*Animal Conservation* (2001) **4**, 157–167  Printed in the United Kingdom

# Competing harvesting strategies in a simulated population under uncertainty

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*(Received 2 August 2000; accepted 5 December 2000)*

## Abstract

We present a case study of the use of simulation modelling to develop and test strategies for managing populations under uncertainty. Strategies that meet a stock conservation criterion under a base case scenario are subjected to a set of robustness trials, including biased and highly variable abundance estimates and poaching. Strategy performance is assessed with respect to a conservation criterion, the revenues achieved and their variability. Strategies that harvest heavily, even when the population is apparently very large, perform badly in the robustness trials. Setting a threshold below which harvesting does not take place, and above which all individuals are harvested, does not provide effective protection against over-harvesting. Strategies that rely on population growth rates rather than estimates of population size are more robust to biased estimates. The strategies that are most robust to uncertainty are simple, involving harvesting a relatively small proportion of the population each year. The simulation modelling approach to exploring harvesting strategies is suggested as a useful tool for the assessment of the performance of competing strategies under uncertainty.

## INTRODUCTION

A major current focus in population management is how best to ensure the sustainability of harvesting under uncertainty. Approaches to this problem include creating no-take areas (Roberts, 1997; Allison, Lubchenco & Carr, 1998; Mangel, 1998; Tuck & Possingham, 2000) and active adaptive management (MacNab, 1983; Walters, 1986; Parma *et al*., 1998). Another approach uses simulation models as a model world within which the performance of management strategies is explored under a broad range of assumptions. Management strategies are tested on a hidden population model, and their robustness is probed with respect to different performance criteria. This approach has received comparatively little attention outside the fisheries literature, although fisheries scientists are increasingly aware of its potential (Hilborn &Walters, 1992; Kirkwood & Smith, 1996; McAllister *et al*., 1999). The Scientific Committee of the International Whaling Commission (IWC-SC) used this approach when devising the Revised Management Procedure for whale stocks (Cooke, 1995; Kirkwood, 1997). Simulation trials can assess strategy performance before risking a strategy on the population itself, highlighting when strategies are most likely to fail.

We apply the IWC-SC's methods to the saiga antelope (*Saiga tatarica*) population of Betpak-dala, Kazakhstan. The saiga is a nomadic species of the steppe and semi-desert, harvested commercially for its meat, hide and horns (Bekenov, Grachev & Milner-Gulland, 1998). This population was chosen because a long time series of population size estimates and offtakes is available, as well as much biological information (Bekenov *et al*., 1998). Population models have been developed for the species and used to test a simple harvesting strategy (Milner-Gulland, 1994, 1997).

We use performance indicators that distinguish variability within and between simulation runs, and explore the effects of error and bias on the robustness of management strategies. We do not attempt to carry out full optimizations for particular harvesting strategies, which would limit the applicability of the results to the saiga antelope alone. Instead, we test a broad range of

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strategies, developed subjectively by different individuals on the basis of model outputs, using a range of robustness trials. Having identified promising strategies, the next stage would be to optimize them for the particular system under study, but that is not the focus of this paper. Our approach avoids limiting the scope of the management strategies considered to those that might otherwise be considered *a priori* the best, hence allowing us to uncover general heuristic principles for developing management strategies that are robust to uncertainty.

## METHODS

The first step is to choose a model for the dynamics of the population. We used a model for saiga antelope population dynamics developed by Milner-Gulland (1994). It is age- and sex-structured with fecundity and mortality rates varying according to the climate. The independent probabilities of each year being good or bad are estimated from the occurrences of each year type this century. Fecundity rates vary according to a normal distribution, parameterized from Bekenov *et al*. (1998). The model is not presented in detail here, because the specifics of the underlying model are not the focus of this paper; rather we concentrate on our approach to testing management strategies.

The process took the form of a game, in which the junior authors proposed strategies for harvesting the saiga antelope over a 50 year period starting in 1994. The strategies were required to fulfil the following management objectives: (1) maximize total discounted revenues over the 50 year period; (2) minimize variability in revenues; (3) fulfil a stock conservation constraint: the probability of the population falling below 200,000 animals at any point during the 50 year period must be < 5%.

The stock conservation constraint reflects the requirement that the saiga population should remain large enough for the probability of extinction to be negligible. The choice of the threshold and the probability of falling below it is subjective, reflecting the manager's evaluation of the saiga as a component of the ecosystem. A common rule of thumb for the threshold population size is 20% of the unexploited population size (Kirkwood & Smith, 1996); the threshold used here is 20% of the maximum population size in the data.

The profitability objective is expressed in terms of revenues because strategies differ in a non-trivial way in their costs of implementation, and cost data do not exist. The revenue obtained from a harvested saiga is the value of the meat obtained plus the horns of adult males. Revenues are discounted and the mean revenue over 50 years is calculated. The overall mean of the 50 year discounted revenues from 500 simulations is taken as the performance indicator for objective 1. The CV of revenues over the 50 year period is calculated for each of the 500 simulation runs, and the two indicators used for objective 2 are the mean of the CVs, and the CV of the CVs. The former measures variability within runs; keeping variability over time low is important to minimize social and economic instability for harvesters. A run of good years may led to over-investment in the sector, which may then be hard to withdraw in bad years, and low predictability may deter investors. The latter measures variability between simulations, so is a measure of the predictability of the strategy's outcome. A strategy with a very high between-runs variability would not be ideal for use in real life, as it would be hard to predict in advance how it would perform.

There is a tradeoff between maximizing revenues and minimizing variability; however, this varies between strategies. Thus strategy performance is given in terms of all the above indicators, rather than as an integrated summary statistic. However, all strategies were required to pass the stock conservation test, objective 3. Because only 500 runs were performed for each strategy, any strategy for which the population fell below the threshold in less than 7% of the runs was accepted. This ensured that strategies were not failed solely owing to sampling error.

The managers had access to all the data on saiga population biology, climate and harvests published in Bekenov *et al*. (1998). Importantly, this publication does not include information on the structure and parameterization of the population model, which remained hidden from the managers. This ensured the conceptual separation of the strategies and the model against which they were tested.

Managers could base their strategy only on the information which actual saiga managers have at their disposal: an estimate of the population size and proportion of adult males in the population in April of current and previous years, and revenues and climatic conditions in previous years. Using this information, the managers developed strategies that each year recommended the number of animals to be harvested, and their age and sex ratios. The sequence of events each year is shown in Fig. 1. Population counts are subject to varying amounts of observation uncertainty and bias, and are not necessarily performed every year. Thus observation uncertainty is modelled through the flawed data that the management strategy must use, while environmental uncertainty is modelled through the probabilistic nature of the underlying population model. The framework of the process is shown in Fig. 2.

