Evaluation of different harvest strategies for a vendace population with highly variable recruitment: a simulation approach

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In the auto-regulative commercial vendace fishery, the fishing effort is increased if stock decreases in order to reduce interannual variation in supply and revenue. When the revenue per unit effort reaches a profitability threshold, fishing ceases. The performance of this strategy was compared with constant effort and constant revenue strategies combined with different threshold levels of fishing shut-down. A simulation model of an age-structured vendace population was applied. Qualitatively the results were very similar for the Ricker and Cushing stock-recruitment curves with or without negative dependence between consecutive recruitments. The interannual variability of revenue increased with an increase in mean revenue when approaching maximum mean annual revenue. Given a low threshold, the constant effort strategy performed best and constant yield worst with respect to the objectives of maximum mean revenue, low mean effort, and low risk for spawning biomass. For the constant effort strategy, the revenue variation was already high at low revenue levels. For the strategy aiming at constant revenue, the variation was low at a low revenue level but increased rapidly with increasing revenue. At a moderate revenue level, the intermediate strategy produced good trade-offs of rather high mean revenue with reasonable variation and risk to reproduction. A tendency for two-year-cyclicity appeared at a low mean spawning stock level. When the threshold of fishery shut-down was increased, the variability in revenue increased for every strategy and differences in their performance decreased. Simultaneously, the risk of low spawning stock decreased. The threshold regulation increased the instability of stock in cases of high fishing effort. Means for regulating the access to fishing should be established in order to ensure the possibility of flexibility of fishing effort and tolerable revenue variation. Some threshold regulation to protect the spawning stock is also necessary.

Introduction

Considerable interannual variation in recruitment is typical of vendace (*Coregonus albula* (L.)). The variation is largely stochastic, caused by unpredictable mortality in prerecruitment stages (Viljanen 1988, Karjalainen *et al.* 2000) due to several external factors (e.g. Auvinen 1988, Marjomäki 2004). Recruitment is also regulated by a compensatory relationship between spawning

stock and recruitment (Valtonen and Marjomäki 1988, Viljanen 1988, Salojärvi 1991, Salmi and Huusko 1995, Marjomäki 2004). Recruitment success has also been shown to be negatively associated with previous-year recruitment, which implies delayed density-dependence due to intra-specific competition (Hamrin and Persson 1986, Helminen and Sarvala 1994, Auvinen *et al.* 2000, Marjomäki 2004) Vendace is a short-lived fish and therefore its recruitment variability is reflected strongly in variation of the harvestable biomass. On the other hand, this variation is damped by strong density-dependence in growth (e.g. Viljanen 1986, Marjomäki and Kirjasniemi 1995).

Most of the commercial fisheries in Finnish inland waters are targeted on vendace and the stock fluctuations make their maintenance and development difficult (Salmi 1998). Stock assessment and fisheries management are not common because the fishing is spatially diffuse across many lakes and basins with separate populations. Rather, the fisheries can be considered auto-regulative, as the fishermen respond adaptively to changes in stock by flexibly adjusting their effort according to catch success (Jurvelius *et al.* 1992, Marjomäki *et al.* 1995, Sipponen *et al.* 1999, Sipponen and Valkeajärvi 2002). From the point of view of individual fisherman, it is rational to try to keep the yield and revenue constant, or at least decrease its fluctuation by regulating fishing effort. The benefits of constant supply are that the established marketing contacts remain and the consequences of over-supply, such as decrease in price and extra marketing costs, can be avoided. To achieve constancy of supply and revenue, the effort must be increased with decrease in yield per unit effort (YPUE) and stock (assuming constant catchability) which induces depensatory fishing mortality and instability (Marjomäki *et al.* 1995). When the revenue per unit effort reaches a certain lower threshold, fishing must eventually cease. This threshold is a function of the unit price of fish and the costs of fishing.

There are three simple harvest strategies that are dependent on stock size (e.g. Hilborn and Walters 1992): constant stock size (or escapement), constant exploitation rate (or effort if assuming constant catchability) and constant yield (or revenue). The auto-regulative strategy of commercial vendace fisheries can be considered as their fusion. It is an intermediate between the constant yield and constant effort strategies in its tendency to decrease yield and revenue variation by some adjustment of effort and it resembles the constant-stock strategy in that there is a minimum threshold stock below which fishing ceases. The higher this threshold, the smaller is the difference in constant effort and constant yield strategies in terms of fishing effort.

Several performance criteria have been used for evaluation of the different strategies and sets of parameters within a certain strategy, such as the total or average yield or economic return over a period, their interannual stability or variance, the preservation or risk of collapse of the stock or fisheries and the sensitivity of the strategy to parameter and model uncertainty and its ability to decrease these (e.g. Allen 1973, Walters 1975, Walters and Hilborn 1976).

In general, for any given level of environmental stochasticity, population numbers and yield exhibit greater year-to-year variation as fishing effort increases (e.g. Ricker 1958, Walters 1975, Doubleday 1976, Beddington and May 1977, May *et al.* 1978). These effects become increasingly severe if effort inadvertently exceeds the maximum sustainable yield (MSY) level. The probability of stock collapse or economic extinction increases with variation and the policy is therefore often a matter of choosing how much average yield to give up in order to obtain less variability and risk over time (e.g. Walters 1975, Doubleday 1976).

Previous applications of alternative harvest strategies to stochastic population models have shown that in the presence of fluctuations in production the optimal harvest strategy is usually the constant stock size strategy in that it maximises the average yield (Ricker 1958, Larkin and Ricker 1964, Gatto and Rinaldi 1976) or expected revenue under certain cost assumptions (Reed 1974). However, one problem is that it also maximises the variance of yield which could cause economic chaos (Ricker 1958, Allen 1973, Gatto and Rinaldi 1976). It is, therefore, considered unsuitable for vendace fisheries management. It is also difficult to implement because it requires up-to-date knowledge of the stock size (Evans 1981) but is itself particularly uninformative (Hilborn and Walters 1992).

The constant yield strategy outperforms the others in reducing the variability in annual yield. Many of the moderately-sized yields produced under constant-yield management have significantly lower associated coefficients of variation than do similar yields produced under constant effort or stock-size management strategies. However, this advantage diminishes rapidly when the stock is overexploited and the strategy invariably results in lower average yield with high variation and risks of stock collapse (Walters 1975, Doubleday 1976, Goh 1976, Beddington and May 1977, May *et al.* 1978, Reed 1978, Evans 1981, Swartzman *et al.* 1983, Ruppert *et al.* 1985, Sissenwine *et al.* 1988).

The performance of the constant effort strategy lies between those of constant stock and constant yield (Doubleday 1976) combining lower risk for collapse than the constant yield strategy (Doubleday 1976, Reed 1978, Swartzman *et al.* 1983, Sissenwine *et al.* 1988) with lower variation in yield than the constant stock strategy (Evans 1981, Getz *et al.* 1987). One problem with the constant effort strategy is that it maximises the time-series bias in the analysis of stock-recruitment data and minimises informative contrast in fishing mortality rate (Hilborn and Walters 1992).

Several fusions and modifications of the basic strategies have also been analysed. (e.g. Walters 1975, Aron 1979, Ludwig 1980, Swartzman *et al.* 1983, Ruppert *et al.* 1985, Getz *et al.* 1987, Hall *et al.* 1988, Quinn *et al.* 1990, Hjerne and Hansson 2001). In many cases a certain minimum threshold stock level under which the fishing is decreased or stopped to reduce the risk of collapse is merged with effort or yield regulation above it in order to utilise the advantages of basic strategies. Some fusions have given promising results in combining almost optimal mean yields with tolerable variation and risk of collapse.

