population processes can give rise to one more criterion characterizing the harvest steadiness, which can be important both from the economic and ecological points of view. The Pareto approach offers methods for analysing such problems and finding the payoffs of different strategies. It does not give a single solution but a set of strategies that cannot be improved for one criterion without worsening for others. This approach originated in economics by Vilfredo Pareto where it is now a standard way to analyse optimization problems under multiple criteria, and it has been applied to ecology and fisheries (Baumol & Oates 1975; Walters 1986; Getz & Haight 1989). In this paper, the specific stationary multicriteria problem is that of maximizing the harvest value and minimizing the extinction risk.

Lande, Engen & Sæther (1995) and, studying a more general case, Whittle & Horwood (1995) incorporated harvest return and extinction risk into a single criterion in the framework of a stochastic dynamic programming model. They proposed the use of such utility functions as the total expected harvest before extinction and the average expected harvest over the time to extinction. Unfortunately, such a strategy requires the precise knowledge of the population size every year and perfect control over the fishing effort which must be adjusted every year. Both are impossible to obtain in the case of the Azov Sea in Russia. Defining some constant, long-term harvesting policy is more realistic, making it impossible to combine the two criteria into a single utility function.

The problem of extinction risk assessment for a single population was formulated accurately by Bartlett (1960). Normally, the viability analysis of a biological population that can be modelled by a simple mathematical model, can be performed analytically with the study of the sensitivity of model stability to the parameter values. The results of such stability analysis should be seen and understood in terms of population viability. The risk of population extinction and of possible qualitative population changes should be analysed. The practical tasks of conservation biology have brought ecology to probability models that can be applied to population extinction risk assessment. The simplest model of this type is the Markov chain model describing transitions of population size with an absorbing zero state. More developed models of this kind can include age, stage, body size, and genetic structures.

Unfortunately, realistic models can only be investigated with the help of simulation techniques. The concept of quasi-extinction probability, i.e. the probability that population density drops below a given pre-assigned level (Ginzburg *et al.* 1982) has been applied to several case studies using software specifically developed for numerical risk assessment (Ferson & Akçakaya 1990; Akçakaya & Ginzburg 1991a,b; Akçakaya 1991; Akçakaya & Ferson 1992; Burgman, Ferson & Akçakaya 1992).

Here, we will follow an approach developed by some of us (Tyutyunov *et al.* 1993). A piece of user-friendly software was built, allowing the description of the dynamics of an isolated age-and sex-structured, exploited, population of fish with density-dependent reproduction. The mathematical model includes non-linear reproduction, individual growth, and harvesting intensity for specific individual sizes. On the basis of stochastic simulations, the program offers application of a wide spectrum of mathematical methods, from the calculation of simple time series statistics to bifurcation analysis of the model and comparative examination of different exploitation strategies with graphical display of multicriteria optimization.

The biological system we consider here consists of two competing fish species. Multiple species harvesting models are quite rare. An early, theoretical, approach was developed by Clark (1976). More recently, optimal harvesting models on age-structured populations and on multispecies fish stocks were developed by Horwood & Whittle (1986) and Horwood (1990), but with no consideration for extinction risks.

In the present paper, we further develop the multicriteria optimization approach used by Tyutyunov *et al.* (1993) to apply it to multiple species harvesting of fish in the Azov Sea. We will study population viability under the double threat of harvesting and stochastic environmental impacts. The consideration of stochasticity is very important, as it makes the optimal harvesting strategy more cautious and allows for more exact evaluation of the risk of population extermination. Harvesting optimization must comprise catch stabilization and reduction of its variation, as far as environmental conditions and flexibility of the harvesting strategy make it possible.

The biological system

We have analysed the relatively complex situation of two species being harvested simultaneously in the Azov Sea, Russia: anchovy *Engraulis encrasicholus maeoticus* Pus and sprat *Clupeonella delicatula delicatula* Nordm. The Azov Sea (46°N by 37°E) is a shallow (7 m deep), brackish and very productive water body, located east of the Crimea peninsula on the north of the Black Sea. It communicates with the latter by the Kerch straits (16 km wide) which is the only outlet. The water exchange between the two seas (and the resulting salinity regime) depends strongly on the winds and on the inflow of freshwater into the Azov Sea. This freshwater is brought mainly by the River Don, flowing into the Taganrog Bay, the eastern extremity of the Azov Sea, and the River Kuban, flowing into the Azov Sea on its south-eastern side.

Ichthyological sources indicate that, in the Azov Sea, sprat and anchovy compete for common food resources (Bronfman, Dubinina & Makarova 1979). Preliminary statistical analysis of the available data and identification of the model parameters have also confirmed this fact. For this reason, both species must be modelled as an interacting community.