All strategies were tested under a simple 'base case' scenario, consisting of our best estimate of the parameter values, with no biases in the observation errors and no poaching (Table 1). Many strategies were submitted; most failed to meet the criteria for success. Managers were informed about the outcome of the tests and allowed to revise their strategies, but were not informed about other managers' strategies, to ensure a broad range of approaches was considered. Strategies that fulfilled the stock conservation constraint were allowed to continue to the next round, regardless of their performance against the other two objectives. Hopeless strategies were rejected, while strategies which just failed to meet the stock conservation constraint were revised. This

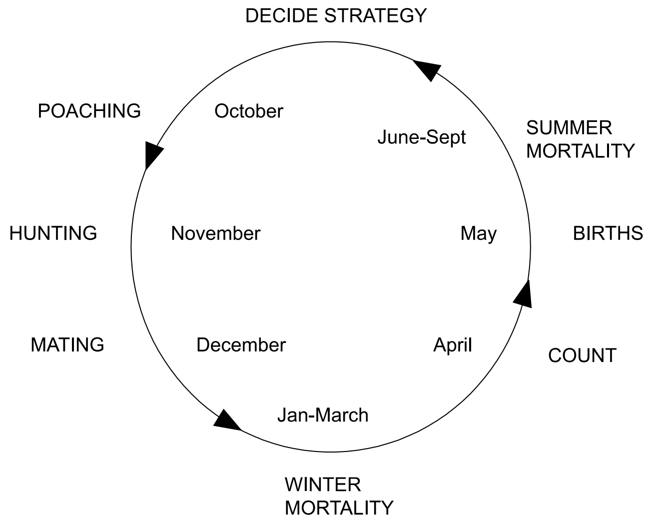


**Fig. 1.** The saiga manager's year. Winter mortality and births are potentially density dependent, the latter being the base case assumption. Mating success is constrained by male numbers; a simple harem mating system is assumed, whereby if there are more than 12 adult females per adult male, the surplus females go unmated (Milner-Gulland, 1997). Poaching is assumed to occur between the year's hunting strategy being decided and the legal harvest actually taking place; this maximizes the impact of poaching on the success of the hunting strategy.

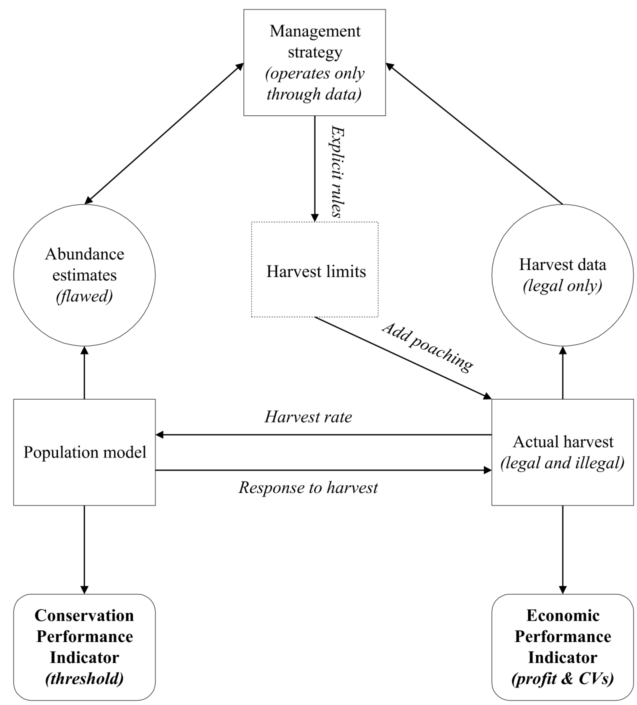


**Fig. 2.** A flow diagram showing the relationship between the population model and the management strategy (based on Cooke, 1995). Each year, the inputs to the management strategy are the legal harvest data and the flawed abundance estimates. The strategy uses these data in a set of explicit rules to produce a number of animals that can be legally harvested. Poaching is added to the harvest limit given by the management strategy to give an actual harvest rate. This harvest rate is fed into the population model, leading to an actual number of animals killed through the population's response to harvest. The population is then censused, giving the next set of input data to the management strategy. Unlike the data available to the management strategy, the performance indicators are true reflections of the state of the system, comprising the revenues produced by the strategy and the true population size each year.

crude optimization procedure ensured that all the strategies continuing to the robustness trials had low enough hunting mortalities to be counted as sustainable, while not constraining strategy performance against other objectives. This avoided rejecting strategies that might be very robust despite giving low revenues in the base case. Two rounds of strategy submission, 'base case' tests and refinement were carried out.

### Robustness trials

The robustness trials (Table 1) were chosen both to reflect the uncertainties that afflict the management of the saiga antelope and to provide a severe test of the strategies. Although ideally a wide range of independently determined trials should be used, because of time constraints we chose a few key trials addressing uncertainties that are known to afflict saiga management. Performance in the robustness trials was assessed against all three management objectives, with the stock conservation objective used as a simple measure of performance rather than a constraint. This allowed consideration of strategies which just failed the stock conservation constraint, but nonetheless were worthy of further investigation. The trials involved every combination of each of the scenarios listed in Table 1. This required a very large number of trials to be run, but was necessary for correct assessment of strategy performance. Sensitivity analyses that simply change one variable at a time are misleading because they cannot pick up interactions between variables (Kremer, 1983; Mangel, 1993). Interactions between variables were particularly important as we were attempting to identify scenarios under which strategies are likely to fail, rather than calculating the elasticity of results to single variables.

## RESULTS

### Strategy development

Table 2 lists the management strategies satisfying the stock conservation constraint in the base case, which proceeded to the robustness trials. Strategies were relatively consistent in their reliance on population size data (Table 3). Some strategies used other data, such as the climate in previous years or the proportion of adult males in the population count, but were rejected. All the strategies reaching the robustness trials used the most recent population size estimate, and many calculated population growth rates as a guide to the hunting mortality rate

**Table 1.** The alternative scenarios to which strategies were subjected in the robustness trials. The base case scenario is given in bold.

| Model component | Scenarios |
|---|---|
| Population model | Base carrying capacity (K) is 1 million, **2 million.** |
| | Linear trend in K to 1.5 or 0.5 of base, or **stays at base.** |
| | Density dependence acts on **neonatal survival** or whole population in winter. |
| Abundance and sex ratio estimates | Abundance estimates are consistent under- or overestimates, or are accurate. Estimate multiplied by 0.5, **1**, 1.5. |
| | Bias in abundance estimates increases or decreases linearly with time. 1 – 0.5 and 1 – 1.5, or **no bias**. |
| | Abundance estimate **every year** or in only 50% of years. |
| | Error in abundance and sex ratio estimates is **CV = 20%**, CV = 40%. |
| Economic variables | Discount rates 0% and **5%.** |
| | Price differential between horns and meat: horns **100×** and 10× more expensive per kilo than meat. |
| Poaching | Poaching at **0%,** 50% and 100% of legal hunting or 2.5%, 5% of actual population size. |
| | Poachers hunt unselectively or the chance of being hunted by a poacher is proportional to the revenues obtainable from the animal. |

that could be applied. Unlike the IWC-SC strategies (IWC-SC, 1993), those developed here were simple models not based on statistical analysis of the data, and relying on short time series of population size data. This allowed us to draw broad generalizations about the performance of different model types, but means that the strategy set is unlikely to contain the optimal strategy.