An interesting question is also what kind of effects different strategies have on population dynamics. Theoretically, strategies aiming at constant yield induce depensatory (boosting the stock change) mortality and therefore instability. Depensatory mortality could be involved in maintenance of cyclicity in population dynamics (Eggers and Rogers 1987). A tendency to generation cyclicity (e.g. Godfray and Hassell 1987, Knell 1998) at a high level of mortality has been demonstrated even in cases of constant mortality and no delayed density-dependence in recruitment (e.g. Townsend *et al.* 1990, Myers *et al.* 1998). Further, threshold-strategies can be considered as extremely nonlinear, compensatory, density-dependent population regulation which can induce instability in population dynamics.

In this paper an example of auto-regulative fishing strategies aiming at reduction of revenue variation is compared with constant effort and constant revenue strategies combined with several threshold revenue levels. The objective variables for comparison are long-term average revenue and its interannual variation, fishing effort and its variation, and the risk of stock collapse indicated by the level of spawning biomass. The aim is to illustrate how the strategies trade off the advantages and disadvantages and to seek improvements in vendace fisheries management that might ensure the maintenance of commercial fishing. The consequences of fishing for the population dynamics are also considered. To explore the performance of the strategies, a simulation model was developed which incorporates several key features of vendace population dynamics: an age-structured population, a stochastic spawner-recruit relationship, density-dependent growth, fish-size dependent gear-selectivity and value of yield.

Methods

The vendace population simulation model consisted of seven age groups (0+ to 6+) and the model was updated at discrete time units of one month. The biomass ($B_{a,m,y}$, kg km^{-2}) of a certain age group a at the beginning of month m of year y was calculated as follows:

$$B_{a,m,y} = D_{a,m,y} w_{a,m,y} \qquad (1)$$

where $D_{a,m,y}$ = density of age-group a (individuals km^{-2}) and

$$w_{a,m,y} = \mathrm{GR}_{a,m-1,y} w_{a,m-1,y} \qquad (2)$$

where $w_{a,m-1,y}$ = the mean weight of fish at the beginning of the previous month, $\mathrm{GR}_{a,m-1,y}$ = growth rate during the previous month (for January, the subscripts for the previous month are a

– 1,12,y – 1). The annual pattern of growth was assumed to be such that growth takes place during May–September, no growth occurs in October and fish lose weight during November–April. Growth was assumed to be dependent on density and fish size according to a modification of the model of Marjomäki and Kirjasniemi (1995). The weight (g) of young-of-the-year (YOY) vendace at the beginning of July was assumed to be 1 g and the growth rate from then on was calculated as follows:

$$GR_{a,m,y} = \frac{1}{\left(\alpha w_{a,m-1,y}^{-1/3.1} + \beta\right)^{-3.1} + \kappa Dy_{m,y} + \tau Do_{m,y}} \quad (3)$$

where $Dy_{m,y}$ = the density of YOY vendace (individuals km^{-2}) at the beginning of month m in year y and $Do_{m,y}$ = the density (individuals km^{-2}) of vendace older than YOY. The values of the parameters (Appendix 1) were tuned to mimic the slow growth pattern of vendace in an oligotrophic lake.

The instantaneous growth rate ($G_{a,m,y}$) was

$$G_{a,m,y} = \ln(GR_{a,m,y}) \quad (4)$$

The density of age a fish in the beginning of month m + 1 of year y was

$$D_{a,m+1,y} = D_{a,m,y}\exp(-M_{a,m,y} - F_{a,m,y}) \quad (5)$$

where $M_{a,m,y}$ = instantaneous total mortality of age a fish during month m (Appendix 2). In the first year of life, M was approximated from the results in Karjalainen *et al.* (2000) and for the older age groups the selected values express the increase in M with age (e.g. Valkeajärvi 1983, Marjomäki and Huolila 1994) and are a level typically found in Finnish lakes (e.g. Viljanen 1986). At a given age and month, M was assumed to be constant in different years.

Fishing was assumed to be carried out by a trawl-type gear. Fishing takes place during June–October. The fishing mortality $F_{a,m,y}$ depends on catchability (q), fish-size-dependent gear selectivity $s(l_{a,m,y})$ and fishing effort f that is dependent on revenue per unit effort ($U_{m,y}$):

$$F_{a,m,y} = qs(l_{a,m,y})f(U_{m,y}) \quad (6)$$

The q of the trawl per trawling hour in

fully recruited (selectivity = 1) size groups is assumed to be 0.2, based on the fact that the fish occupy the pelagic areas of the lake (Marjomäki and Huolila 1995) (over 10 m in depth). There this is assumed to be 50% of the lake area, where their catchability per area swept by trawl is assumed to be about 50% (based on Marjomäki and Huolila 1995). The swept area of one trawling hour is assumed to be 0.2 km^2.

The selectivity function of the gear is assumed to be a sigmoid function of total length of fish (Paloheimo and Cadima 1964):

$$s\left(l_{a,m,y}\right) = \frac{\exp\left(-20 + 2l_{a,m,y}\right)}{1 + \exp\left(-20 + 2l_{a,m,y}\right)} \quad (7)$$

Thus the 25%, 50% and 75% selectivities occur at lengths of 9.44, 10.0 and 10.56 cm, respectively.

The average weight ($w_{a,m,y}$, g) was converted to length ($l_{a,m,y}$, cm) for the selectivity function as follows:

$$l_{a,m,y} = (303w_{a,m,y})^{0.305} \quad (8)$$

where the parameter values were obtained from mean length–mean weight regression of different age-groups from Lake Puulavesi vendace catch samples of years 1984–1990 (Marjomäki and Huolila 1994).

The revenue per trawling hour ($U_{m,y}$) was estimated at the beginning of each month based on the unit price of fish $p(w_{a,m,y})$ and the yield per unit of effort (YPUE$_{m,y}$, kg/trawling hour) as follows:

$$U_{m,y} = \sum_{a=0}^{6+} p\left(w_{a,m,y}\right)YPUE_{a,m,y} \quad (9)$$

where $p(w_{a,m,y})$ = 1 price unit if the weight of the fish is at least 10 g (11.5 cm) and 0.75 for smaller fish. This relative difference in price is approximated from an enquiry to one fish wholesale dealer in 2002.

Yield per unit effort (YPUE) is calculated as follows:

$$YPUE_{a,m,y} = qs(l_{a,m,y})B_{a,m,y}. \quad (10)$$

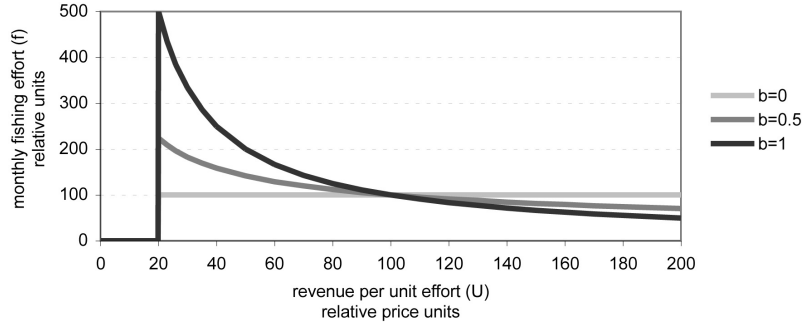The fishing effort during month m, $f_{m,y}$, as a function of $U_{m,y}$ in June–October was

Fig. 1. The dependence of monthly fishing effort on the revenue per unit effort at the beginning of the month with different values of b (Eqs. 11 and 12). In this example the threshold is 20.

$$f_{m,y} = aU_{m,y}^{-b} \text{ if } U_{m,y} > T \qquad (11)$$

$$f_{m,y} = 0 \text{ if } U_{m,y} \leq T \qquad (12)$$

where T = threshold level of $U_{m,y}$. Three threshold levels (T-strategies) were used: 20, 40 and 80 revenue units/hour of trawling resembling the stock biomass of at least 100, 200 and 400 kg km^{-2}, respectively (assuming $s(w_{a,m,y}) = 1$ and $p(w_{a,m,y}) = 1$ price unit). Three different values for b (b-strategies) were considered (Fig. 1):

$b = 0 => f = a$	constant monthly effort strategy, revenue relative to mean monthly U,
$b = 0.5$	increasing f with decreasing U, slower decrease in revenue than in U,
$b = 1 =>$ revenue $\approx a$	(semi-)constant monthly revenue, increasing f with decreasing U.

