

Harvesting strategies for Norwegian spring-spawning herring

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The overfishing of an increasing number of fish populations has put focus on the need for development of robust sustainable harvest strategies that can be easily implemented. This requires estimates and modelling of the deterministic and stochastic components of the population dynamics as well as an evaluation of the contribution of different harvest strategies to future population fluctuations. Here we present an example of such an approach, using the collapse of Norwegian spring-spawning herring stock as a case. We demonstrate that the collapse probably was due to overfishing, and that the large influence of the environmental stochasticity could only influence the timing of the collapse. We suggest that a proportional threshold strategy with a threshold around 14 billion individuals (4 200 000 tons), combined with a harvest of 30–40% of the individuals above this threshold will give a sustainable yield with little annual variation. The choice of harvest strategy should also be strongly influenced by the uncertainty in the assessment of stock size. When the population stock is estimated with uncertainty, the proportional threshold strategy give a mean annual yield close to the optimum for known population size.

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In recent years we have experienced large declines of many commercial fish stocks (Pauly et al. 2001, 2002, 2003, Christensen et al. 2003, Myers and Worm 2003) with important ecological consequences (Pauly et al. 1998, 2003, Pauly and Watson 2003, Worm and Myers 2003). In many cases over-harvesting is suspected to be the major driving force for the declines. It is therefore surprising that few studies have quantitatively analysed the contribution of the fishing to the rate of decrease, with Hutchings and Myers (1994), Myers et al. (1997), Jonzén et al. (2001, 2002) and Kaitala et al. (2003) as some notable exceptions. One reason is that such analyses require that effects on the population dynamics of density dependent feed-back mechanisms within the population as well as natural variation in environment are estimated and properly modelled. For instance, even when Canadian populations of the Atlantic cod (*Gadus morhua*) declined to a level where a moratorium was

declared on fishing with profound commercial and social consequences, the importance of over-fishing for the collapse was not generally accepted (Myers et al. 1996, 1997).

Theoretical analyses of the long term success of different harvesting strategies in a stochastic environment have been performed for populations without age structure (Beddington and May 1977, May et al. 1978, Lande et al. 1995, 1997, Engen et al. 1997). The most important conclusions valid for a large class of population dynamics and several optimization criteria are that no harvest should occur when the estimated population size is below a certain level. If the population size is large and exactly known, all individuals above this threshold can be removed. Such a threshold harvest strategy maximizes the mean annual yield (Getz and Haight 1989, Lande et al. 1995, Whittle and Horwood 1995), and gives lower risk of reducing the population sizes to

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(quasi-) extinction (Sæther et al. 1996, Lande et al. 1997, 2001, 2003).

Admittedly, these results are based on models with several simplifying assumptions that should severely reduce their applicability to complex natural systems. However, analyses of more complicated models including both sex and age-structure (Sæther et al. 2001) have shown that these results are extremely useful for deriving general principles for harvesting populations in fluctuating environments.

These analyses have also illustrated some basic problems in determining a sustainable harvest strategy. First, the choice of tactic will depend on the criteria of optimization. Shorter term economic maximization can cause rapid stock-depletion, dependent on the interest rate (Clark 1973, Lande et al. 1994). A threshold harvesting strategy gives a higher mean annual yield and lower risk of (quasi-) extinction, but gives higher annual variability in the yield (often with periods without any harvest) than proportional harvesting (Getz and Haight 1989, Lande et al. 1995, 1997, Quinn and Deriso 1999, Sæther et al. 2001). Second, uncertainties in population estimates will strongly affect the choice of harvest strategy. Engen et al. (1997) demonstrated that under low to moderate environmental stochasticity proportional threshold harvesting, i.e. no harvest below a decreased threshold and only removing a proportion of the excess individuals above the threshold, will be superior to a pure threshold strategy when there are large sampling errors in the population estimates. Similarly, Frederick and Peterman (1995) and Parma (2002) illustrated how uncertainty in population estimates is essential to include when choosing the harvesting strategy. Third, the optimal harvesting strategy depends, even in models without age-structure, on several population parameters such as the specific population growth rate, the form of the density regulation and the carrying capacity as well as the magnitude of the environmental stochasticity (Sæther et al. 1996, Lande et al. 1997, 2001). These parameters have shown to be extremely difficult to estimate precisely in most fish stocks, even when long time series of population series are available (Mertz and Myers 1996, Myers and Mertz 1998, Myers et al. 1999, 2001, MacKenzie et al. 2003).

Our purpose here is to analyse quantitatively the relative contribution of natural fluctuation in the environment and fishing to the collapse of the Norwegian spring-spawning herring (*Clupea harengus*) stock during the middle of the last century. This is a herring stock with an oceanic distribution. It is currently the largest herring stock in the world with a spawning stock of about 7 million tons (ICES 2001), and distributes from the south-western parts of Norway to the Barents Sea and across the Norwegian Sea to the north coast of Iceland. The Norwegian

spring-spawning herring is a stock with huge temporal fluctuations in stock size. Toresen and Østvedt (2000) analysed the stock size fluctuations through the 20th century and found that the stock has undergone long term natural stock size fluctuations throughout the last century. Figure 1 (the solid line) shows the historical fluctuations of the spawning stock size. One billion individuals represent approximately 300 000 tons. The reason for the focus on spawning stock size is that only this stock is harvested, and we will assume that all age groups in this stock are equally vulnerable.