Many strategies used a threshold population size below which harvesting was prohibited, and some used a cap on harvest rates. Simple harvesting theory suggests that a hunting mortality rate proportional to population size is less destabilizing, and can provide higher sustainable yields, than harvesting the same number of individuals each year, and the results of these trials tend to support this (see Hilborn & Walters, 1992 or Milner-Gulland & Mace, 1998 for expositions; the result was first identified in the 1970s). The decision rules used were relatively simple and transparent, which can be a major advantage in practical application. Strategies 9 and 10 were included specifically to test the performance of the 'rule of ¾' proposed by Roughgarden & Smith (1996). These authors proposed that fish stocks should be allowed to recover to ¾ of their carrying capacity and then be harvested in perpetuity at a constant rate, with the aim of maintaining the population size at this level. This rule was intended to be simple but extremely robust, allowing sustainable harvesting with a sufficiently large margin of error to be precautionary.

## Base case performance

Strategy performance in the base case scenario is shown in Fig. 3 and Table 4. The threshold probabilities are not shown, because all the strategies had passed the stock conservation constraint. A cluster of strategies performed very well, giving high revenues with relatively low within-run variability (strategies 0–3 at 10% hunting mortality, strategies 6, 12, 13; Fig. 3a); two performed badly, giving low revenues and high within-run variability (strategies 5 and 9). Apart from these two strategies, there is no clear overall relationship between revenues, within-run and between-run variability; it is possible to have both high revenues and relatively low variability in revenue, rather than having to trade them off.

However, among the cluster of strategies producing high revenues there is a strong positive relationship between revenue and between-run variability, and an inverse relationship between within-run and between-run variability; within this cluster there is a trade-off between predictability within simulations, revenues, and predictability between simulations. If the population is able to recover from its low level at the beginning of the simulation, owing to favourable values of the stochastic parameters in a given run, it is able to withstand heavy harvesting and produce high revenues. Otherwise, if the early years are poor, the population quickly falls below the threshold under heavy harvesting. Discounting leads to revenues produced early in the simulation having most influence on mean revenues, weighting in favour of early heavy harvesting. Thus a strategy that harvests heavily regardless of population size (e.g. S0b) has both high between-run variability, high mean revenues, and lower within-run variability, while a strategy with a harvest rate that tracks population size (e.g. S13) has higher within-runs variability. This trade-off means it is not possible to pick a clear best strategy in the base case scenario, only to suggest that it is likely to be chosen from within the cluster of high-revenue strategies.

## Overall performance in robustness trials

Figure 4 summarizes the overall performance of the strategies in the robustness trials. There is a weak positive relationship between the probability of the population falling below the threshold size and the revenues obtained from hunting, because high hunting mortalities both give high revenues and cause population decline (Fig. 4a). Strategy 9 (an implementation of the rule of ¾) produces inordinately low revenues given its threshold probability. The best strategies, from Fig. 4a, are those producing high revenues while still fulfilling the

**Table 2a.** Strategies tested in the robustness trials. $E$ = Estimated population size last year. If there was no count last year, $E$ = 0. $T$ = threshold population size. $R$ = Population growth rate; $E_{t-1}/E_{t-2}$. $G$ = Logarithmic growth rate; $\ln(E_{t-1})/\ln(E_{t-2})$. Strategies 4a–c, 5a, 8a, 12a are less successful variants of very similar strategies, and are therefore not discussed further.

| Strategy | Rules |
|---|---|
| S0 | Harvest (a) 4% or (b) 10% of population, 100% males in harvest. If no count, no hunting. |
| S1 | $T$ = 250,000. The harvest must never reduce the estimated population size below $T$. If $E > T$, take either (a) 4% or (b) 10% of $E$-200,000, 100% males. If no count, no hunting. |
| S2 | $T$ = 250,000. If $R > 1$ take (a) 4% or (b) 10% of $E$-200,000, otherwise take 50% of this percentage of $E$-200,000, 100% males. If no count this year, no hunting. If no count last year, use the last available count to calculate $R$. |
| S3 | Starting hunting mortality is (a) 4% or (b) 10%, 100% males. Every 3 years, calculate mean $G$ for the 3 year period. If mean $G \leq 1$ reduce hunting mortality by 50% for the next 3 years. Otherwise keep hunting mortality at the original level. If a year has no count, any $G$ involving that year is zero. |
| S4 | $T$ = 300,000. The harvest must never reduce the estimated population size below $T$. At time $t = 1$, if $R > 1$, take 50,000 animals, otherwise take 30,000 animals. At time $t > 1$, if $R > 1$ increase harvest by 10,000 animals, if $R < 1$ reduce harvest by 10,000 animals. Harvest may not exceed 0.2*($E$-200,000). 100% males. If no count, no hunting. If no count in a previous year, use most recent available count. |
| S4a | $T$ = 300,000. The harvest must never reduce the estimated population size below $T$. At time t = 1, if $R > 1$, take 50,000 animals, otherwise take 30,000 animals. At time $t > 1$, if $R > 1$ increase harvest by 10,000 animals, if $R < 1$ reduce harvest by 10,000 animals. Harvest may not exceed 100,000 animals. 100% males. If no count, no hunting. If no count in a previous year, use most recent available count. |
| S4b | Same as 4, but start at 60% male in the harvest (females and juvenile proportions as in population). At each time-step, if $R > 1$, increase proportion of males by 5%, up to a maximum of 95%. If $R \leq 1$, reduce proportion of males by 5%. |
| S4c | Same as 4a, but start at 60% male in the harvest (females and juvenile proportions as in population). At each time-step, if $R > 1$, increase proportion of males by 5%, up to a maximum of 95%. If $R \leq 1$, reduce proportion of males by 5%. |
| S5 | Start with 6% hunting mortality. Calculate mean $G$ as a 3 year running mean. If mean $G > 1.02$, increase hunting mortality by 1%, if mean $G < 1.01$, decrease hunting mortality by 1%, otherwise leave it the same. 100% males. If a year has no count, any mean $G$ involving that year is zero. |
| S5a | Same as above but calculate mean $G$ every 3 years rather than as a running mean. |
| S6 | Calculate number of juveniles and adult females ($N_{j+f}$) = total count ($N$) – adult males ($N_m$). Calculate the number of adult females in the population ($N_f$): Following a poor winter $N_f = 0.4*N_{j+f}$. Following a good winter $N_f = 0.3*N_{j+f}$. Calculate the total number of adults in the population $N_a = N_f + N_m$. Do not cull below $T$ ($N_a$ = 375,000). Above $T$, $p = 0.0006(N_a/1000) + 0.02$. Calculate $t = p*N$ to estimate how many to kill. Calculate from the spring count $y = (N_f / N_m) * 0.2$. Harvest $yt / (1+y)$ females and $t/(1+y)$ males. If there are no count data in the spring prior to the cull remove 20,000 females and 20,000 males. |
| S7 | If $E > 300{,}000$ then cull 50,000 individuals. 90% males in cull. Proportion of females and juveniles as in the population. If no count, no hunting. |
| S8 | $T$ = 300,000. If $E > T$, kill 20,000 adult males. If no count, no hunting. |
| S8a | $T$ = 220,000. If $E > T$, kill 10,000 adult males. If no count, no hunting. |
| S9 | $T = 0.75K$. If $E > T$ then kill $E$–$T$ animals, only adults. Males in the sex ratio found in the population, females the rest. If no count, no hunting. |
| S10 | Do not hunt for 5 years. After 5 years, or after 5 counts are available (whichever is the longer), calculate the mean $R$. Find $r = \ln(\text{mean } R)$. Harvest in perpetuity at a rate of $0.25r$, unselectively. |
| S11 | Harvest in year 1 ($H_1$) is 18,000. In subsequent years, $H_{t+1} = H_t \times R$. Harvest only adults, 70% male, 30% female. If no count in either the current or previous year, no hunting. |
| S12 | Harvest is 90% males, harvest females and juveniles unselectively. Initial harvest mortality is 5%. Calculate the fraction harvested ($H_t$) in subsequent years as: $H_t = H_{t-1} * (E_t + 0.7E_{t-1} + 0.5E_{t-2})/(E_{t-1} + 0.7E_{t-2} + 0.5E_{t-3})$. For $t < 3$, use the historical counts. If there are no counts in certain years, use the most recent available counts. Bound $H_t$ between 2% and 10%, and bound the change in hunting mortality ($H_t/H_{t-1}$) between 0.6 and 1.25. |
| S12a | Same as 12 but bound the change in hunting mortality ($H_t/H_{t-1}$) between 0.8 and 1.1. |
| S13 | Do not harvest until you have the first three population estimates. Then for each year with a new population estimate select this count and the two previous counts. Scale the earliest of the three estimates to year zero and scale the other years accordingly. Divide the total number of individuals estimated to be in the population by 1000. Fit a regression line through these three points. Harvest rates are determined by residual pattern, slope and intercept of the regression line (see Table 2b). If there is no population estimate: If you harvested in the year when the population was last estimated remove 4% of animals, 100% males. If you did not harvest in the year when the population was last estimated remove 1.5% of animals, 100% males. |
| S14 | Start harvesting at 8%, with 90% males, 10% females. Harvest no juveniles. $T$ = 300,000. If $E \leq T$, reduce hunting mortality by 50% for 1 year. Otherwise, calculate a 3 year running mean growth rate. If counts are not available in a particular year, ignore that year. If mean $G > 1.01$, increase hm by 1%, if mean $G < 1$ decrease hm by 1.5%. If the estimated proportion of males in the population is < 1/12, reduce male proportion in harvest by 10%. If it is > 0.5, increase male proportion by 10%. |