The last case is not exactly constant monthly revenue, as the monthly f is determined by U at the beginning of the month. If U changes considerably during the month, for example because of high growth rate, the mean monthly U differs considerably from U at the beginning. The strategy of updating f once a month was, however, considered more realistic than more frequent updating, as it reflects the fact that there is always some time-lag in the decisions and rapid changes in the stock may not be anticipated.

The monthly revenue (ρ) is

$$\rho_{m,y} = \sum_{a=0+}^{6+} p\left(w_{a,m,y}\right) F_{a,m,y} \text{ mean}\left(B_{a,m,y}\right) \quad (13)$$

where the mean monthly biomass (mean($B_{a,m,y}$))

is

$$\text{mean}\left(B_{a,m,y}\right) = \frac{B_{a,m,y}\left[\exp\left(-M_{a,m,y} - F_{a,m,y} + G_{a,m,y}\right) - 1\right]}{\left(-M_{a,m,y} - F_{a,m,y} + G_{a,m,y}\right)}. (14)$$

The number of young of the year vendace at the beginning of July in year $y + 1$ (R_{y+1}, individuals km^{-2}) was simulated by the Ricker (1954) and Cushing (1971) recruitment functions modified from Marjomäki (2004) (Fig. 2)

$$R_{y+1} = 390\text{SB}_y\exp(-0.0018\text{SB}_y) \qquad (15)$$

$$R_{y+1} = 9748\text{SB}_y^{0.27} \qquad (16)$$

where SB_y = the biomass of older than one year old fish (kg km^{-2}) in the beginning of November in year y.

The negative dependence between recruitment in consecutive years was simulated by including a hypothetical delayed density-dependence into the SB-R relationship $f(\text{SB}_y)$ (Fig. 2)

$$R_{y+1} = f(\text{SB}_y)1.1\exp(0.00004R_y) \qquad (17)$$

The random component ε of the recruitment was assumed to be log-normal (theoretical justification: Walters and Hilborn (1976); empirical justification: Hennemuth *et al.* (1980) and Peterman (1981)) with mean 0:

$$R_{y+1} = f(\text{SB}_y)e^{\varepsilon}, \varepsilon \sim \text{N}(0,\delta_{\varepsilon}^2). \qquad (18)$$

As the random variation of vendace recruitment is usually considered high (Marjomäki *et al.* 2004) a high value of $\delta_{\varepsilon} = 1.2$ was assumed. A lower value $\delta_{\varepsilon} = 0.6$ and a deterministic case $\delta_{\varepsilon} = 0$ were also tested. The range of ε was truncated
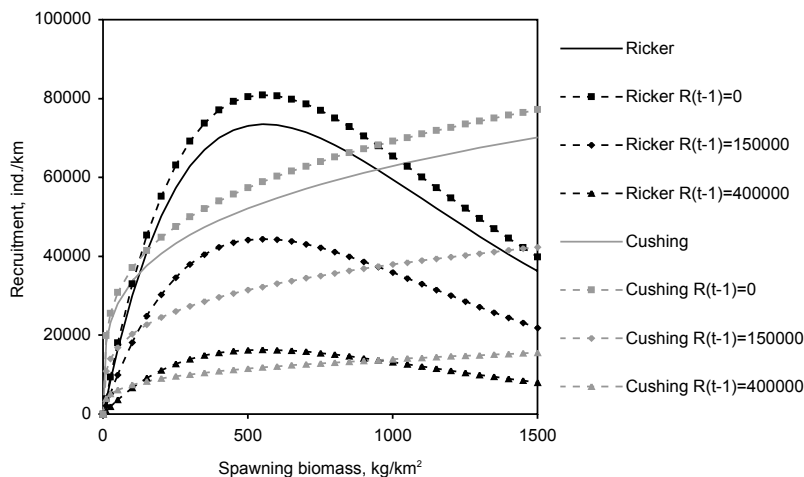
Fig. 2. The spawning biomass–recruitment relationships used in the study (solid lines): Ricker (Eq. 15), Cushing (Eq. 16). The curves for different $R(t-1)$ (dashed lines) assuming delayed density dependence are examples of the expected recruitment with different levels of previous year recruitment (Eq. 17).

to ±1.7 (range of e^ε from 0.18 to 5.5) in order to keep the maximum number of recruits within the range observed in nature.

To compare different harvesting strategies, a set of evaluation criteria is needed. Following the pattern of other harvest strategy studies (e.g. Hall *et al.* 1988), the mean annual revenue (in many studies catch or yield) was used as a primary criterion. Zero discount rate was used in all cases. This presumes that fishery resources will generally be managed with long-term, resource husbandry objectives. The coefficient of variation (CV) of revenue compares revenue variability between different levels of the same harvest strategy and between different strategies. Risk of collapse of fisheries was measured by monitoring the mean spawning population biomass, its CV and the proportion of years when the spawning population was below 200 kg km^{-2}, which was clearly on the steep-sloped section of both SB-*R* functions (Fig. 2). Also, mean recruitment and its CV were recorded. The criteria for evaluation of strategies were the mean annual effort and its CV and the maximum monthly effort needed to apply a certain strategy. An example of trade-offs between mean annual revenue (ρ) and its variation (sd = standard deviation) was illustrated by an objective function (*O*) by Quinn *et al.* (1990):

$$O = \mathrm{mean}(\rho)(1-\lambda) - \lambda \mathrm{sd}(\rho), \qquad (19)$$

where the penalty factor representing the cost of variation $\lambda = 0.5$.

The number of recruitment-sequences where $r_t > r_{t+1} < r_{t+2} > r_{t+3} < r_{t+4} > r_{t+5}$ ($t = 1 - 100$) was used as an index of a tendency for two-year cyclicity of recruitment. The results were compared with the expected number (8) in a sequence of normally distributed random variables.

With each parameter combination (*b*- and *T*-strategies, δ_ε) and varying number of fishermen, 150 years were simulated. The simulator was allowed to "warm up" for the first 50 years after which the state variables were independent of their initial values. The values of the criterion variables were recorded for each run. The procedure was repeated 500 times and the medians of these values, each representing a 100 year sequence, were used in the analysis.