Observations (Lutz 1986) suggest that intraspecific competition acts only among the adults while interspecific competition is exerted by the total population of the alternate species. This difference is due to the migration cycles of the species. In the winter, sprats do not leave the Azov Sea but remain in the central region, whereas anchovies move to the warmer Black Sea. Thus, the two species are separated during the period when they build up their fat reserves. The viability of the offspring is largely determined by the fat content of the spawning individuals (Lutz 1986). Therefore, intraspecific competition is assumed to occur mainly among adults. Interspecific competition occurs mainly in the spring, when both species swim to the Taganrog Bay, where environmental conditions for spawning are optimal (water salinity is lower) (Lutz 1986). In the Taganrog Bay, all age groups compete for a common food resource. For this reason, interspecific competition is assumed to depend on the total abundance of the alternate species.

Two environmental factors must be accounted for: the average annual salinity of the Azov Sea and the total annual inflow of the rivers Don and Kuban. This is mainly due to their direct influence on the spawning process of both populations. If the inflow from the rivers in the spring is too strong, it will wash out the eggs. If the inflow is too weak, it will result in drying of the spawn products. High salinity also reduces recruitment because it impairs spermatozoa mobility. These facts are known from ichthyological sources (Lutz 1986). Since the construction of the Tzimlyansk Reservoir in the 1950s, salinity has remained too high and water flow too low.

Data available for this study consist of several time series running from 1953 to 1981 (i.e. 29 yearly observations) provided by the Azov Fisheries Research Institute. The series include estimates of the annual abundance of juveniles and adults of both species, yearly catches of each species, average annual salinity of the Azov Sea and total annual inflow of the rivers Don and Kuban.

The model

DETERMINISTIC MODEL

Let N denote anchovy and K sprat. Both populations are subdivided into two stage groups. Population dynamics are assumed to proceed as follows: in year t, group 2 (adults) reproduce following Ricker-type competition (Ricker 1954) and produce the group 1

(juveniles) of year $t + 1$. We use superscripts to denote the time. (They are not exponents.)

Thus, the recruitment equation for anchovy is:

$$N_1^{t+1} = a_N N_2^t \, e^{-b_N N_2^t} e^{-\gamma_N (K_1^t + K_2^t)},$$

where a_N is the fecundity in optimal conditions, and b_N and γ_N quantify intraspecific and interspecific competition, respectively. Adults are harvested after reproduction. They result from ageing juveniles and from surviving adults. The equation for adult anchovies is:

$$N_2^{t+1} = (p_N N_1^t + q_N N_2^t)(1 - h_N^t),$$

where p_N and q_N are the juvenile and adult survival rate, and h_N^t is the harvesting effort.

The influence of S^t, the average annual salinity of the Azov Sea and Q^t, the total annual inflow of rivers Don and Kuban is modelled with Gaussian functions, as multiplicative reducers of recruitment. These two environmental factors S^t and Q^t are time series, with different values every year. For anchovy, these multipliers are:

$$e^{-((S^t - S_{N,0})/\sigma_N^S)^2} \quad \text{and} \quad e^{-((Q^t - Q_{N,0})/\sigma_N^Q)^2},$$

where $S_{N,0}$ and $Q_{N,0}$ are the optimal values, and σ_N^S and σ_N^Q are the tolerances.

Writing analogous equations for sprat, the full model is finally:

$$N_1^{t+1} = a_N N_2^t \, e^{-b_N N_2^t} e^{-\gamma_N (K_1^t + K_2^t)}$$
$$\times e^{-((S^t - S_{N,0})/\sigma_N^S)^2} e^{-((Q^t - Q_{N,0})/\sigma_N^Q)^2} \quad \text{eqn 1a}$$

$$N_2^{t+1} = (p_N N_1^t + q_N N_2^t)(1 - h_N^t) \quad \text{eqn 1b}$$

$$K_1^{t+1} = a_K K_2^t \, e^{-b_K K_2^t} e^{-\gamma_K (N_1^t + N_2^t)}$$
$$\times e^{-((S^t - S_{K,0})/\sigma_N^S)^2} e^{-((Q^t - Q_{K,0})/\sigma_K^Q)^2} \quad \text{eqn 1c}$$

$$K_2^{t+1} = (p_K K_1^t + q_K K_2^t)(1 - h_K^t). \quad \text{eqn 1d}$$

The catches are:

$$C_N^t = m_N h_N^t (p_N N_1^t + q_N N_2^t)$$

$$C_K^t = m_K h_K^t (p_K K_1^t + q_K K_2^t)$$

with m_N and m_K being the individual weights of anchovy and sprat.

Parameter estimation

For parameter identification, we used recorded measurements of salinity and river inflow as inputs. The optimal values of environmental factors S_0 and Q_0 providing the best conditions for spawning were taken from ichthyological sources (Lutz 1986). The mortality values q_N and q_K were determined from the knowledge of the life expectancy of each species (Lutz 1986). These values are given in Table 1.