It is central to obtain estimates of the parameters describing expected changes in the dynamics as well as the stochastic part of the population fluctuations due to environmental variability. Such estimates are difficult to obtain in natural populations, mainly because extrapolation often is necessary over a large range of population sizes, e. g. to obtain estimates of the density regulation or the population growth rates at small population sizes (Hilborn and Walters 1992, Aanes et al. 2002). Here we show that analyses of declining populations can provide important information because the range of variation in population size often are much larger than in populations with stationary fluctuations around an equilibrium population size. We will then use these estimates to analyse alternative strategies for a sustainable harvest of this stock. In this way we will quantitative explore the relative contribution of different harvesting strategies as well as natural dynamical characteristics of the population to the fluctuations in the size of this herring stock. As data we use estimated numbers-at-age from a long term (1921–1996) virtual population analysis (VPA) made for Norwegian spring-spawning herring (Toresen and Østvedt 2000).

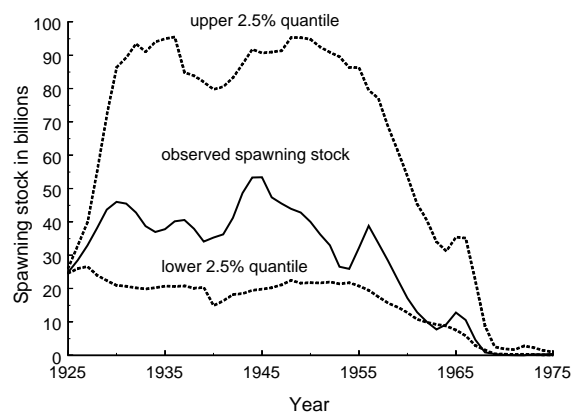


Fig. 1. Estimated spawning stock in billions of individuals for the Norwegian spring-spawning herring with corresponding population prediction intervals (dotted lines) for a population subject to the same proportional harvesting pressure as for the realized harvesting during the same period. The data source was the estimates from the virtual population analysis (Quinn and Deriso 1999) of Toresen and Østvedt (2000).

Harvesting strategies for Norwegian spring-spawning herring have also been discussed by Kaitala et al. (2003). Using a dynamic model they compare three different strategies with respect to risk of extinction as well as mean and variation of the annual yield. The novel contribution in our paper is the focus on modelling of the stochastic influences on population dynamics, including stochasticity in recruitment, survival and age of maturity. Using bootstrap samples of residuals, the stochastic terms will have the same properties as those driving the real population fluctuations. We also take into account the effect sea temperature, modelled as a stochastic process, has on the recruitment. Then we are able to simulate the large fluctuations in abundance that have been observed historically, fluctuations which influence the choice of harvesting strategy. We also use stochastic simulations to analyse the population collapse in the 1960s, and derive a diffusion approximation for the spawning stock process, giving estimates for the stochastic growth rate and the environmental variance.

Population model with no harvesting

Let N_{ij} be the number of individuals of age i in year j so that the number of new recruits in year j is $R_j = N_{0j}$. Stochastic stock-recruitment models can be written on the form $R_{j+1} = g(S_j)\exp(\varepsilon_j)$, where S_j is the spawning stock at year j and ε_j is the environmental noise in the reproduction, which is often assumed to be approximately normally distributed with zero mean and variance σ^2 . Two of the most commonly used models in fisheries biology (Myers 2001) are the Beverton-Holt model given by $g(S) = \alpha S / (1 + \beta S)$, and the Ricker model given by

$$g(S) = \alpha S \exp(-\beta S) \quad (1)$$

Generally, the stochastic fluctuations described by ε_j may partly be determined by physical and biological factors such as sea temperature, the large scale climate patterns such as the North Atlantic Oscillation (NAO) (Ottersen et al. 2001), or the abundance of competing species or predators (Lande et al. 2003). For instance, the recruitment of the spring-spawning herring is known to be strongly influenced by sea temperature (Torensen and Østvedt 2000, Fiksen and Slotte 2002, Sætre et al. 2002). These kind of effects may be modelled by writing ε_j as a linear combination of such covariates and a new stochastic error term δ_j ,

$$\varepsilon_j = \sum \gamma_i z_i + \delta_j,$$

where the γ_i are constants and z_i are the covariates partly explaining the stochastic fluctuations. Similar methods for modeling environmental covariates for recruitment are used by Maunder and Watters (2003).

If the abundances of other species were important for the recruitment one should expect to find temporal autocorrelations in the noise ε_j since the corresponding covariate in that case is not a 'white noise' process but for most species a process with positive autocorrelations. If important biological covariates have been excluded from the model, this can be revealed by investigating the temporal autocorrelations in the residuals after fitting the model. Analyses of fish dynamics have shown that annual fluctuations in sea temperatures (Alheit and Hagen 2001) as well as large scale climate phenomenon as the NAO (Drinkwater et al. 2003) can explain fluctuations in size of northern temperate fish stocks.

We used as covariates in the two models given above the mean annual sea temperature in the "Kola section" of the Barents sea, which stretches from 70°30'N to 72°30'N along the 33°30'E meridian, and the winter NAO index (<http://www.cgd.ucar.edu/cas/NAO/nao.html>). The temperature turned out to have a significant effect ($\hat{\gamma} = 1.17$, 95% confidence interval [0.58, 1.75]) in accordance with the findings of Torensen and Østvedt (2000), whereas NAO had no effect apart from its possible effect on temperature. The temperature explained 17% of the variance of the noise term. The residual variance was estimated to be $\hat{\sigma}_\delta^2 = 1.13$. Furthermore, an analysis of the residuals showed that there was practically no temporal autocorrelations in the residuals, indicating that abundance of single predators or competitors are not crucial for the dynamics of herring. Hence, the noise in reproduction was modelled as

$$\varepsilon_j = \gamma(t_j - \bar{t}) + \delta_j$$

where \bar{t} is the mean temperature in the region through time.