Results

For the four spawning biomass-recruitment hypotheses exemplified, Ricker and Cushing without (Figs. 3 and 4) and with negative dependence (not presented) between the consecutive recruitment, the qualitative results were very similar, and the quantitative results differed only slightly for most of the criterion variables. A clear difference occurred between the Ricker and Cushing models only at an effort exceeding that producing maximum mean annual revenue. There, the decrease in mean revenue with the increase in effort is slower for the Cushing model (Fig. 4) than for the Ricker model (Fig. 3). This was expected from Fig. 2: the relative difference
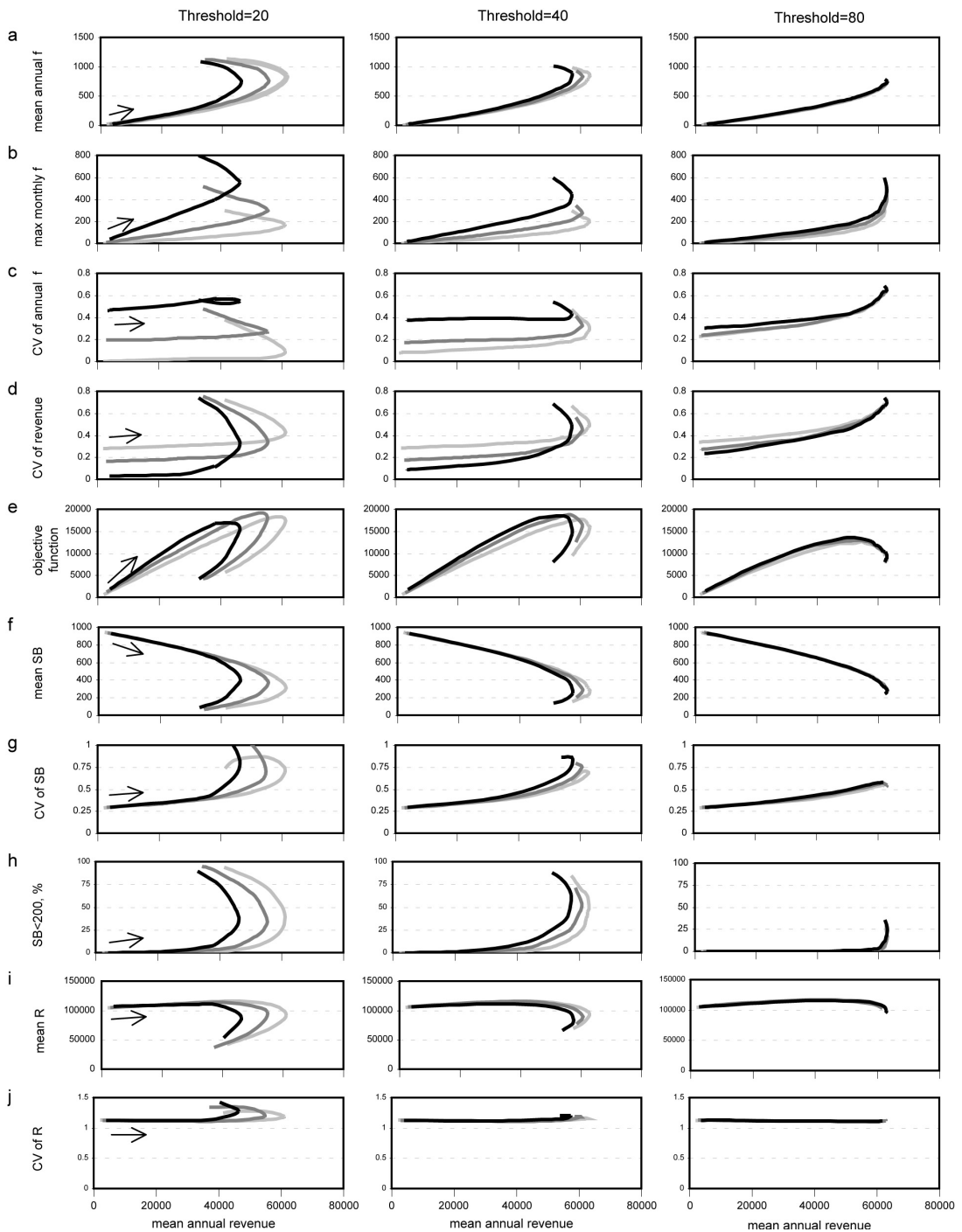
Fig. 3. The relationship between performance criteria and mean annual revenue for the Ricker *S-R* function (Eq. 15) with random variation sd = 1.2 for different harvesting strategies. Light grey line *b* = 0 constant effort, dark grey *b* = 0.5, black *b* = 1 constant revenue. The arrow shows the direction of the effect of an increase in the number of fishermen.
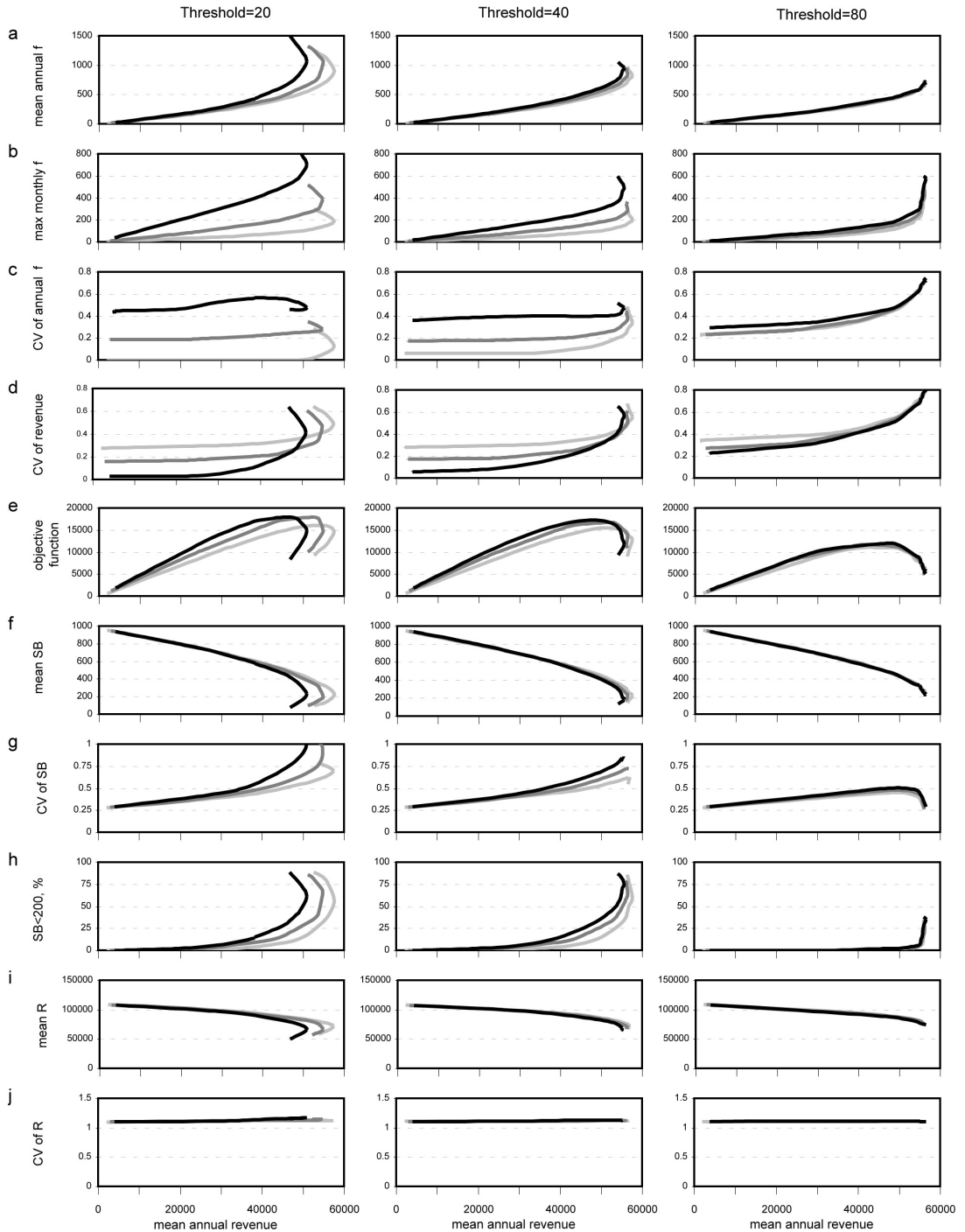
Fig. 4. The relationship between performance criteria and mean annual revenue for the Cushing *S-R* function (Eq. 16) with random variation sd = 1.2 for different harvesting strategies. Light grey line *b* = 0 constant effort, dark grey *b* = 0.5, black *b* = 1 constant revenue.

in expected recruitment between the models is highest at very low level of spawning biomass. The only difference between the results from the *S-R*-functions without and with delayed density-dependence in the case of high random variation was the marginally lower coefficient of variation in annual effort, and revenue in cases of delayed-density dependence.

In all cases the highest mean annual revenue (Figs. 3 and 4) was provided by the constant effort strategy ($b = 0$) and the lowest by the strategy aiming at constant revenue ($b = 1$). The difference in mean revenue between different *b*-strategies was most striking when the threshold (*T*-strategy) for shutting down fishing was low and the effect of the value of *b* on the performance became negligible when a high threshold was selected. From the point of view of different threshold levels this means that, for the strategies of increasing effort with decreasing stock ($b > 0$), especially constant revenue ($b = 1$), threshold adjustment has a clear effect on the maximum mean revenue, whereas the revenue from the constant effort strategy is rather insensitive to threshold level.