We have used a two-step procedure for parameter estimation. First, a multiple linear regression was

Table 1. Parameter values for the deterministic model. Standard errors are given for the estimated parameters

Parameter	Anchovy	Sprat	Source
Optimal fecundity (a)	$18{\cdot}12 \pm 1{\cdot}98$	$9{\cdot}19 \pm 0{\cdot}79$	Linear regression
Intraspecific competition (b)	$0{\cdot}195 \pm 0{\cdot}01$	$0{\cdot}02 \pm 5{\cdot}10^{-4}$	Linear regression
Interspecific competition (γ)	$0{\cdot}005 \pm 5{\cdot}10^{-4}$	$0{\cdot}012 \pm 0{\cdot}002$	Linear regression
Juvenile survival (p)	$0{\cdot}319$	$0{\cdot}448$	Calibration
Adult survival (q)	$0{\cdot}32$	$0{\cdot}5$	(Lutz 1986)
Salinity tolerance (σ^S)	$2{\cdot}56 \pm 0{\cdot}34$	$2{\cdot}62 \pm 0{\cdot}31$	Linear regression
Inflow tolerance (σ^Q)	$64{\cdot}09 \pm 16{\cdot}37$	$97{\cdot}83 \pm 32{\cdot}34$	Linear regression
Optimal salinity (S_0)	$12{\cdot}2$	$12{\cdot}1$	(Lutz 1986)
Optimal inflow (Q_0)	$32{\cdot}0$	$35{\cdot}6$	(Lutz 1986)

applied to the reproduction equations as follows. Dividing eqn 1a by N_2^t and taking logarithms, we obtain a multiple linear equation. Regressing this equation on available data provides estimates of parameters a_N, b_N, γ_N, σ_N^S, σ_N^Q. Proceeding similarly for sprat, the parameters a_K, b_K, γ_K, σ_K^S, σ_K^Q were estimated. On the two steps, the procedures that were used gave the standard error of the fitted parameters. Table 1 gives the values of all estimated parameters with their standard errors (SE). On the second step, the parameters p_N and p_K were calibrated simultaneously by fitting the whole model trajectories to the observed time series, using the least squares criterion. Starting from initial estimates of p_N and p_K, roughly determined from demographic field data, an iterative procedure was applied to the model (eqn 1a–d). The final estimates are not sensitive to the choice of the initial estimates.

An analytical study of all possible equilibria was performed for the model (eqn 1a–d) without environmental effects. To exclude the influence of salinity and inflow fluctuation, and to obtain an autonomous system, we fixed S^t and Q^t (as well as harvesting efforts) to their average values. Four possible equilibria exist: the trivial zero equilibrium, two single-species equilibria and one non-trivial equilibrium with both species coexisting. The analytical conditions for stability of each equilibrium have been derived but, because of their huge size, these formulae are not given here. Using these formulae, we have checked that the set of estimated parameters (Table 1) fulfils the conditions for a stable non-trivial equilibrium. As the system does not exhibit chaos with the parameter values being used, its dynamics do not depend much on initial conditions, which were set to the observed values of 1953. Therefore, it is likely that the observed population fluctuations (see Fig. 1, broken curves) are due to environmental causes. This seems reasonable in the case of the Azov Sea because salinity is close to the upper limit of the tolerance of the fish species considered. The critical importance of salinity and freshwater inflow have been demonstrated earlier for the Azov Sea ecosystem (Vorovich *et al.* 1981).

STOCHASTIC MODEL

Successful and unsuccessful reproduction

Other environmental factors that could be important, like temperature, winds at the time of fry hatching, and fluctuations in plankton productivity, have been ignored. The variety of complex processes affecting larval survivorship cannot be modelled completely. Following Vorovich *et al.* (1989) we use a reduced approach considering that, besides the influence of salinity and river inflow, each year can be either favourable or unfavourable for reproduction. A similar scheme of random transitions between several environmental regimes was used by Whittle & Horwood (1995). The set of observations is divided into two groups: successful and unsuccessful years. The value of recruitment calculated with the parameters estimated over the whole set of observations (see Table 1) is used as a criterion for this subdivision. If the observed number of recruits is higher than predicted, then the corresponding year is considered as successful. Otherwise it is unsuccessful. Note that the same year can be successful for one species and unsuccessful for the other species. Working separately on the two subsets of observations, and using the same technique as above, we then estimated two ensembles of parameters for the successful and the unsuccessful years (see Table 2). Now S_0 and Q_0 were no longer set to known values but they were determined by calibration, constraining them within the limits of natural fluctuations. The standard errors were computed for all estimated parameters except S_0 and Q_0. A sensitivity analysis was performed on all parameters (see below).