stock conservation constraint; these are the cluster of strategies 0–3 at 4% hunting mortality. The within-run and between-run variabilities are plotted for the best-performing strategies in Fig. 4b. Again, there is an inverse relationship between the two measures of revenue stability.

The difference between the outcomes of the base case and robustness trials varies from strategy to strategy, and between performance indicators (Table 4). Some strategies performed noticeably better in the ranking of threshold probabilities in the robustness trials than in the base case (strategy 1 at 4%, strategy 5), others were much worse (strategies 6, 9). These changes in performance indicate how robust the strategies are to external factors. The cluster of strategies 0–3 performs well in the base case at high hunting mortalities and indifferently at low hunting mortalities (Fig. 3). By contrast, in the robustness trials the high hunting mortalities perform very

**Table 2b.** The decision rules for strategy 13. In each cell, the first figure is the proportional hunting mortality, the second is the proportion of males among the harvested individuals.
(i) Residual pattern + – +

| Slope | <–35 | –35 ≤ *x* ≤ 35 | >35 |
|---|---|---|---|
| INTERCEPT | | | |
| <400 | 0 | 0 | 0.03,1 |
| 400 ≤ *x* ≤ 1000 | 0 | 0.05,1 | 0.09,0.9 |
| >1000 | 0.06,1 | 0.12,0.9 | 0.15,0.9 |

(ii) Residual pattern – + –

| Slope | <–35 | –35 ≤ *x* ≤ 35 | >35 |
|---|---|---|---|
| INTERCEPT | | | |
| <400 | 0 | 0 | 0 |
| 400 ≤ *x* ≤ 1000 | 0 | 0.04,1 | 0.06,0.9 |
| >1000 | 0.06,1 | 0.1,0.75 | 0.15,0.75 |

poorly, the low hunting mortalities very well (Fig. 4). Strategies 12 and 13 do not fulfil the stock conservation constraint under the robustness trials but none the less perform relatively well.

A key predictor of a strategy's overall performance is the proportion of males in the harvest. Generally strategies perform well in terms of both the revenues produced and the threshold criterion if they harvest mostly males. This is because saiga males are particularly valuable for their horns, as well as providing more meat than females. They also do not contribute to the population growth rate in the model until the ratio of adult males to adult females is ≤ 1/12, because saigas are harem breeders. There are no other simple indicators of strategy performance, so in order to elucidate the factors affecting performance, we now examine the individual robustness trials.

## Factors affecting strategy performance

The robustness trials assess strategy performance under a severe but realistic range of challenges (Table 1). We examine the results only in terms of the effect on threshold probability (the probability of falling below the threshold population size of 200,000), rather than the other performance indicators. This is because the threshold probability is the indicator most closely related to strategy sustainability. The factors that most affect the strategies' threshold probabilities are poaching and biased abundance estimates.

Two kinds of poaching were tested; poaching independent of the strategy's harvesting rate and poaching linked to the strategy's harvesting rate. The former tends to have a more severe effect on threshold probability than the latter, because when strategies compensate for reductions in population size, the linked poaching does so too. However, if strategies do not compensate for reduced population size they are more strongly affected by linked poaching; for example strategies 7 and 9, which harvest a number of individuals, rather than a proportion of the population. Table 5 shows how poaching of each kind affects the threshold probabilities of each strategy; strategy 13 is the most robust to poaching. Some strategies appear to perform well because their legal hunting mortality is so high that poaching is a comparatively minor source of mortality (S0–S3 at 10%), while the converse is true for S1 and S2 at 4%.