A certain level of mean annual revenue was always produced by the smallest mean annual effort (Figs. 3 and 4a) under the constant-effort strategy. Thus, it is economically the most effective strategy if the profit is only dependent on average revenue and average effort (= variation induces no cost). The performance of the constant revenue strategy ($b = 1$) was again worst and that of $b = 0.5$ intermediate. The maximal monthly effort (Figs. 3 and 4b) and the coefficient of variation of effort (Figs. 3 and 4c) needed to produce a certain revenue were obviously highest for the constant-revenue strategy ($b = 1$) as the constancy was achieved by a varying fishing effort. The variation in effort remained very low for the strategy combining constant effort with low threshold until the maximum yield was achieved. After that the variation increased dramatically as the fishing was shut down more often due to low stock. For higher threshold levels, the variation of effort was higher already for lowest mean revenues as fishing shutdown became more frequent.

The difference between strategies was also clear for the essential criterion of coefficient of variation of revenue (Figs. 3 and 4d). For low levels of mean revenue, the variation was obviously highest for the constant effort strategy ($b = 0$), which follows closely the variation of stock, intermediate with $b = 0.5$ and lowest for constant revenue. The variation for every strategy increased with increase in mean effort. This effect was most dramatic for the strategy targeting constant revenue and from the level of effort producing highest mean revenue onwards, the variation for that strategy became highest due to frequent fishing shutdown. Again, increasing the threshold level generally increased the variation of revenue for all *b*-strategies and diminished their difference.

The values of the objective functions (Figs. 3 and 4e) providing the trade-off between the revenue and variation of revenue depend on the value of the penalty factor λ representing the cost of variation. Assuming the penalty $\lambda = 0.5$, the value of the objective function at low mean effort and revenue was highest for the constant revenue strategy because of the low variation in revenue at that level. The function was maximised for the intermediate *b*-strategy if the Ricker recruitment model and low to intermediate threshold levels are assumed. For the Cushing model and high threshold the differences in maximum levels were minor. The maximum was always found at 10%–20% lower mean revenue level compared with maximum mean revenue because of the sharp increase in revenue variation near the maximum. The maximum of the objective function would be gained by a constant effort strategy if λ was less than about 0.4 and 0.3 for the Ricker and Cushing models, respectively. The constant revenue strategy would maximise the function starting from the value of λ of about 0.6 and 0.5.

Judging by the risk of low spawning stock (Figs. 3 and 4f–h), the combined strategy of constant revenue and low threshold showed the worst performance. As yield increased towards its maximum, the variation of spawning stock and risk of low stock increased rapidly. The risk also increased for intermediate and constant effort strategies, but more slowly. Obviously, increasing the threshold decreased the risk of low stock and CV of the stock.

As an example of the effect on the criteria of the level of random variation of recruitment, the

results for different strategies with the Ricker recruitment function and $\delta_\varepsilon = 0.6$ are presented (Fig. 5). The results did not differ qualitatively from $\delta_\varepsilon = 1.2$ (Fig. 3) but naturally all the coefficients of variation and risks of low spawning stocks are lower.

To demonstrate the sole effect of the level of threshold for the dynamics of the model, the performance was calculated for the model in a deterministic case ($\delta_\varepsilon = 0$). In the case of no threshold, all strategies converted to case-specific constant population size and revenue (no interannual variation). With high effort the stock collapsed to extinction. When the threshold was added, the constancy was still achieved with low fishing effort (Fig. 6). With the increase of effort, however, interannual variation emerged. In some cases the variation was cyclical but sometimes chaotic "pseudo-random". Sometimes, as in the case of threshold = 80 and constant effort, the relationship between mean revenue and its variation was very peculiar (Fig. 6d). After an interannual constant revenue up to a maximum revenue, a section of highly variable revenues emerged when the potential effort was increased. Then, with overfishing another situation of interannually constant effort and revenue emerged. After that variation increased again. Typically the non-constant zone emerged in all studied cases only in the zone where the revenue was maximised or after that in an over-fishing situation. The behaviour emphasises the fact that introduction of "boom-and-bust" stopping rules into the fishery can decrease the stability of the resource dynamics.

An increased tendency for two-year cyclicity was detected with decrease of mean spawning stock except for the very low spawning stock level (Fig. 7). For the Ricker model (Fig. 7a), in cases of high mean spawning biomass (negative slope in *S-R*-model), cyclicity was less than expected from a sequence of random numbers (expected = 8), which implies cyclicity longer than 2 years. For lower mean spawning biomass (positive slope of the Ricker model), the tendency was higher than in a random sequence. For the continuously increasing (positive slope) Cushing function (Fig. 7e), the cyclicity was also higher than in a random sequence for high spawning stocks. For both models, however, the tendency decreased at very low spawning stock levels. This was due to breaking the pattern by the shutdown of the fishery when the threshold was approached. For the same reason, with a higher threshold the overall tendency was lower (compare Fig. 7a and b). In case of high random variation, the *b*-strategy did not much affect the level of cyclicity, but for lower variation the cyclicity was highest for constant effort strategy and lowest for constant revenue strategy (Fig. 7c). This was due to the higher frequency of fishery shutdown breaking the two-year-pattern in the case of constant revenue strategy. In the case of delayed density-dependence by the previous year-class (Fig. 7d), the cyclicity was somewhat higher for high spawning stock level but almost at the same level as without delayed-density dependence for low spawning stock.

Discussion

The results are generally in agreement with the theory of the basic strategies (*see* Introduction) of constant stock, effort and yield in that (1) fixing one of these aspects will make the other two absorb the variation in recruitment and risk (e.g. Evans 1981), and (2) the variation of revenue increases with increase in effort (e.g. Beddington and May 1978). In this study, however, all the strategies studied were fusions of at least two of the three aspects, e.g. constant effort or constant revenue combined with minimum biomass control by a threshold under which fishing is prohibited or shut down completely. Further, the case of somewhat adjustable fishing effort ($b = 0.5$) was a compromise of all three and therefore produces interesting trade-offs of the performance criteria.