The comparison of observed and predicted time series of anchovy and sprat juveniles is shown in Fig. 1. The correlation coefficient between observations and model predictions is equal to $0{\cdot}7$ for anchovy and $0{\cdot}81$ for sprat. Besides, in order to assess the quality of the fit, a simple linear regression $y = ax + b$ of predicted vs. observed values was performed. For both species, the regression coefficient a was found not to be significantly different from 1 and the constant b not significantly different from 0.

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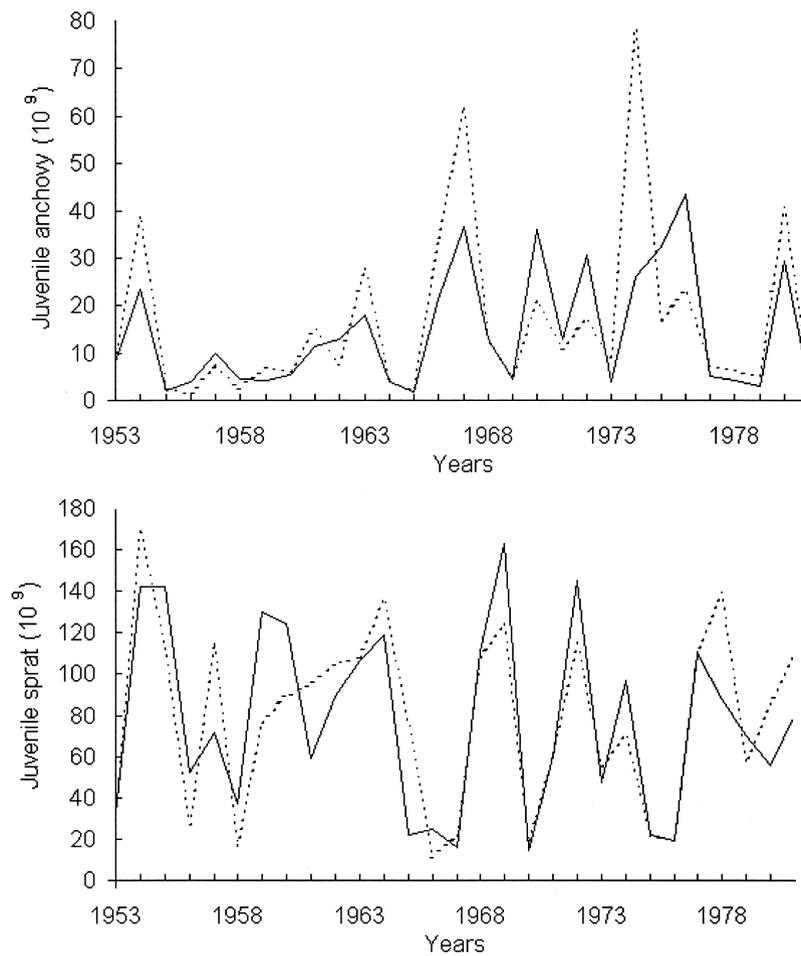
Fig. 1. Broken lines are the observed time series of abundances of juvenile anchovy and juvenile sprat in the Azov Sea. Unbroken lines are the values predicted by the full model (accounting for successful or unsuccessful reproduction).

Table 2. Parameter values for the model with subdivision in successful and unsuccessful years. Standard errors are given for the estimated parameters

Parameter	Successful years Anchovy	Sprat	Unsuccessful years Anchovy	Sprat
Optimal fecundity (a)	$32{\cdot}27 \pm 2{\cdot}59$	$17{\cdot}45 \pm 0{\cdot}77$	$1{\cdot}72 \pm 0{\cdot}26$	$5{\cdot}67 \pm 0{\cdot}65$
Intraspecific competition (b)	$0{\cdot}181 \pm 0{\cdot}008$	$0{\cdot}022 \pm 3{\cdot}10^{-4}$	$0{\cdot}117 \pm 0{\cdot}015$	$0{\cdot}027 \pm 0{\cdot}002$
Interspecific competition (γ)	$0{\cdot}005 \pm 4{\cdot}10^{-4}$	$0{\cdot}01 \pm 0{\cdot}001$	$0{\cdot}001 \pm 1{\cdot}10^{-4}$	$0{\cdot}005 \pm 3{\cdot}10^{-4}$
Juvenile survival (p)	$0{\cdot}286$	$0{\cdot}353$	$0{\cdot}220$	$0{\cdot}336$
Salinity tolerance (σ^S)	$5{\cdot}94 \pm 1{\cdot}28$	$4{\cdot}60 \pm 0{\cdot}72$	$4{\cdot}88 \pm 1{\cdot}39$	$1{\cdot}29 \pm 0{\cdot}1$
Inflow tolerance (σ^Q)	$298{\cdot}24 \pm 81{\cdot}5$	$25{\cdot}86 \pm 1{\cdot}75$	$95{\cdot}85 \pm 32{\cdot}8$	$215{\cdot}65 \pm 91{\cdot}9$
Optimal salinity (S_0)	$12{\cdot}9$	$12{\cdot}1$	$12{\cdot}6$	$12{\cdot}1$
Optimal inflow (Q_0)	$26{\cdot}8$	$35{\cdot}6$	$33{\cdot}5$	$40{\cdot}4$