Consistent overestimation of population size is a major problem for many strategies; this was also the case in the IWC-SC trials (Cooke, 1995). Strategies that harvest a relatively large proportion of the population are sensitive to this (S1 and S2 at 10%, Table 5). Strategies that rely on threshold populations above which harvests are allowed are also more susceptible to bias (S9). The strategies that are least susceptible to bias are those

**Table 3.** Methods employed and information used by the strategies to control harvest rates. The methods are: a threshold below which the population may not fall (Threshold), a cap on the total number of individuals that can be harvested in a year (Cap), a hunting mortality rate proportional to the population size (Propnl hm), harvesting a given number of individuals (Number). All strategies used the latest population size estimate. The other types of information used are: the growth rate of the population (Growth rate), the number of years of population size estimates used (No. years), and the sex ratio of the population (Sex ratio). Some strategies had harvest rates that changed as the strategy learnt more about the system (Learning); the others had their harvest rates for each state of the system fixed from the start. Performance is shown as the mean probability of the strategy causing the population to fall below 200,000 at any point in the 50 year simulation, averaged over all the robustness trials (Threshold prob), and the mean discounted revenues over the 50 year period, averaged over all the robustness trials (Revenue, shown in million roubles). The results for strategies 0–4 are shown for a 4% hunting mortality.

| Strategy | Threshold | Cap | Propnl hm | Number | Growth rate | No. years | Sex ratio | Learning | Threshold prob | Revenue |
|---|---|---|---|---|---|---|---|---|---|---|
| 0 | | | X | | | 1 | | | 0.07 | 1.17 |
| 1 | X | | X | | | 1 | | | 0.04 | 0.97 |
| 2 | X | | X | | X | 2 | | | 0.05 | 1.06 |
| 3 | | | X | | X | 3 | | | 0.06 | 0.92 |
| 4 | X | X | | X | X | 2 | | X | 0.08 | 0.57 |
| 5 | | | X | | X | 3 | | X | 0.07 | 1.90 |
| 6 | X | | X | X | | 1 | X | | 0.38 | 1.12 |
| 7 | X | | | X | | 1 | | | 0.27 | 1.00 |
| 8 | X | | | X | | 1 | | | 0.05 | 0.57 |
| 9 | X | | | | | 1 | X | | 0.23 | 0.47 |
| 10 | | | X | | X | 5 | | X | 0.07 | 0.24 |
| 11 | | | | X | X | 2 | | | 0.32 | 1.02 |
| 12 | X | X | X | | X | 3 | | X | 0.10 | 1.53 |
| 13 | | | X | | X | 3 | | | 0.11 | 1.49 |
| 14 | X | | X | | X | 3 | X | X | 0.09 | 0.37 |

**Table 4.** Ranking of the performance of each strategy in the base case and of overall performance in the robustness trials (the mean of the performances in each trial); in each case, 1 is the best performance, 19 is the worst performance. Strategies that perform well have low probabilities of falling below the threshold population size, low within-run and between-run variabilities, but high revenues. The strategies whose overall performance in the robustness trials fulfils the stock conservation constraint (a probability of ≤ 0.07 of the population going below 200,000 individuals) are shown in bold.

| | Base case | | | | Overall | | | |
|---|---|---|---|---|---|---|---|---|
| Strategy | Threshold | Revenue | Within-run var | Between-run var | Threshold | Revenue | Within-run var | Between-run var |
| **S0 (4%)** | **11** | **8** | **1** | **14** | **6** | **7** | **3** | **14** |
| **S1 (4%)** | **18** | **12** | **5** | **8** | **1** | **12** | **7** | **5** |
| **S2 (4%)** | **4** | **14** | **11** | **5** | **2** | **9** | **2** | **4** |
| **S3 (4%)** | **1** | **11** | **6** | **6** | **4** | **13** | **4** | **11** |
| S0 (10%) | 13 | 1 | 4 | 19 | 19 | 3 | 14 | 12 |
| S1 (10%) | 10 | 3 | 6 | 15 | 12 | 2 | 10 | 9 |
| S2 (10%) | 4 | 7 | 12 | 7 | 13 | 1 | 5 | 8 |
| S3 (10%) | 16 | 2 | 8 | 17 | 16 | 6 | 11 | 13 |
| S4 | 7 | 13 | 10 | 13 | 8 | 15 | 12 | 7 |
| **S5** | **14** | **18** | **18** | **1** | **7** | **19** | **18** | **1** |
| S6 | 7 | 6 | 16 | 2 | 18 | 8 | 17 | 6 |
| S7 | 16 | 10 | 14 | 10 | 15 | 11 | 15 | 15 |
| **S8** | **1** | **16** | **13** | **11** | **3** | **14** | **6** | **16** |
| S9 | 1 | 17 | 19 | 3 | 14 | 16 | 19 | 18 |
| **S10** | **4** | **19** | **2** | **16** | **5** | **18** | **1** | **17** |
| S11 | 19 | 9 | 3 | 18 | 17 | 10 | 8 | 19 |
| S12 | 15 | 5 | 9 | 12 | 10 | 4 | 9 | 10 |
| S13 | 11 | 4 | 15 | 9 | 11 | 5 | 13 | 3 |
| S14 | 7 | 15 | 17 | 4 | 9 | 17 | 16 | 2 |

which rely on population growth rates rather than actual population size estimates to calculate their hunting mortalities (S3 at 4%, S5).

The strategies are generally not sensitive to a doubling of the CV of abundance and sex ratio estimates. Strategy 9 is most sensitive because it has a threshold above which all individuals are harvested; if by chance abundance estimates are seriously inflated one year, massive over-harvesting can take place. Several strategies of this type were eliminated early on; strategy 9 was the only one to proceed to the robustness trials, because the threshold is so high. The major effect of changes in discount rate is on revenues rather than threshold probabilities; strategies that obtain a comparatively large proportion of their revenues early in the simulation are less affected by a reduction in discount rate. The results are generally not sensitive to changes in carrying capacity because the population size at the start of the simulation is well below both the Ks tested. The effect of not counting the population in 50% of years depends on how the strategies deal with missing abundance estimates. In most cases, they are very precautionary, either not hunting or hunting at a much lower rate in these years, thus the probability of failing the stock conservation criterion tends to reduce slightly when counts are missing. The age group at which density dependence acts has little effect on the result, nor does a change in the relative prices of meat and horns.

## DISCUSSION

Although the strategies tested here are all relatively simple, their responses to bias, high levels of uncertainty, trending variables and poaching vary greatly. We have shown that the performance of a management strategy under a 'best guess' scenario is not an adequate guide to its performance under more realistic conditions of

**Table 5.** A ranking of the sensitivity of the strategies to poaching and bias in abundance estimates. For each scenario, the deviation of the threshold probability with poaching from the threshold probability without poaching was calculated ((probability with poaching – probability without poaching)/probability without poaching), and similarly for bias. The deviations were then ranked from the smallest magnitude deviation at rank 1 to the largest at rank 19. The rank shown here is the strategy's overall average rank for each group of scenarios; poaching independent of the strategy (at a rate of 0.025 and 0.05, selective and unselective) and linked to the strategy (at a rate of 50% and 100% of the strategy's hunting mortality, selective and unselective), and a constant level of bias (at 1.5 and 0.5) and trended bias (to 1.5 and 0.5). This ranking gives an indication of the relative robustness of the strategies; 1 is the best performer, 19 the worst.