Many studies (e.g. Aron 1979, Ruppert *et al.* 1985, Hall *et al.* 1988, Quinn *et al.* 1990, Hjerne and Hansson 2001) support the inclusion of a minimum threshold stock in the strategy for its safety against extinction and in some cases also higher average yield. Yet these benefits depend much on the life-history of the species studied and must therefore be evaluated separately for each species. For example, Quinn *et al.* (1990) compared different threshold levels for walleye pollock (*Theragra chalcogramma*) and found
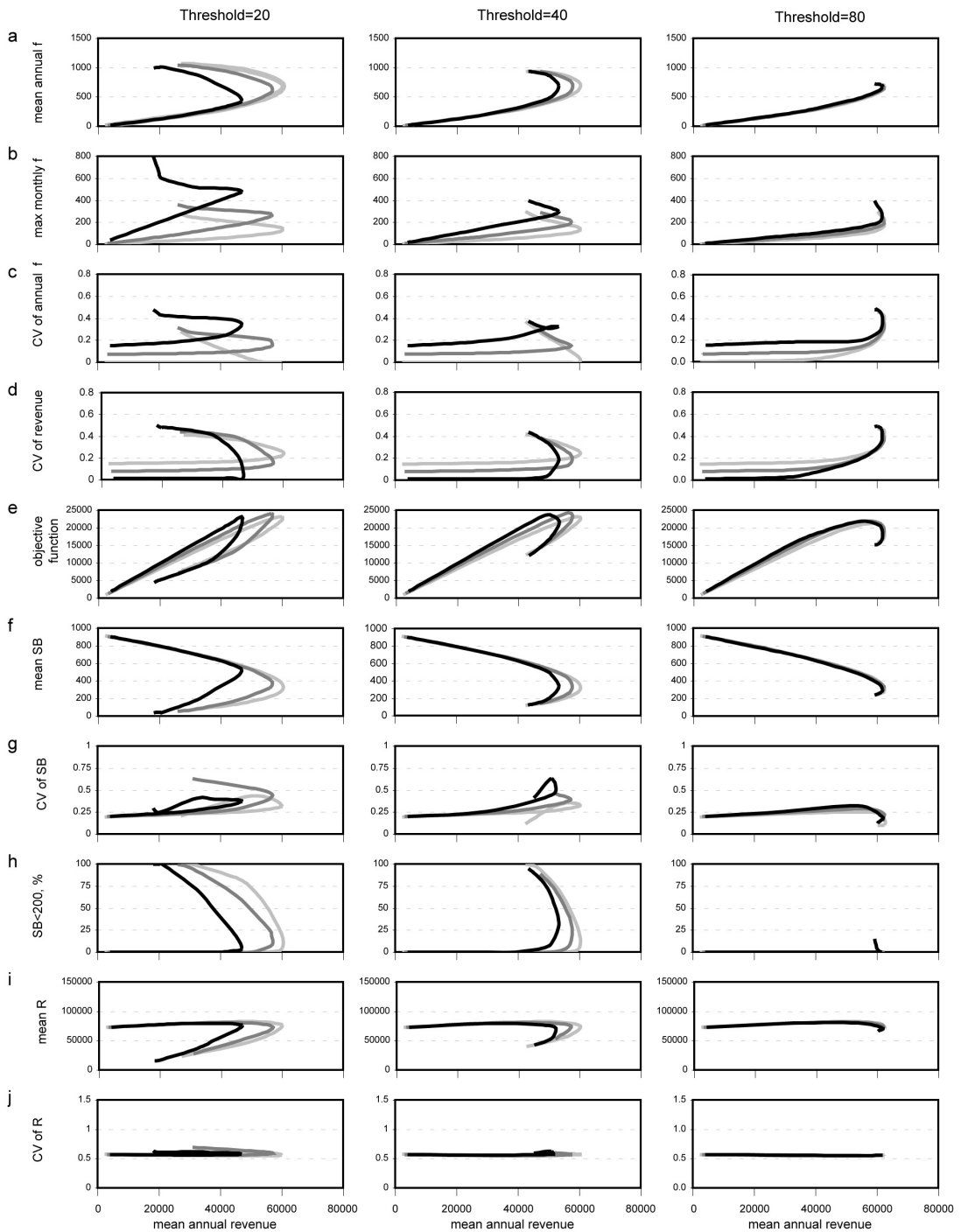
Fig. 5. The relationship between performance criteria and mean annual revenue for the Ricker *S-R* function (Eq. 15) with random variation sd = 0.6 for different harvesting strategies. Light grey line *b* = 0 constant effort, dark grey *b* = 0.5, black *b* = 1 constant revenue.
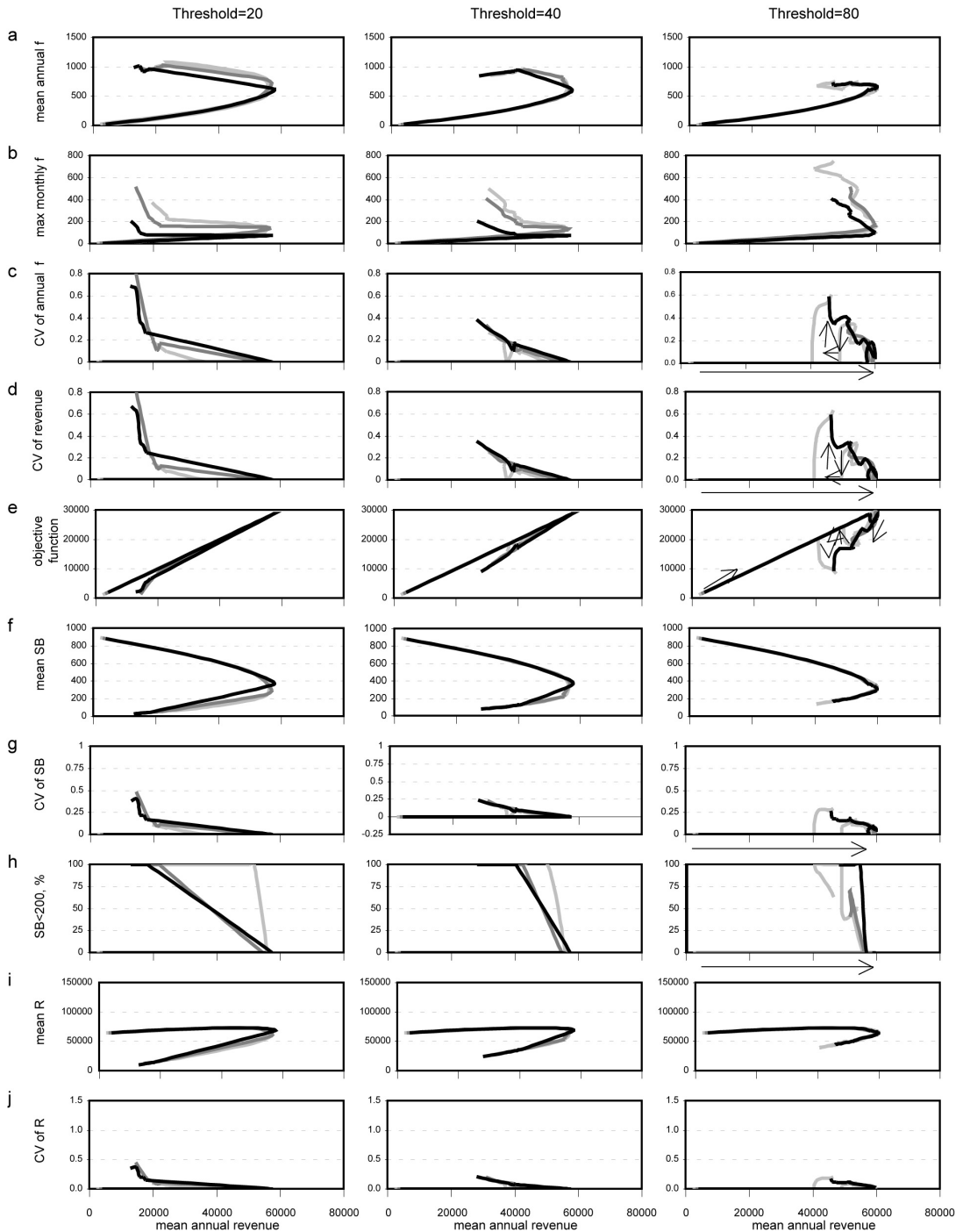
Fig. 6. The relationship between performance criteria and mean annual revenue for the Ricker *S-R* function (Eq. 15) with no random variation for different harvesting strategies. Light grey line *b* = 0 constant effort, dark grey *b* = 0.5, black *b* = 1 constant revenue.

that a threshold policy combined with constant effort strategy increased average yield over a non-threshold policy. The effect was most pronounced with high fishing effort and the success was due to relatively rapid rebuilding of the population after decline. Interestingly, in the case of vendace, the effect of different thresholds on average revenue was marginal with a constant effort ($b = 0$) strategy. This difference is understandable when the life-histories of pollock and vendace are compared. Pollock is a longer-lived and later-maturing fish than vendace and the fishing is started at an older age, so the rebuilding time is shortened effectively by thresholds. The rebuilding time for a vendace population model is always short as vendace mature at less than 2 years and the fishing starts also early. Thus, for this kind of species the benefits of threshold for mean revenue are less obvious.

For strategies of increasing effort with decreasing stock ($b > 0$), especially constant revenue ($b = 1$), the benefits of a threshold on maximum average revenue became apparent. Strategies resembling these have been studied previously. The optimal strategies for minimising variance of catches of Skeena River Pacific salmon around a moderate mean value were typically such that the exploitation rate should be increased with the decrease of the stock to a certain point below which it should be decreased rapidly (Walters 1975). The threshold of no fishing was higher and the need for increase in effort smaller with higher desired mean catches. For Atlantic menhaden (*Brevoortia tyrannus*) fisheries, the optimal intermediate egg escapement strategy, resembling the case of $b = 0.5$ in this paper, produced somewhat lower catch variations than optimal constant escapement policies, but the difference in typical utility was small (Ruppert *et al*. 1985).