It is important to notice that the purpose of including the temperature when examining different harvesting strategies was not as a predictor of future population sizes. Temperature does not increase the predictive power because it cannot itself be predicted with any accuracy. However, we can analyse the temperature fluctuations by a time series analysis and utilize this when simulating the population process. Actually, stochastic fluctuations in temperature may create temporal autocovariances in the noise process ε_j which can be included by incorporating realistic simulations of the temperature process t_j . Fitting auto-regressive models (Shumway 1988) to the observed temperature during the period 1921–1996 gave a first order process with no significant higher order terms

$$t_j - \bar{t} = \tau(t_{j-1} - \bar{t}) + w_j \quad (2)$$

where the innovations w_j are normally distributed with zero mean and variance $\sigma_w^2 = 0.155$ while $\bar{t} = 3.97$ and $\tau = 0.388$. The coefficient τ represents the temporal autocorrelation at time lag 1, while $\tau^2 = 0.151$ is the correlation at lag 2. The variance in the stationary

distribution of temperature through time, say σ_t^2 , is given by $\sigma_t^2 = \tau^2 \sigma_t^2 + \sigma_w^2$ giving $\sigma_t^2 = 0.183$ and standard deviation $\sigma_t = 0.427$. The autocorrelation at lag one in the noise process is found to be

$$\text{corr}(\varepsilon_{j+1}, \varepsilon_j) = \frac{\tau \gamma^2 \sigma_t^2}{\tau \gamma^2 \sigma_t^2 + \sigma_\delta^2} = 0.079$$

We see from this expression that the inclusion of temperature in the population model generate a temporal autocorrelation in the population process. However, the residuals δ_j , after correcting for temperature, are a white noise process.

We now include age-structure into the model. Let p_i be the proportion of i year old herring surviving from one year to the next, that is $N_{i+1,j+1} = p_i N_{ij}$. The survival is not known exactly, but Toresen and Østvedt (2000) have estimated this, using results from Lea (1930), to be approximately 0.41 for 0–2 years old and 0.86 for individuals of 3 years and older. Accordingly we write $p_i = p'$ for $i = 0, 1, 2$ and $p_i = p$ for $i \geq 3$. It is realistic to assume that the mortality rates are subject to some stochastic fluctuations among years generated by fluctuations in environmental conditions. We modelled this by assuming that p' and p are stochastic variables with expectation $E(p') = 0.41$, $E(p) = 0.86$ and $\text{var}(\ln p') = \text{var}(\ln p)$ which means that all death rates have the same between-year variation. The environment is assumed to have the same effect on the death rate of all individuals so that $p/p' = 2.12$ is constant over years.

The spawning stock in year j is given by

$$S_j = \sum_{i=0} N_{ij} M_{ij}$$

where M_{ij} is the proportion mature herring with age i in year j . The maturity M_{ij} of herring is dependent on the body growth (Toresen 1990, Toresen and Østvedt 2000). When the individuals reach a certain size the maturation process starts. Weak year-classes may reach maturation size as 3-year-olds, while rich year-classes with poor growth may mature as late as 10-year-olds although the “normal” age at maturation for Norwegian spring-spawning herring is 6 years. The age at first maturation therefore varies with growth and year-class strength. The length at first maturation also varies somewhat, depending on the age of the fish.

Let $M = M(i, n_0, h)$ be the proportion mature of i year old herring where the year-class originally has n_0 recruits and the total catch from the year-class up to age i is h . We chose to fit a logistic function (Hastie and Tibshirani 1990)

$$\ln\left(\frac{M}{1-M}\right) = \omega_0 + \omega_1 i + \omega_2 \ln n_0 + \omega_3 h n_0^{-1} + u$$

where u is normally distributed with zero mean and variance σ_u^2 . The data are the proportion mature for year-classes born in 1947–91, 3–6 years old. With a

slight modification, $\hat{M} = 1$ or 0 being replaced by 0.99 and 0.01, respectively, to avoid taking the logarithm of zero, the maximum likelihood estimation gave

$$\hat{\omega}_0 = 2.35, \hat{\omega}_1 = 1.95, \hat{\omega}_2 = -0.62, \hat{\omega}_3 = -2.63 \text{ and } \hat{\sigma}_u^2 = 2.31.$$

This model was used for individuals of age 3–6 years, whereas $M = 0$ for the younger ones and $M = 1$ for those older than 6 years.

The stock-recruitment curve was related to the mean temperatures (Fig. 2). Larger recruitment was recorded in years with high temperatures. When simulating this model, using a normal distribution for the δ_j , the number of recruits occasionally became unrealistically high. This indicates that the corresponding log-normal distribution for variation in the number of recruits has a too heavy tail to be realistic. We therefore chose a robust approach simulating the process using non-parametric resampling with replacement of the observed residuals rather than simulating from the log-normal distribution. Adopting the Ricker model the number of recruits in year $j+1$ was simulated as

$$R_{j+1} = \exp[\ln \hat{\alpha} + \hat{\gamma}(t_j - \bar{t}) + \ln S_j - \hat{\beta} S_j + \delta_j^*]$$

where δ_j^* is the j th resampled residual. Spawning stock S_j and temperature t_j was simulated from the models described above. Figure 3 shows a single simulation of the spawning stock over a 500 year period with no harvesting using the Ricker model. We found this model to give the same fit (same variance in residuals) as the Beverton-Holt model to the data. However, we chose to apply the Ricker model with temperature as covariate for the rest of this analysis.