| | Poaching | | Bias | |
|---|---|---|---|---|
| Strategy | Independent | Linked | Constant | Trended |
| S0 (4%) | 14 | 14 | 3 | 6 |
| S1 (4%) | 19 | 1 | 3 | 5 |
| S2 (4%) | 18 | 3 | 6 | 4 |
| S3 (4%) | 17 | 10 | 2 | 3 |
| S0 (10%) | 2 | 9 | 13 | 15 |
| S1 (10%) | 5 | 4 | 18 | 18 |
| S2 (10%) | 4 | 6 | 17 | 16 |
| S3 (10%) | 7 | 12 | 14 | 13 |
| S4 | 10 | 15 | 15 | 10 |
| S5 | 13 | 18 | 5 | 1 |
| S6 | 5 | 13 | 8 | 14 |
| S7 | 9 | 19 | 15 | 10 |
| S8 | 15 | 5 | 8 | 7 |
| S9 | 1 | 8 | 19 | 18 |
| S10 | 10 | 6 | 7 | 12 |
| S11 | 8 | 11 | 1 | 8 |
| S12 | 12 | 16 | 11 | 9 |
| S13 | 3 | 1 | 12 | 16 |
| S14 | 15 | 16 | 10 | 1 |

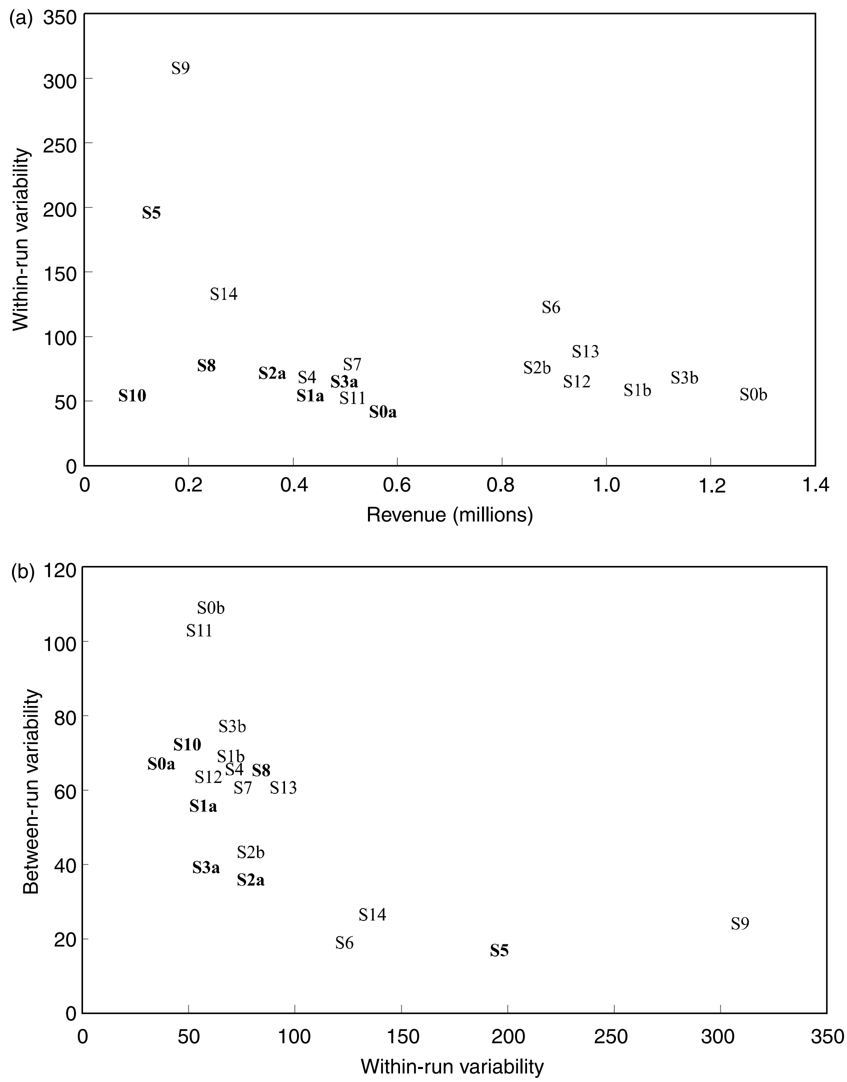


**Fig. 3.** The performance indicators for the strategies under the base case scenario (Table 1). The strategies are numbered as in Table 2, with strategies 0–3a involving a 4% hunting mortality, and strategies 0–3b involving a 10% hunting mortality. The strategies that pass the stock conservation criterion (those with an overall mean probability of ≤ 0.07 of going below the threshold population size at any point during the 50 year period) are shown in bold. (a) The mean discounted 50 year revenue against the within-run variability of the strategies. (b) The between-run variability against the within-run variability of the strategies. Within-run variability is measured as the mean CV of the revenues; between-run variability is measured as the CV of the CVs of the revenues.

uncertainty, and that the strategies perform differently depending on the criteria by which they are assessed. Testing strategies over a wide range of plausible scenarios reveals that those which at first sight appear to be ideal may in fact perform badly (e.g. S0b). Despite this, it is rare for modellers to test their strategies under a broad range of robustness trials, rather than with single-parameter sensitivity analyses, and even rarer for people to compare the performances of several different strategies.

We use two indicators of variability in revenues: variability between and within runs. These indicators have very different policy implications; the former measures the predictability of the results between different realisations, the latter the variability of revenues over time. We show that the two indicators are generally inversely related to one another, but that performance measured on one indicator is a poor predictor of performance on the other (Table 4). Both indicators are important for assessing strategy performance.

Our study is purposefully subjective, with individual ‘managers’ competing in a game to harvest a simulated population under uncertainty. This approach was used to maximise the diversity of strategies produced. We use only one population model and one set of management objectives. Therefore our specific conclusions relate only to this case study. Furthermore, ours is a broad exploratory analysis not designed to make concrete recommendations for the management of a particular resource. Before making such recommendations, eco-