The mixed strategies resembling a constant stock size strategy, where the effort is increased with the increase in the stock size in the zone above the threshold, have been found to produce the highest average catches because of their ability to capitalise fully on occasional large positive recruitment fluctuations (e.g. Swartzman *et al*. 1983, Hall *et al*. 1988). These strategies were not studied in this paper because it was considered
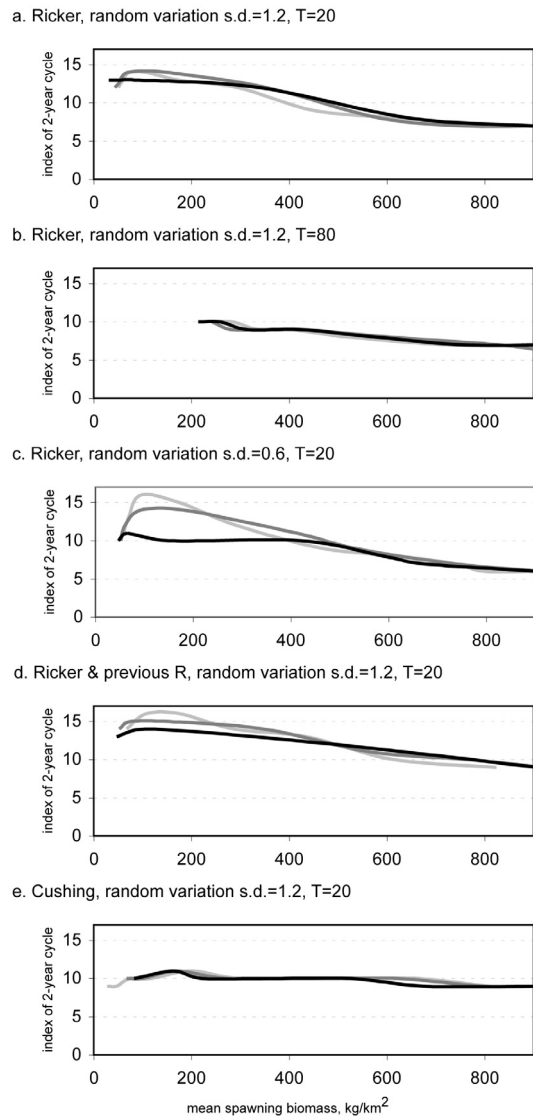

Fig. 7. The relationship between a tendency for a 2-year cycle and the mean spawning biomass in cases of different recruitment models, thresholds and levels of random variation. Light grey line $b = 0$ constant effort, dark grey $b = 0.5$, black $b = 1$ constant revenue.

that the ability of the vendace fisheries and markets to absorb these high yields and generally higher variance is very limited.

It was assumed in the model that the effort was adjusted on grounds of revenue per unit effort which was assumed directly proportional to the biomass levels of different sized fish. The unit effort-based proxies sometimes contain considerable error so that Walters (1975) pro-

posed a simplified strategy which was a fusion of constant effort and a sharp decline below a threshold instead of the stock dependent optimal strategy. Hjerne and Hansson (2001) found a mixture of threshold and constant catch strategies to be especially favourable over constant effort in fisheries where CPUE's dependence on the stock size is weak (hyperstability). However, vendace trawl yield per swept area seems to be closely comparable to results from other assessment methods of vendace stock (Marjomäki and Huolila 1995) and the stock fluctuations are vast. Therefore, if considered necessary, yield per unit effort might be an accurate enough index for effective effort or threshold regulation.

For schooling fish like vendace, it is possible that the assumption of constant catchability fails and fishing mortality per unit effort increases with stock decrease, causing bias of hyperstability of yield per unit effort (e.g. Gulland 1977). In that case the increase in fishing mortality with stock decrease is greater than the increase of nominal effort with decrease of yield per unit effort, and the estimates of spawning biomass are further biased upwards at low stock levels. Both of these biases increase the risk of stock collapse. This bias has not been shown to exist in assessment of vendace stocks but calls for a systematic study comparing the CPUE and echosounding estimates in different lakes and at different vendace densities.

As emphasised by Horwood and Shepherd (1981), models intended for the study of dynamic behaviour need to be very carefully constructed. In this study, emphasis was put on careful modelling of the compensatory density-dependence in growth and its economical consequences. This compensation limits the stock increase in cases of already high biomass and limits the relative value of dense stock due to the lower price of small fish. Without the density-dependence in growth the biomass variation would have been much higher, especially at the highest level of spawning stock. This would have induced bias, especially in the performance of the constant effort strategy, by increasing its average yield and revenue and its variance. Concerning optimal harvest, strong density dependence in growth calls for an immediate thinning of year-class at an early date (Hannesson 1986). Vendace

is recruited to trawl or seine fishing during its first year of life but, unfortunately, in practice the thinning operates depensatorily: due to their slow growth, abundant year-classes become vulnerable to gear later and fishing is sometimes stopped due to their low price and demand.

Age- and month-specific natural mortality was assumed to be constant in different years. In reality, however, it may be compensatorily density dependent, although no observations exist for vendace. The effect of compensatory natural mortality on the dynamics of the model is, however, much the same as that of density-dependent growth in that it reduces the increase of already dense spawning stock and makes the stock more resistant to overfishing. Therefore, constancy of *M* is a conservative assumption considering the risk of over-exploitation.

A serious problem for practical fisheries management may be that the details of the trade-off between revenue and risk depend heavily on the assumed stock-recruitment curves (Aron 1979). In this study, the differences in results from the Ricker and the Cushing recruitment models were minor over a large range of spawning stocks and thus the uncertainty of the recruitment model seems not to be critical to management. This difference was due to the fact that the stochastic variation around the models was assumed large in comparison with the differences of model predictions, thereby masking the effect of the model. In cases of a smaller proportion of stochastic variation, the differences between models and between different levels of compensation would be more evident. However, for all models the uncertainty about the slope and shape (e.g. possible depensation) of the model at very low spawning stocks is critical considering the risk of collapse if overfishing occurs. If the uncertainty is high, there is a need for management schemes which require less detailed knowledge; one class of such schemes is protection policies which do not permit harvesting if stocks drop below a certain threshold level (Aron 1979).

The suggested delayed density-dependence that induces negative autocorrelation in vendace recruitment was produced in this study by introducing negative dependence of recruitment on the recruitment in the previous year. In the case of negative lag-1 autocorrelation, the probability

of a series of extremely low or high recruitment is reduced and the yield variability, therefore, is lower than with white noise (Quinn *et al.* 1990). This was detected to some extent in this study. However, independent of delayed density-dependence, there was a tendency for two-year-cyclicity which increased with increase of fishing mortality and decrease in spawning stock. This result is in accordance with the results of Townsend *et al.* (1990) and Myers *et al.* (1998) who demonstrated the tendency for generation cycles after perturbation and further, positive correlation between the life span of the cycle and fishing mortality. In this study, the cyclicity in cases of low spawning stock was almost as common without delayed density dependence as with it. This result should, however, be considered preliminary as the applied model for delayed density-dependence was hypothetical.

Alternatively, a low frequency positive autocorrelation in recruitment variability may emerge, for example due to positively autocorrelated environmental forcing (e.g. Steele 1985) or mortality by long-lived predator stock. Valkeajärvi and Marjomäki (2004) described a sequence of low recruitment of vendace and suggested that this was due to perch (*Perca fluviatilis*) predation. The consequences of positively autocorrelated variation in recruitment have been studied extensively (Sissenwine 1977, Steele and Henderson 1984, Getz *et al.* 1987, Hall *et al.* 1988, Koslow 1989, Parma 1990, Quinn *et al.* 1990, Walters and Parma 1996 and Spencer 1997). Koslow (1989) concluded that recruitment periodicity does not directly affect estimates of long-term sustainable yield or the levels of effort required to obtain this. Instead, the variance of yield and stock biomass increases substantially, thereby increasing the risk of fishery closure and the incidence of very low stock levels. As the period length exceeded the populations generation time, the amplitude of change in stock biomass increased rapidly. This makes the shorter-lived species sensitive to environmental variability at an additional range of frequencies than longer-lived species. Risk of stock collapse may be minimised with either optimal stock biomass management or a mix of optimal effort management at high stock levels and base-stock management during periods of poor recruitment.