This stochastic age-structured model is rather complicated with a large number of parameters. The main properties of such models can, however, be expressed by some few parameters. We then considered only the

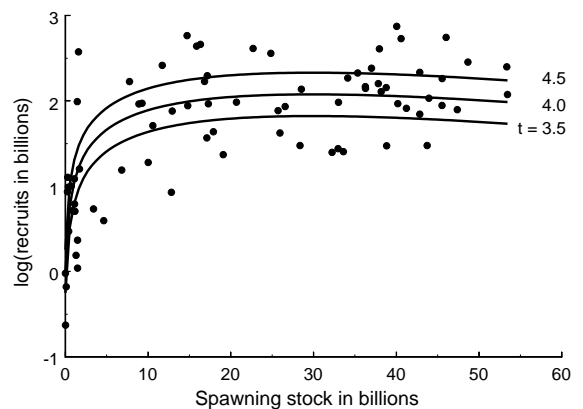


Fig. 2. Number of recruits in relation to the size of spawning stock in billions of individuals of Norwegian spring-spawning herring. The solid lines represent the estimated Ricker model for different mean sea temperatures. The estimated parameters of the Ricker model are $\hat{\alpha} = 10.51$, $\hat{\beta} = 3.35 \times 10^{-8}$ and $\hat{\gamma} = 1.17$.

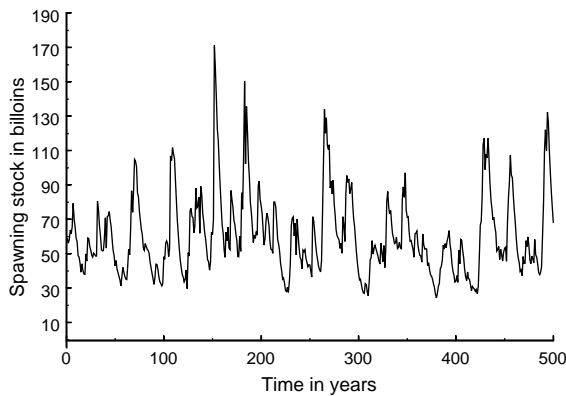


Fig. 3. Simulated fluctuations of the Norwegian spring-spawning herring subject to no harvesting. Recruitment is given by the Ricker model (Eq. 1) with temperature simulated from the first order autoregressive model (Eq. 2) and error terms drawn at random from the observed residuals. The estimated parameters of the Ricker model are $\hat{\alpha} = 10.51$, $\hat{\beta} = 3.35 \times 10^{-8}$ and $\hat{\gamma} = 1.17$.

spawning stock process S_j . An approximation to this process by a process with white noise can be found by fitting parametric models to $E(\Delta \ln S|S)$ and the variance $\text{var}(\Delta \ln S|S)$, and using these functions as the infinitesimal mean and variance in the diffusion approximation (Lande et al. 2003). The mean value as a function of S can be found by stochastic simulations of the full age structured model and evaluating the mean values of $\Delta \ln S$. Fortunately, this function was quite similar (Fig. 4a) to the theta-logistic approximation (Lande et al. 2003)

$$E(\Delta \ln S|S) = r \left(1 - \frac{S^\theta - 1}{K^\theta - 1} \right) \quad (3)$$

where r is the stochastic growth rate at small densities, K is the carrying capacity, and θ is a parameter determining the shape of the density regulation. Using constant adult survival, the fitted curve (Fig. 4a) has parameters $r = 0.264$, $K = 57.3$ billion individuals (17 million tons), and $\theta = 0.573$. Thus, the Ricker model with parameters estimated for the herring corresponds to a type of density regulation just between the logistic ($\theta = 1$) and the Gompertz type ($\theta = 0$). The environmental variance σ_c^2 for the process was determined in a similar way by estimating the variance of $\Delta \ln S$ for different values of S . The environmental variance decreased with increasing population size (Fig. 4b) and increasing between-year variation in mortality rate (Fig. 4c).

Analysis of the population collapse

To analyse the historic collapse of the Norwegian spring-spawning herring (Fig. 1) we simulated the stochastic population model with the same harvesting that actually

was used. It is not obvious how to do this, because repeated simulations of the process gave rather different abundances, and we have no exact knowledge of how the population would have been harvested under other environmental conditions than those that actually were present. Technically we specified the harvesting by first calculating the proportion of the various age-classes that were harvested each year from 1921 to 1968. Then we performed the simulations of the process assuming the same age- and time-dependent harvested proportions. By performing these simulations a large number of times we derived population prediction intervals, given by the dotted lines in Fig. 1, for the size of the spawning