Notice that this new model has a greater number of parameters than the first deterministic model. Therefore, it is necessary to examine whether it provides a significantly better fit due to the improved model structure. To assess the advantage of a complicated model over a simpler model, one can use the likelihood ratio test (e.g. Hilborn & Mangel 1997). This test requires that the models being compared be nested; that is, the more complex model reduces to the simpler one by setting some parameters to 0. Let L_A be the negative log-likelihood of the simpler model, and L_B for the more complex (subdivided) model. Then, $R = 2(L_A - L_B)$ has a chi-square distribution with the number of degrees of freedom v equal to the difference in the numbers of parameters between models B and A. In our case $v = 14$, and $R = 28{\cdot}3$ for anchovy and $R = 36{\cdot}2$ for sprat. Both of these values are significant at the 5% level.

Environmental stochasticity

Two sources of stochasticity were accounted for in the model. The first one is reproduction stochasticity and the second one is environmental stochasticity. Regarding reproduction, stochastic simulations were performed with random occurrence of a successful or unsuccessful year. The probability of occurrence of an unsuccessful year was set equal to the proportion of unsuccessful years in the sample (0·39 for sprat and 0·40 for anchovy).

Stochasticity of accounted environmental factors was modelled following Ratkovich & Ya (1977), Bronfman & Surkov (1976), and Surkov *et al.* (1977): starting from the initial values of 1953, time series of river inflow and salinity are built stochastically, while keeping the same serial correlation structure as in the observed data. The river inflow was modelled as a Markov stochastic process (details can be found in Ratkovich & Ya 1977), while for the sea salinity, the following multiple linear equation was used (Bronfman & Surkov 1976):

$$S^t = 3·928 + 0·771 S^{t-1} - 0·022 Q^t - 0·015 Q^{t-1}.$$

These submodels were simply incorporated into the simulation program. Using the Monte-Carlo method, the trajectories were averaged over 50 replications of stochastic simulations. The results obtained were used to solve numerically the stationary problem of extinction risk assessment and optimal harvesting for the two species community.

SENSITIVITY ANALYSIS

Sensitivity measures the response of model variables to small variations in parameter values (Beck 1983). In practice, sensitivity can be estimated as the ratio of the relative variation of model variables to the relative variation of parameters. Sensitivity was analysed as follows. Starting from the values of Table 2, each parameter was varied in turn by $\delta = 15\%$. For every parameter, 50 stochastic replications of 30-year forecasts of the model were performed. The average deviations of modelled abundances of anchovy juveniles were calculated according to the expression:

$$\overline{\Delta N_1} = \frac{1}{1500} \sum_{k=1}^{50} \sum_{t=1}^{30} |N_1^{t,k} - \overline{N_1}|,$$

where $\overline{N_1} = \frac{1}{1500} \sum_{k=1}^{50} \sum_{t=1}^{30} N_1^{t,k}$ is the average value of anchovy juveniles obtained as a result of simulations with the basic parameter values. The sensitivity of variable N_1 to the parameter being varied is finally calculated as:

$$\zeta_N = \frac{1}{\delta} \frac{\overline{\Delta N_1}}{\overline{N_1}}. \qquad \text{eqn 2}$$

An analogous expression is calculated for sprat juveniles.

The values of ζ computed for both species and for all parameters are given in Table 3. This analysis shows a generally low sensitivity of the model to parameter variations. The most important parameters (those for which the sensitivity is highest) are the fecundities, the intraspecific competition coefficients and the salinity tolerance.

Optimal management of the two-species community

The model that has just been described was used to solve numerically the problem of extinction risk minimization and optimal harvesting with a fixed effort strategy. It is well known that harvesting a fixed quota appears to be more unstable than harvesting a fixed proportion of a population and can push the population out of the basin of attraction of the stable equilibrium (e.g. Begon, Harper & Townsend 1990). We consider the two-criteria problem of finding the combination of fishing efforts (h_N, h_K) that maximizes the total harvest $C_{NK} = C_N + C_K$ (the market prices for both species are equal) while minimizing the probability (risk) that either population falls below the quasi-extinction threshold within the simulation horizon T (Ginzburg *et al.* 1982). The second criterion (the probability that at least one population drops below its critical level) can be expressed as $P_{NK} = P_N + P_K - P_N P_K$ where P_N and P_K are the probabilities of quasi-extinction computed for each species. For each stochastic realization, the catches are averaged over the simulation horizon T:

$$C_N = \frac{m_N h_N}{T} \sum_{t=1}^{T} (p_N N_1^t + q_N N_2^t)$$

Table 3. Sensitivity coefficients (eqn 2) of modelled anchovy (N) and sprat (K) juveniles to variations of parameters