According to Steele and Henderson (1984) and Spencer (1997), multiple equilibria of the stock can result if a non-linear rate of predation is forced with positively autocorrelated noise.

It was assumed in the model that fishing does not induce indirect fishing mortality, which for vendace fisheries means mortality caused by fishing that does not result in landings but causes lethal injury to fish passing through the cod-end. Considerable mortality of young-of-the-year juvenile vendace has been shown to occur in vendace trawling experiments (Suuronen *et al.* 1995). Its consequences for the population dynamics are, however, difficult to evaluate as the spatio-temporal overlap between distribution of trawling effort and juveniles is currently obscure. Furthermore, the total mortality of juveniles during the first summer is typically large and unpredictable (Karjalainen *et al.* 2000) which suggests that the significance of indirect mortality may not be decisive. No symptoms of recruitment failure connected to trawling were found in a case study comparing zones of a lake with different trawling intensities (Marjomäki and Huolila 2001). Thus, this simplifying assumption hardly compromises the applicability of the results in the case of trawling. Naturally, in assessment and management of real fisheries the effect of indirect mortality must be taken into account (e.g. Auvinen *et al.* 2001).

Improving vendace fisheries management

Answering the question what would be the single most desirable strategy for vendace harvesting is beyond the scope of this study. The optimal strategy must be determined by balancing the utility of the different levels of yields, the cost of fishing and the cost of variation in effort and yield, the risk of the stock or fishery collapsing at different levels of spawning biomass and the opportunity losses due to model and parameter uncertainties in the models *et cetera*. As noted by Hilborn and Walters (1977), when a specific question is asked, such as "would fisherman prefer a lower variation in annual catch to the current high variation?", there usually are no data available to answer the question. Many dif-

ferent utility functions in relation to risk have been studied and the form of this function has a significant effect on optimal strategy (e.g. Mendelssohn 1982). In this paper, a risk neutral utility function $U(\rho) = \rho$ was assumed for the main criterion of mean annual revenue, but choosing a risk averse utility function e.g. $U(\rho) = \log (\rho + 1)$ instead decreases the utility for the strategies with higher interannual variation in revenue. The cost of variance was illustrated with the objective function trading off the variance and mean revenue with arbitrarily chosen $\lambda = 0.5$ to demonstrate that the optimal strategy choice depends on the trade-off between benefits and losses.

However, instead of proposing a single optimal strategy for vendace fisheries management, certain guidelines, that are robust to the uncertainties, can be given. Given the basic assumption that the interannual variation in stock is too large to be absorbed by the fisheries system without severe complications (costs), the ability to adjust fishing effort ($b \gg 0$) in order to dampen the fluctuation in revenue is essential for the fishermen. The results demonstrate clearly the fact that prerequisites for effective adjustability are (1) a much lower than maximum mean annual revenue, and thus also number of fishermen (2) a certain amount of over-capacity of potential fishing effort in the case of individual fisherman during the high stock period and (3) a low or moderate threshold level. When the number of fishermen, and thus mean effort and average revenue, increase, the possibility of high values of b decreases, which means less opportunity for adjustment. Thus first of all, the means for regulation of the maximum total fishing effort by regulating the access to fishing should be established. This decreases the need for restricting fishing effort during the stock decline. Because the stock fluctuations are vast and the parameters of the production functions are difficult to estimate for optimisation, the increase in the amount of fishermen (and target revenue) must be cautious (*see* Evans 1981). If for some reason the number of fishermen and also the target revenue is already large (near to maximum annual revenue level), then the flexibility of effort must be limited close to constant effort ($b = 0$) to ensure the sustainability of average expected yield. The limitations can be made by regulating maximum

gear dimensions and daily fishing time. Sustainability may still become impossible in this case due to increased yield and revenue variation because this case is contrary to the previously stated basic assumption.

From the viewpoint of the trade-off between revenue and its variation, there seems to be little need for threshold control, if the number of fishermen and therefore the total target revenue can be limited. In all studied cases, the variation in revenue increased as the threshold was increased due to higher frequency of fishing shutdown. Yet one should bear in mind that strategies aiming at constant yield invariably result in a high risk of stock collapse in an over-fishing situation (e.g. Beddington and May 1977). In economically auto-regulative vendace fisheries, increase in price or decrease in cost decreases the threshold by ensuring profitable fishing from ever sparser stock, as suggested by Marjomäki *et al.* (1995). If considerable potential for increase in effort is present, this can lead to overexploitation and collapse of fisheries, which supports the use of a threshold level that is not connected to economic variables, such as minimum spawning biomass. If the recruitment variability is suspected to be positively autocorrelated, the protection of spawning biomass may be even more desirable. In a typical case of high uncertainty about the recruitment model at low spawning stock, it may be worth trading off revenue variability with lower risk associated with higher threshold levels. Helminen *et al.* (1997) and Karjalainen *et al.* (2000) have shown that the number of recruits is positively dependent on spawning stock and larval density at low stock levels. This calls for protection of sufficient spawning stock by a threshold strategy to ensure ample recruitment. Stock-recruitment studies should be targeted at defining the sufficient level.

The suggested guidelines are in good agreement with the attitudes of the fishermen themselves towards fishery management. According to Salmi (1998), limiting the access of new enterprises to the fishery was most often considered the best course of action for vendace fisheries management among trawlers and winter seiners whereas gear regulations and catch quotas were often regarded as the least desired management tools. Overall, the development of fisheries

according to these guidelines demands some re-arrangement of the fishing license system (*see* Sipponen and Valkeajärvi 2002) and above all proper assessment of the long-term average potential yield of the vendace stocks.

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Appendix 1. Parameter values for the growth model (Eq. 3) for different months and age groups.

Month	Young of the year				Older			
	α	β	κ	τ	α	β	κ	τ
1					0	0.995	0	0
2					0	0.995	0	0
3					0	0.995	0	0
4					0	0.995	0	0
5					0.46	0.885	0	1E–06
6					0.46	0.885	0	1E–06
7	0.6	0.83	7E–07	1E–06	0.46	0.885	7E–07	1E–06
8	0.6	0.83	7E–07	1E–06	0.46	0.885	7E–07	1E–06
9	0.6	0.83	7E–07	1E–06	0.46	0.885	7E–07	1E–06
10	0	1	0	0	0	1	0	0
11	0	0.995	0	0	0	0.975	0	0
12	0	0.995	0	0	0	0.995	0	0

Appendix 2. Parameter values for natural mortality *M* in different months and age groups.

Month	Age						
	0+	1+	2+	3+	4+	5+	6+
1		0.042	0.058	0.075	0.092	0.108	0.125
2		0.042	0.058	0.075	0.092	0.108	0.125
3		0.042	0.058	0.075	0.092	0.108	0.125
4		0.042	0.058	0.075	0.092	0.108	0.125
5		0.042	0.058	0.075	0.092	0.108	0.125
6		0.042	0.058	0.075	0.092	0.108	0.125
7	0.280	0.042	0.058	0.075	0.092	0.108	0.125
8	0.140	0.042	0.058	0.075	0.092	0.108	0.125
9	0.070	0.042	0.058	0.075	0.092	0.108	0.125
10	0.042	0.042	0.058	0.075	0.092	0.108	0.125
11	0.042	0.042	0.058	0.075	0.092	0.108	0.125
12	0.042	0.042	0.058	0.075	0.092	0.108	0.125
Sum	0.936	0.504	0.696	0.9	1.104	1.296	1.5