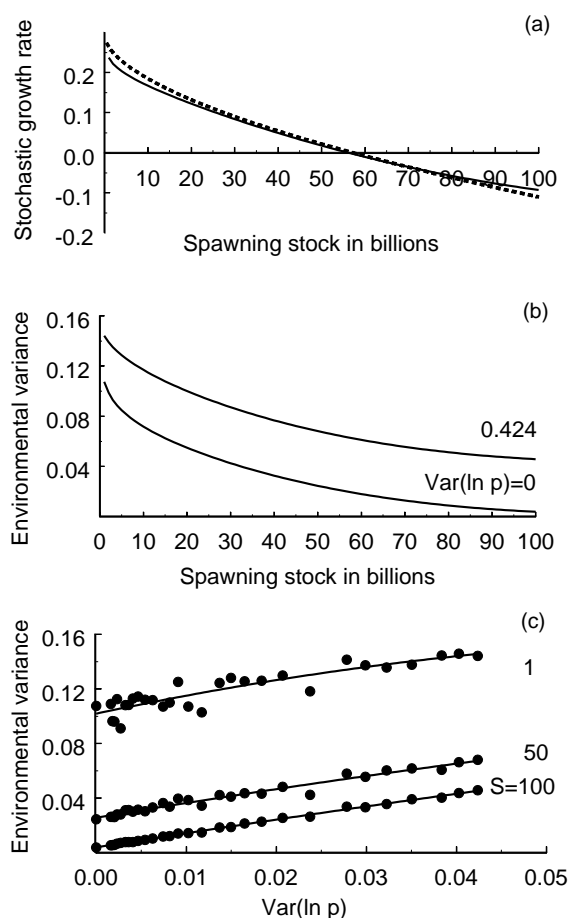


Fig. 4. (a) The stochastic growth rate in relation to the spawning stock size of the Norwegian spring-spawning herring. The solid line assumes no among-year variance in survival, whereas the dashed line shows the fitted theta-logistic model (Eq. 3) with parameters $r = 0.264$, $K = 57.3$ (billions of individuals) and $\theta = 0.573$. The relation for $\text{var}(\ln p) = 0.0424$ is almost undistinguishable from the solid line. (b) The environmental variance σ_c^2 in relation to stock size for different levels of variance in annual survival rate $\text{var}(\ln p)$. (c) The environmental variance σ_c^2 in relation to variance in annual survival rate $\text{var}(\ln p)$ for different spawning stock sizes S in billions of individuals.

stock (Sæther et al. 2000, Engen et al. 2001, Sæther and Engen 2002).

Under the theoretical assumption that harvest ratio is independent of stock size, the analyses showed that the adopted harvesting tactic could not give another result than a collapse of the stock. The collapse could have occurred some few years earlier or later under other environmental conditions than those that occurred, but it could not have been avoided by chance.

Sustainable harvesting strategies

Continuous vs immediate harvesting

All results to be presented assume harvesting immediately after reproduction. If harvesting is performed continuously over some time interval during the year all the results are still applicable. However, the yield and the optimal harvest rate will vary depending on when harvesting occurs in the annual cycle (Jonzén and Lundberg 1999), hence the yield has to be transformed according to the actual interval to give a harvest rate leading to the same spawning stock at the end of the year.

Let the time run from zero at reproduction to one during the year and assume that harvesting is performed at a constant rate during the time interval [a, b]. The continuous harvest rate (harvested amount per time unit) equivalent to immediate harvesting y is then $m = -\ln(1 - y/S)/(b - a)$ and the total harvest during the year relative to the spawning stock turns out to be

$$y[a, b]/S = \frac{p^a \ln(1 - y/S)[1 - (1 - y/S)p^{b-a}]}{\ln(1 - y/S) + (b - a)\ln p}$$

Numerical calculations show that this is very close to the linearization at zero for $0 < y/S < 1$, which leads to the simple linear expression

$$y[a, b] \approx -\frac{p^a - p^b}{(b - a)\ln p} y$$

For continuous sampling through the whole season we find for $p = 0.86$, that $y[0, 1] \approx 0.929y$, whereas harvesting only the second half of the season give $y[0.5, 1] \approx 0.894y$.

Proportional harvesting

Some harvesting strategies can be performed without knowing the population size and even without having an estimate of the spawning stock. This is a useful property that has caught the attraction of fisheries biologists (Hilborn and Walters 1992). In particular this is the case when harvesting a constant amount each year. If the harvest is proportional to the effort the strategy called

proportional harvesting also has this property. This is defined as

$$y(S, b) = bS \quad (4)$$

where y denotes the yield and b is a constant factor that in practice is unknown when a given effort is used. When an estimate of the spawning stock \hat{S} is available one can alternatively choose $y(\hat{S}, b) = b\hat{S}$.

Threshold harvesting

If population size is exactly known, an approach that generally gives larger mean annual yield (Getz and Haight 1989, Lande et al. 1995, 1997, Whittle and Horwood 1995, Quinn and Deriso 1999) is threshold harvesting defined as

$$y(S, c) = \begin{cases} S - c & \text{for } S > c \\ 0 & \text{otherwise} \end{cases} \quad (5)$$

In practice quotas must be determined on the bases of an uncertain population estimate. In this situation Engen et al. (1997) proposed using so called proportional threshold harvesting

$$y(\hat{S}, q, c) = \begin{cases} q(\hat{S} - c) & \text{for } \hat{S} > c \\ 0 & \text{otherwise} \end{cases} \quad (6)$$

The parameter q , which is between zero and one, is the proportion of the individuals in excess of the threshold that can be harvested. Choosing a relatively small value of q , an appropriate choice of c then gives large mean annual yield as well as rather small between years variance in the yield.

Restricted threshold harvesting

There is generally a logical conflict between the demand for large annual yield and small between years variation. However, for populations with large production (large growth rate), strategies that gives rather small variation in yield may also give large annual yield relative to what is optimal (Sæther et al. 2001). One such strategy is to use a maximum quota m

$$y(\hat{S}, m, b) = \begin{cases} 0 & \text{for } \hat{S} < c \\ q(\hat{S} - c) & \text{for } c \leq \hat{S} < c + m/q \\ m & \text{for } \hat{S} \geq c + m/q \end{cases} \quad (7)$$

Provided that m is not chosen too large the yield may be equal to m most of the time giving almost a constant harvest.