Parameter	Anchovy juveniles	Sprat juveniles
Optimal fecundity (a_N)	0·42	0·22
Optimal fecundity (a_K)	0·25	0·73
Intraspecific competition (b_N)	0·48	0·23
Intraspecific competition (b_K)	0·36	0·61
Interspecific competition (γ_N)	0·34	0·10
Interspecific competition (γ_K)	0·13	0·22
Juvenile survival (p_N)	0·12	0·19
Juvenile survival (p_K)	0·12	0·14
Adult survival (q_N)	0·11	0·24
Adult survival (q_K)	0·19	0·15
Salinity tolerance (σ_N^S)	0·23	0·13
Salinity tolerance (σ_K^S)	0·33	1·19
Inflow tolerance (σ_K^Q)	0·16	0·14
Inflow tolerance (σ_K^Q)	0·16	0·17
Optimal salinity ($S_{N,0}$)	0·35	0·21
Optimal salinity ($S_{K,0}$)	0·34	0·61
Optimal inflow ($Q_{N,0}$)	0·07	0·14
Optimal inflow ($Q_{K,0}$)	0·16	0·46

$$C_K = \frac{m_K h_K}{T} \sum_{t=1}^{T} (p_K K_1^t + q_K K_2^t),$$

with the individual weights of anchovy $m_N = 7$ g and sprat $m_N = 5$ g. The critical values N_{cr} and K_{cr} were set equal to 5% of the average number of adults observed in the time series.

The simulation length of 30 years is the length of the time series that we used for parameter identification. Stochastic simulations over the same length of time are not intended to be forecasts over a 30-year horizon, but rather a retrospective assessment of the extinction risk and harvest returns.

The isopleths of the combined catches C_{NK} and of the extinction risk P_{NK} against harvesting rates are presented in Figs 2 and 3. These results suggest that the current practice (harvests of 20% and 30%, respectively, for adult anchovy and for adult sprat populations) can be increased without great danger. According to the model, the fishing efforts can almost be doubled while keeping the level of risk relatively low. With the chosen thresholds of quasi-extinction, the chance of falling under N_{cr} or K_{cr} over the simulation horizon $T = 30$ years did not exceed 0·07. However, one should notice that higher values would lead to overcatch and strong increase of the quasi-extinction risk, which would be even greater if higher values of the critical population sizes (N_{cr}, K_{cr}) had been chosen (see Fig. 3).

The isopleth diagrams in Figs 2 and 3 show how fishing strategies determine each criterion separately. In order to view the trade-off between the two criteria,

another presentation of this information is necessary, i.e. the so-called Pareto diagrams (Fig. 4). This figure presents occurrences of combined catch C_{NK} and minimal number of individuals of the competing community of anchovy and sprat. This second criterion is calculated as $X_{min} = \min_t\{N_2^t/N_{cr}, K_2^t/K_{cr}\}$. Hence, it is just the lowest adult abundance of sprat or anchovy (as measured in units of critical population size) occurring during the simulation period T. This value is closely related to the extinction probability of either species. Every point of the diagram is the result of the 50 stochastic replications with a given fishing strategy: the fishing efforts h_N and h_K were varied independently from 0 to 1 by increments of 0·03. The values of the control parameters h_N and h_K that maximize the conservation criterion X_{min} while maximizing the economic criterion C_{NK} determine the top-right border of the cloud, known as the Pareto frontier. This frontier (i.e. the set of non-improvable criteria) gives the trade-off. For a given catch C_{NK}, the frontier gives the highest value of X_{min} that can be obtained; or, for a given value of X_{min}, it gives the highest combined catch C_{NK} that can be expected. All strategies below the Pareto frontier are less efficient. Our simulation software allows the user to work interactively with the Pareto diagram, returning for any selected point the corresponding combination of fishing efforts h_N and h_K.