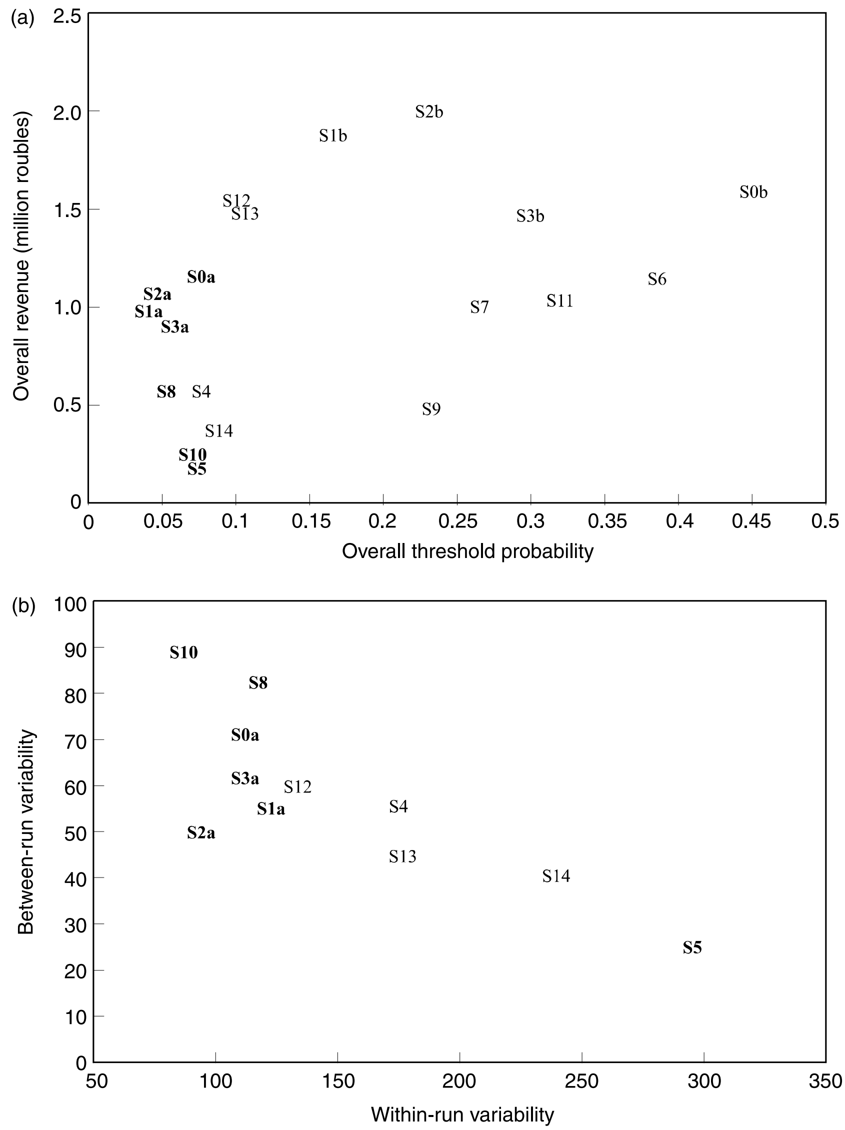


**Fig. 4.** The performance indicators for the strategies under the robustness trials. The strategies are numbered as in Table 2, with strategies 0–3a involving a 4% hunting mortality, and strategies 0–3b involving a 10% hunting mortality. The strategies that pass the stock conservation criterion (those with an overall mean probability of $\leq 0.07$ of going below the threshold population size at any point during the 50 year period) are shown in bold. (a) The overall mean probability of falling below the threshold population size plotted against the overall mean revenue. (b) The within-run variability against the between-run variability, plotted for the best-performing strategies only (those with a probability of falling below the threshold of $< 0.15$). Within-run variability is measured as the mean CV of the revenues; between-run variability is measured as the CV of the CVs of the revenues.

nomic and social issues (such as the costs of implementation and enforcement, strategy acceptability and practicability) would have to be fully investigated, along with a more systematic analysis of management options.

The performance criteria against which management strategies are assessed, and the importance that managers attach to particular objectives, depend on the social goals of policy makers. Thus any overall ranking of strategies depends on the particular situation; both on the factors affecting the population (such as poaching or biased abundance estimates), and on the manager's aims. However, once managers have decided on their objectives, the best strategy can be chosen using subjective weighting of the performance indicators or tools such as multi-criteria analysis. A very simple example of such a procedure is shown in Table 6.

Although some of our findings are specific to the saiga antelope, for example the importance of harvesting a relatively high proportion of males, many of the issues we highlight are much more general. In particular, we carried out extensive testing of the 'rule of ¾', which was proposed by Roughgarden & Smith (1996) as a robust and precautionary approach to fisheries management in

**Table 6.** A simple assessment of overall strategy performance on each of the four performance indicators, with an overall ranking assuming that each indicator has equal weight for the manager's decision-making. Three stars is the best performance, down to a zero for the worst performance.

| Strategy | Threshold | Revenue | Within run | Between run | Overall |
|---|---|---|---|---|---|
| S0 (4%) | * * * | * * | * * | * | * * |
| S1 (4%) | * * * | * | * * | * * | * * |
| S2 (4%) | * * * | * * | * * * | * * * | * * * |
| S3 (4%) | * * * | * | * * | * | * * |
| S0 (10%) | 0 | * * * | * | * | * |
| S1 (10%) | * | * * * | * * | * * | * * |
| S2 (10%) | * | * * * | * * | * * | * * |
| S3 (10%) | 0 | * * | * | * | * |
| S4 | * * | * | * | * * | * (*) |
| S5 | * * | 0 | 0 | * * * | * |
| S6 | 0 | * * | 0 | * * | * |
| S7 | 0 | * | 0 | * | (*) |
| S8 | * * * | * | * * | 0 | * (*) |
| S9 | * | 0 | 0 | 0 | 0 |
| S10 | * * * | 0 | * * * | 0 | * (*) |
| S11 | 0 | * * | * * | 0 | * |
| S12 | * * | * * * | * * | * * | * * |
| S13 | * * | * * | * | * * * | * * |
| S14 | * * | 0 | 0 | * * * | * |

the face of uncertainty. We included two realizations of the strategy; one (S9) had access to the exact value of the carrying capacity of the population at the beginning of the simulation, the other (S10) declared a 5 year moratorium and estimated the number of individuals to be harvested from the population growth rate during that time. Strategy 8 is also similar in spirit to the suggestions of Roughgarden & Smith (1996), harvesting a constant small number of individuals whenever the population exceeds a threshold. The performance of strategies that harvest a small number of individuals each year (S8, S10) is excellent on the stock conservation criterion, but very poor in terms of the revenues obtained and variability between runs. These conservative strategies have the advantage of simplicity and robustness in implementation and could be useful if revenues were not a prime concern of managers. However, the revenues produced are much lower than those of some of the other strategies, including some which performed very well on the robustness trials.

Strategy 9, which involves harvesting all individuals above a threshold of ¾K, also appears to be a conservative strategy. However, it both provides low revenues and performs very badly on the stock conservation criterion. One problem is that there is no reassessment once the harvest rate has been fixed, which is problematical under conditions where K or the biases in population estimates are trending. Another problem is that setting a zero quota below ¾K and harvesting all individuals above this level leads to a serious risk of over-harvest under uncertainty. Lande, Engen & Saether (1995) found from theoretical models that harvesting all individuals above a threshold and none below is the optimal strategy for maximizing yields from fluctuating populations. Our results contradict these findings, suggesting that the reason for Lande *et al.*'s (1995) result is that they assume that the population size is known. Further work by Engen, Lande & Saether (1997) showed that when population estimates are uncertain, harvesting a proportion of the difference between a threshold population size and the estimated population size is a better option. This coincides with our findings: a proportional threshold strategy (S1) performed well, but simple threshold strategies performed very badly. This suggests that strategies involving harvesting all individuals above a threshold are of very limited use in the management of real populations.