Results

We investigated the effect of the strategies defined by Eq. 4–7 for the Norwegian spring-spawning herring

adopting the simulation approach earlier used by Sæther et al. (2001) for analysing harvesting strategies of the moose (*Alces alces*). This method is based on simulating the process with a given harvesting strategy for a large number of years. If each simulation is started at the same place, the mean annual yield is a deterministic function of the parameters used. This is a technique sometimes used in statistical methods based on resampling (Bølviken and Skovlund 1996). Applied to harvesting this makes harvesting statistics, such as the mean or variance of the annual yield, smooth functions of the parameters defining the strategy, and any harvesting statistic can be maximized numerically. The numerical results for the spawning stock size are given as the number of individuals, where one billion individuals is approximately 300 000 tons.

For proportional harvesting strategy, stochastic variation among years in survival had a small effect on the optimal mean annual yield (Fig. 5), ranging from about 6.3 billion for large stochasticity to 7 billion when the survival rates are constant. Similarly, the optimal proportion to harvest ranges from 29% to 33% (Fig. 5), where increased stochasticity imply a somewhat less aggressive harvesting. Optimal choice of threshold harvesting gives however larger mean annual yields than a proportional harvesting strategy (Fig. 5, 6). We again experience, also for threshold harvesting, that the mean annual yield decreases with increasing environmental stochasticity (Fig. 6a), whereas the optimal threshold was about 14 billion regardless the magnitude of stochasticity in the death rates. Although the proportion of years without harvesting increases with the environmental stochasticity and the choice of threshold (Fig. 6b), for moderate values of $\text{var}(\ln p)$ harvesting could occur in more than 90% of the years.

Uncertainty in the estimates of the size of the spawning stock strongly affects the optimal choice of

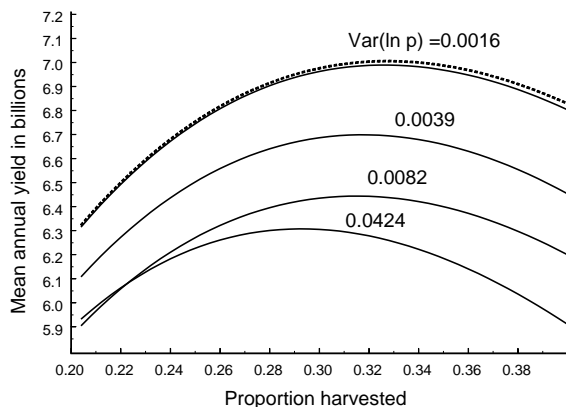


Fig. 5. Mean annual yield of Norwegian spring-spawning herring in billions of individuals in relation to the proportion harvested assuming a proportional harvesting strategy (Eq. 4) for different variances in adult survival rate $\text{var}(\ln p)$. The dotted line corresponds to $\text{var}(\ln p) = 0$.

harvesting strategy (Fig. 7). For small values of CV, the threshold should increase with increasing uncertainty in the population estimates (Fig. 7a). For large environmental stochasticities this increase should continue also for large uncertainties in the population estimates, with a corresponding decrease in the frequency of harvest (Fig. 7c) and in the mean annual yield (Fig. 7d). In contrast, for low to moderate environmental stochasticity, a value of CV is found, above which the threshold should decrease (Fig. 7a), corresponding to a simultaneous reduction in the proportion of excess individuals that can be removed (Fig. 7b). Notice that for $\text{var}(\ln p) = 0.0039$, corresponding to a standard deviation of about 0.06 in the death rates, the mean annual yield was close to 8 billion (Fig. 7d) for coefficients of variation as large as 0.2.

In Fig. 8 we have chosen values for the proportion q and the threshold c that maximize the mean annual yield for a given maximum quota m . (Eq. 7). From Fig. 8a we see that inclusion of a maximum quota did not increase the mean annual yield. The optimal choice of all three parameters turns out to be at $m = \infty$, corresponding to a proportional threshold strategy. The purpose of using a maximum quota is to reduce the variation in the yield among year. However, when the yield equals the max-

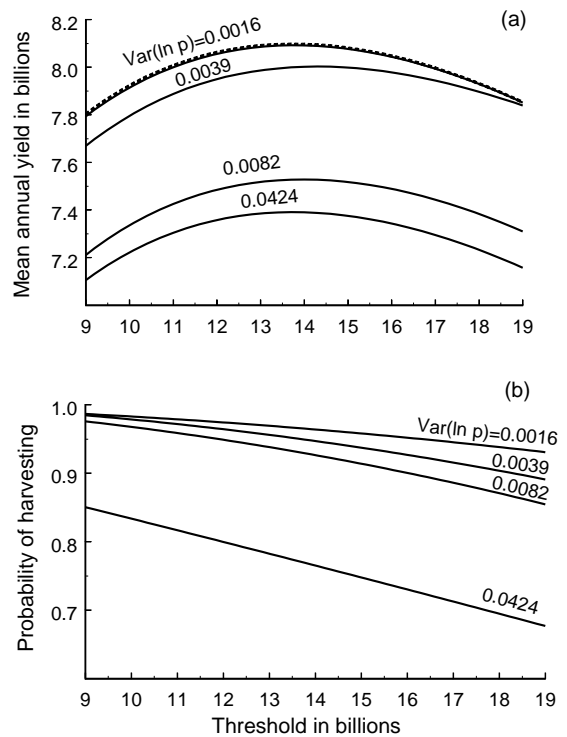


Fig. 6. Mean annual yield for threshold harvesting (a) and relative frequency of years where harvesting can be done (b) in relation to threshold in billions of individuals assuming a threshold harvesting strategy (Eq. 5), based on the assumption of known spawning stock. The dotted line corresponds to $\text{var}(\ln p) = 0$.