Discussion

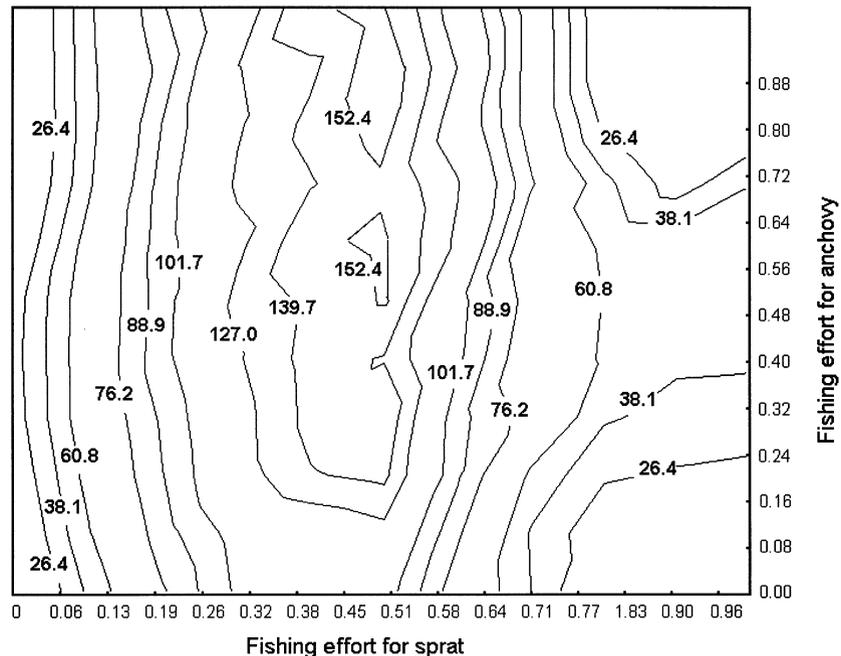A model of the two competing species has been built to solve applied problems of management of pelagic fish

Fig. 2. Isopleths of combined expected yield C_{NK} against the two harvesting rates.
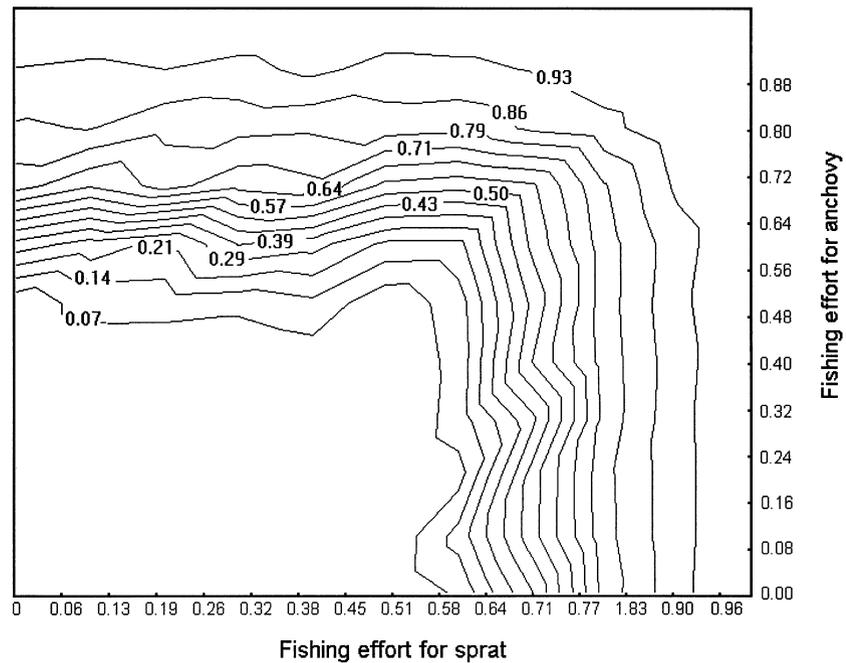
Fig. 3. Isopleths of the quasi-extinction risk P_{NK} (probability that either population drops below its critical level) against the two harvesting rates.
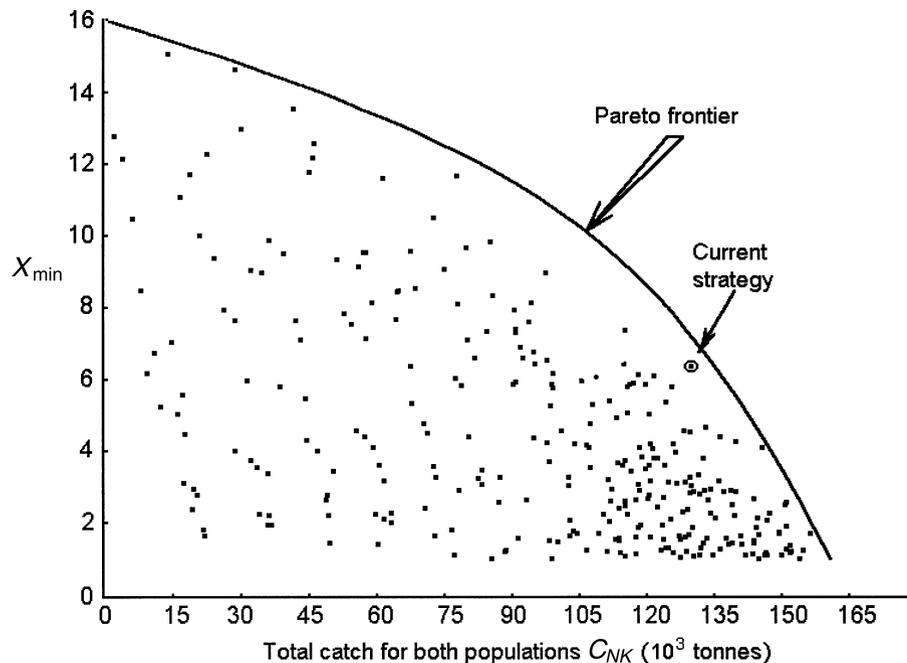