Strategies that used population growth rates were more resistant to bias than those using population estimates as a basis for calculating harvest rates. Those using proportional hunting mortalities were good robust performers, particularly if they reduced hunting mortality for a time if the population growth rate became negative (S2, S3). The simplest strategy of all (harvest a set proportion of the population each year regardless of population size) is perhaps the best performer at low hunting mortalities, but the worst at high hunting mortalities. Generally, we found that strategies that did well never harvested heavily, even when the population was (apparently) very large; the IWC-SC also found this (Cooke, 1995).

The relative success of simple strategies brings into question the value of complex strategies, which may be more susceptible to error and bias. Simple strategies are often more robust to uncertainty than strategies based on models whose assumptions are likely to be broken, even when these models are empirical in origin. Ludwig & Walters (1985) found that a simple model was at least as good as a more complex one at estimating optimal fishing effort, even though the data had been generated by the more complex model in the first place. However, simple strategies do have the disadvantage that they do not allow managers to learn about the system.

In this study, we evaluated the performance of a range of management strategies in a simulated population under realistic levels of uncertainty. We used a decision analysis framework for the study, a key component of which is the initial formulation of clear objectives against which strategy performance can be assessed. Our major finding is that the best performing strategies are very simple, involving harvesting a small proportion of the population each year. Previous theoretical results, suggesting that the best approach to harvesting populations under uncertainty is to harvest all individuals above a threshold, do not stand up under more realistic conditions. We show that the performance of a strategy under the best estimate of parameter values is not an adequate representation of its performance under a feasible range of parameter values. We suggest that performance should be evaluated in terms of the variability of revenues between simulation runs as well as within runs, because strategies perform differently under these two measures and they have different policy implications.

Although most of these results have been found individually in previous work, they are not all as widely appreciated as they should be. Our results contradict the recommendations of other high-profile studies, many of which are derived from rather general models with no particular species or problem in mind. Our work has shown that these recommendations may not be at all precautionary under realistic uncertainty. This exploratory study suggests that the simulation model approach is a valuable tool for the exploration of harvesting strategies under uncertainty. It is a flexible and powerful method that could have wide applicability for the management of populations under uncertainty.

## Acknowledgements

This work was conducted as part of the ‘Managing Variability’ Working Group supported by the National Center for Ecological Analysis and Synthesis, a Center funded by NSF (Grant #DEB-94-21535), the University of California at Santa Barbara, and the State of California. We are very grateful to the NCEAS staff for their help and hospitality. We thank Geoff Kirkwood, Marc Mangel, Mick McCarthy, Joan Roughgarden and our anonymous reviewers for their useful insights and suggestions. The PHLEM group of the University of Adelaide, especially Drew Tyre, provided useful comments on an earlier version of this paper.

## REFERENCES

Allison, G. W., Lubchenco, J. & Carr, M. H. (1998). Marine reserves are necessary but not sufficient for marine conservation. *Ecol. Applic.* **8**: S79–S92.

Bekenov, A. B., Grachev, Iu. A. & Milner-Gulland, E. J. (1998). The ecology and management of the saiga antelope in Kazakhstan. *Mamm. Rev.* **28**: 1–52.

Cooke, J. G. (1995). The International Whaling Commission’s Revised Management Procedure as an example of a new approach to fishery management. In *Whales, seals, fish and man*. Blix, A. S., Walloe, L. & Ulltang, O. (Eds). London: Elsevier Science.

Engen, S., Lande, R. & Saether, B.-E. (1997). Harvesting strategies for fluctuating populations based on uncertain population estimates. *J. Theoretical Biol.* **186**: 201–212.

Hilborn, R. & Walters, C. J. (1992). *Quantitative fisheries stock assessment: choice, dynamics and uncertainty*. New York: Chapman and Hall.

International Whaling Commission Scientific Committee (1993). Report of the Scientific Committee. *Reports of the International Whaling Commission* **43**: 244a.

International Whaling Commission Scientific Committee (1994). Report of the Scientific Committee. Reports of the *International Whaling Commission* **44**: 147–148.

Kirkwood, G. P. (1997). The Revised Management Procedure of the International Whaling Commission. In *Global trends: fishery management*. Pikitch, E. K., Huppert, D. D. & Sissenwine, M. P. (Eds). Bethesda, Maryland, MD: American Fisheries Society Symposium 20.

Kirkwood, G. P. & Smith, A. D. M. (1996). Assessing the precautionary nature of fishery management strategies. *Precautionary approach to fisheries Part 2: Scientific papers*. FAO Fisheries Technical Paper 350/2. Rome: FAO.

Kremer, J. N. (1983). Ecological implications of parameter uncertainty in stochastic simulation. *Ecol. Mod*. **18**: 187–207.

Lande, R., Engen, S. & Saether, B.-E. (1995). Optimal harvesting of fluctuating populations with a risk of extinction. *Am. Nat.* **145**: 728–745.

Ludwig, D. & Walters, C. J. (1985). Are age-structured models appropriate for catch-effort data? *Can. J. Fish. Aq. Sci.* **42**: 1066–1072.

McAllister, M. K., Starr, P. J., Restrepo, V. R. & Kirkwood, G. P. (1999). Formulating quantitative methods to evaluate fishery management systems: what fishery processes should we model and what trade-offs do we make? *ICES J. Marine Sci.* **56**: 900–916.

MacNab, J. (1983). Wildlife management as scientific experimentation. *Wildl. Soc. Bull.* **11**: 397–401

Mangel, M. (1993). Effects of high-seas driftnet fisheries on the Northern Right Whale Dolphin *Lissodelphis borealis. Ecol. Applic.* **3**: 221–229.

Mangel, M. (1998). No-take areas for sustainability of harvested species and a conservation invariant for marine reserves. *Ecol. Letters* **1**: 87–90.

Milner-Gulland, E. J. (1994). A population model for the management of the saiga antelope. *J. Appl. Ecol.* **31**: 25–39.

Milner-Gulland, E. J. (1997). A stochastic dynamic programming model for the management of the saiga antelope. *Ecol. Applic.* **7**: 130–142.

Milner-Gulland, E. J. & Mace, R. (1998). *Conservation of biological resources*. Oxford: Blackwell Science.

Parma, A., Amarasekare, P., Mangel, M., Moore, J., Murdoch, W. W., Noonburg, E., Pascual, M. A., Possingham, H. P., Shea, K., Wilcox, C. W. & Yu, D. (1998). What can adaptive management do for our fish, food, forests and biodiversity? *Integr. Biol.* **1**: 16–26.

Roberts, C. M. (1997). Ecological advice for the global fisheries crisis. *Trends Ecol. Evol.* **12**: 35–38.

Roughgarden, J. & Smith, F. (1996). Why fisheries collapse and what to do about it. *Proc. Nat. Acad. Sci.* **93**: 5078–5083.

Tuck, G. N. & Possingham, H. P. (2000). Marine protected areas for spatially structured stock**.** *Marine Ecol. Progress Series* **192**: 89–101.

Walters, C. J. (1986). *Adaptive management of renewable resources*. New York: Macmillan.