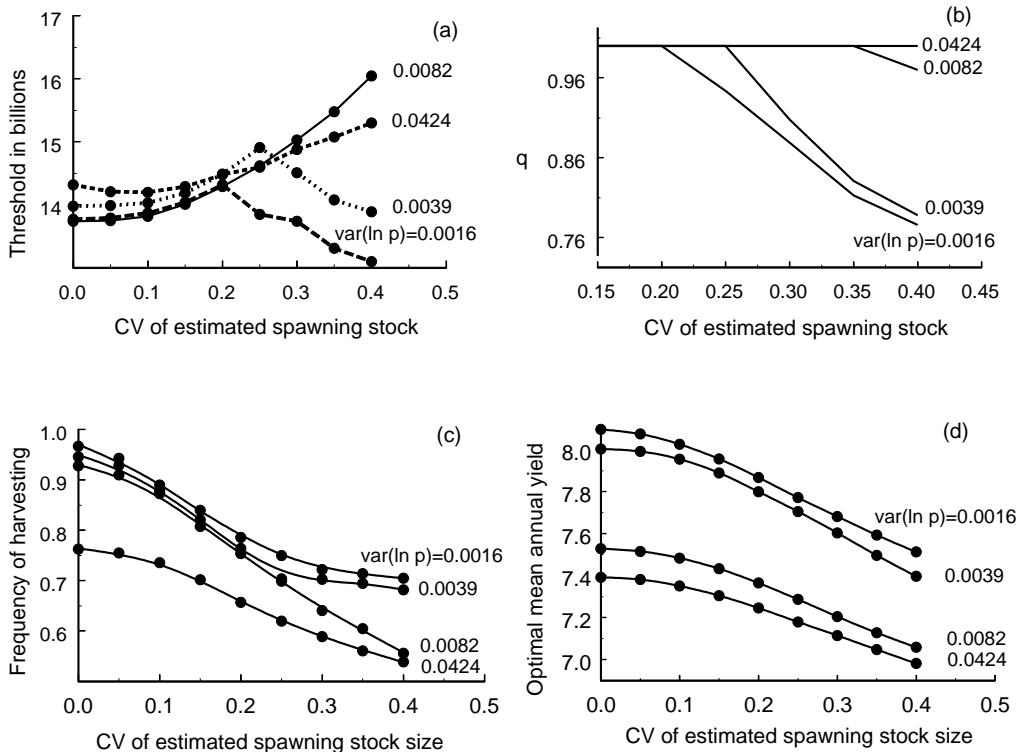


Fig. 7. The threshold in billions (a), the proportion of excess individuals above the threshold that can be removed (b), the proportion of years with harvesting (c), and the mean annual yield (d) in relation to the coefficient of variation (CV) of the estimated spawning stock size of Norwegian spring-spawning herring for different levels of variance in adults survival rate $\text{var}(\ln p)$, assuming a proportional threshold harvesting strategy (Eq. 6).

imum quota for most seasons (Fig. 8b), the corresponding mean annual yield is rather small (Fig. 8a). For instance, to obtain a mean annual yield of 6 billion, the maximum quota must be chosen as large as 8 billion (Fig. 8a). This quota is then only reached at about 50% of the seasons (Fig. 8b), so the yield is far from being constant between years, in contrast to the goal for applying this strategy.

Discussion

This study suggests that the collapse of the Norwegian spring-spawning herring stock was due to overharvesting (Fig. 1), as previously also indicated by Toresen and Østvedt (2000) and Fiksen and Slotte (2002). The large stochastic variation in the population dynamics of this stock (Fig. 3), partly due to variation in sea temperatures (Fig. 2), only affected the timing of the collapse, but could not explain the decrease in stock size. This was due to the large stochastic fluctuations in the growth rate of this population. Our analyses (Fig. 5–8) suggest that proportional threshold harvesting (Eq. 6) represents a superior strategy for a sustainable management of this population.

The Norwegian spring-spawning herring stock has a large stochastic growth rate, $r=0.264$, for small population sizes. This implies that the population generally can recover very rapidly from intense harvesting. However, in many cases r is difficult to estimate because in populations that fluctuate around the carrying capacity (Aanes et al. 2002) it is necessary to interpolate population fluctuations over non-observed values of the population size. In this case, estimating r is facilitated by the population collapse to give population estimates even at small population sizes. This emphasizes the importance of collecting basic population data even when the population levels are below those that permit commercially exploitation of the stocks.