Fig. 4. Pareto diagram of the lowest number of adult anchovy or sprat (as measured in units of critical population size) occurring during the simulation period (X_{min}) vs. expected combined catch (C_{NK}). Each point represents a fishing strategy (a pair of fishing efforts for anchovy and sprat). The best possible trade-off forms the Pareto frontier.

populations in the Azov Sea. In addition to the traditional economic criterion, we considered the ecological criterion of minimizing the quasi-extinction risk. These species are harvested under the strong influence of environmental factors. The model parameters were estimated using a data set that included population and environmental characteristics divided into two groups:

successful and unsuccessful years (Vorovich *et al.* 1989). To some extent, this approach reduces some of the variation in the system. However, the parameter values obtained were used for simulations with stochastic switching between the two environmental regimes and with stochastically generated environmental factors, thereby re-introducing variability.

Analysing just the economic criterion C_{NK}, it is interesting to see how the presence of competing species changes the conclusions about optimal strategies. Clark (1976) noticed that in a competing community, because of bifurcation occurring with increasing harvesting rate, extinction can take place even with harvesting values lower than the optimal fishing effort providing the maximal sustainable yield (MSY). Giving as an example the collapse of the Pacific sardine fishery in the late 1940s, Clark explains this event by the combined effect of heavy fishing and interspecific competition. In the absolute absence of interspecific competition, the stationary optimal harvesting (in the economic sense) would consist in independent harvests of the coexisting species with the efforts providing the MSY of each population ($h_{MSY}^{N} \approx 0.53$ and $h_{MSY}^{K} \approx 0.48$). In our case, where the competition coefficients appear rather low in comparison with the self-regulation coefficient, maximization of the combined harvest C_{NK} can comprise total removal of the less productive anchovy ($h_N = 1$) and exploitation of the sprat population with a harvesting effort $h_K \approx 0.5$ providing the MSY for an isolated population (see Fig. 2). Such a harvesting strategy is 'optimal' in the sense of the single economic criterion (see a similar theoretical example of Clark 1976). Furthermore, one can see in Fig. 2 that a decrease of the harvesting pressure for anchovy from $h_N = 1$ to $h_N \approx 0.5$ must be compensated for by just a very slight decrease of the fishing effort for sprat at $h_K \approx 0.5$ to obtain almost the same level of combined yield $C_{NK} \approx 152000$ tonnes.

It is interesting to see that overcatch of the endemic sprat population results in a strong fall of the total catch, while overcatch and total extinction of its competitor, the migrant anchovy, just increases the criterion C_{NK}.

The isopleth diagram in Fig. 3 illustrates the changes of the extinction risk P_{NK}. Note that, in general, minimization of the extinction risk (or the equivalent maximization of the lowest abundance X_{min} does not necessarily require zero harvesting. For the classical Ricker (1954) model with a high reproduction rate causing chaotic dynamics in the absence of harvesting, the minimal risk of population extinction is obtained with a fishing effort that corresponds to the onset of a stable equilibrium after the 2-year cycle bifurcation (Tyutyunov, Dombrovsky & Obushchenko 1996). This seems to be a general result for Ricker-type nonlinear models. However, as was demonstrated by the deterministic linear analysis of the present model, the set of estimated parameters does not correspond to the chaotic regime. This is why the maximum value of the ecological criterion X_{min} is obtained here with zero harvesting effort for each species.

Using Figs 2 and 3, one can easily compare the effects of different fishing strategies on both economic and ecological criteria. The final choice of catch level should belong to the set of Pareto-optimal strategies (Fig. 4). It is interesting that the current combination of the two harvesting efforts gives a point near the Pareto frontier. This fact can be considered as an indirect validation of the model. However, the model can suggest other strategies that keep a balance between harvesting value and extinction risk. For example, using our software, one could see that an increase in the harvesting effort for the sprat (from 0·3 to 0·46) accompanied by a decrease in the effort for anchovy (from 0·2 to 0·16), which is less productive but more vulnerable to environmental impacts, will lead to a much higher total harvest with just a slightly increased risk level. Certainly, to recommend changes in natural population management solely on the basis of a mathematical model is rather risky. However, the model and software can be useful for fishery experts, providing additional suggestions for management and supporting arguments upon which their decisions are made. In particular, our simulation model can help to assess the trade-off between commercial profits and population security in the long term.

Acknowledgements

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