Large interspecific differences among commercially important fish species are found in the rate of recovery after large reductions in stock size, but clupeids seem to recover more rapidly than many other fish species (Hutchings 2000). For the Norwegian spring spawning herring, a large stochastic growth rate was estimated even though the environmental variance was quite large (Fig. 4b), which should decrease the long term growth rate of the population (Lande et al. 2003). For example, if $\sigma_e^2=0.04$ (Fig. 4b, c), the standard deviation in the growth rates between years is $\sigma_e=0.2$. Thus, the

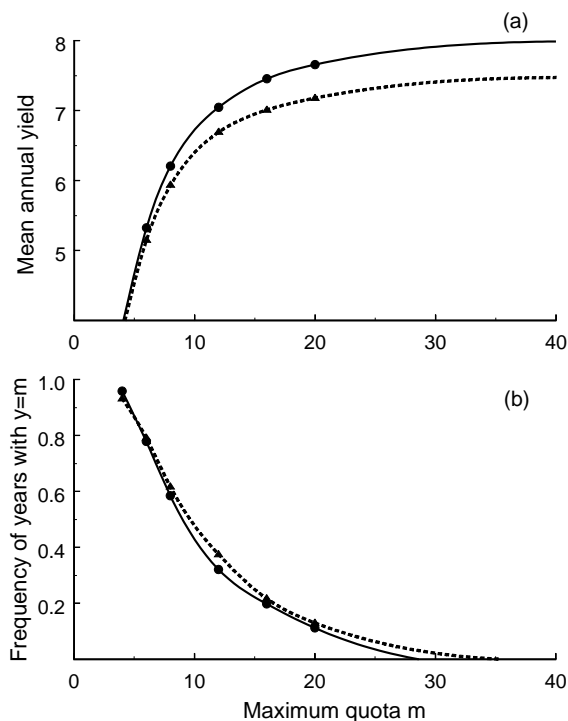


Fig. 8. Mean annual yield (a) and the proportion of years where maximum quota m is harvested (b) of Norwegian spring-spawning herring in relation to maximum quota m . The lower bound for harvesting c and the proportion q is chosen optimally by numerical optimization for each value of m . The solid lines are computed under the assumption of $CV=0.1$, while the dotted lines are for $CV=0.4$. There is no variation in the death rates.

stochastic component of the population fluctuations is large.

In general, large environmental stochasticity often require less aggressive harvesting (Lande et al. 1997, 2001). However, when the stochastic growth rate is large one will sometimes find the opposite conclusion (Sæther et al. 1996, Engen et al. 1997). The reason for this is that large stochastic fluctuations in addition to implying that the population may decrease by chance, also implies that one quite often will experience very large recruitment. If this is to be utilized to increase the mean annual yield, an aggressive harvesting is necessary, provided that the growth rate is large enough to prevent collapse and that an appropriate threshold is used to ensure sustainability. This fact is also demonstrated if we compare our analyses with the work of Kaitala et al. (2003). Using the proportional harvesting strategy they have a maximum mean annual yield of approximately 800 000 tons obtained at a harvest fraction of 0.14. Our analyses gave a nearly three times as high mean annual yield (2.1 million tons) obtained at a harvest fraction of 0.30. The reason is probably that we use a stochastic dynamic model which give years with very large abundances (Fig. 3), giving a higher mean annual yield, and the

possibility of a more aggressive harvesting. It is important to notice that such aggressive harvesting strategies are dependent on precise knowledge of population sizes as well as the basic features of population dynamics. This results in wide prediction intervals (Fig. 1), and hence large uncertainties in the expected time to population recovery (Sæther and Engen 2002).

The recruitment of the spring spawning stock was density dependent (Fig. 2). As is commonly recorded in heavily exploited herring stocks (Myers 2001), the variability was especially large at low densities. As a consequence, environmental variance decreased with the size of the spawning stock (Fig. 4b). This illustrates an important general characteristic of many populations that the impact of environmental fluctuations on the variation in population growth rates is density-dependent. An interaction between density dependence and stochastic variation in survival among the youngest age-classes has also been demonstrated in Norwegian cod populations (Fromentin et al. 2001).

If the only focus is on maximizing the mean annual yield, threshold harvesting will be the optimal strategy for moderate values of the coefficient of variation (CV) in the population estimates (Fig. 7b). However, the frequency of years with harvesting then can be as low as 60%, which will not be acceptable for the fishing industry. As a consequence it is preferable to choose a strategy that is a little more conservative than the optimal strategy for a given CV . Restricted threshold harvesting (Eq. 7) is a strategy where we can achieve an almost constant quota each year, but as the results (Fig. 8) show, the mean annual yield will then be very low. Earlier results for simple population models without age structure implies that proportional threshold harvesting is a good strategy. To reduce the variance in yield between years, Engen et al. (1997) recommended choosing the proportion q less than the one leading to largest mean annual yield. This approach will also to a larger extent be a guarantee against minor population collapses giving many years without harvesting. Our findings together with earlier theoretical results, indicate that a threshold of about 14 billion individuals (4.2 million tons), combined with a harvested proportion of excess individuals from 0.3 to 0.4 can be recommended. This is in agreement with the result of Kaitala et al. (2003) who find the optimal threshold and proportion equal to 3.5 million tons and 0.4, respectively, for the proportional threshold harvesting strategy.

When the proportion is equal to 0.3, the mean annual yield is 5.8 billion individuals (1.7 million tons), and harvesting is allowed in 98% of the years. A more aggressive harvesting strategy, changing the proportion to 0.4, increases the mean annual yield to 6.4 billion individuals (1.9 million tons), but the relative number of years with harvesting decreases to 95%. These results are based on a CV equal to 0.2 in the estimate of the

spawning stock. However, large variation in census error has been recorded among different herring stocks (Kehler et al. 2002). A crucial precondition for developing harvest strategies that in the future will become more sustainable than in the past (Fig. 1) will be to obtain reliable estimates of the uncertainties in the assessment of stock size.

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