Scientific quality is undoubtedly the most important aspect of a contribution to a symposium, but the value of a contribution is also greatly heightened by a vivid and stirring presentation, and the discussion it stimulates. In order to underline the importance of the latter in communicating scientific results, it was decided to give awards for the "best presentations". On the basis of a plenary vote, the awards were presented to H. Gislason (paper) and to M. Tasker, R. Furness, M. Harris, and R. S. Bailey (poster) for their excellent use of audiovisual aids.

The influence of variations in recruitment on multispecies yield predictions in the North Sea

Henrik Gislason


Because of interactions among fish predators and their prey, multispecies predictions of yield are not directly proportional to recruitment as in the single species Y/R model. It is therefore important to examine to what extent changes in recruitment will affect the results. A Monte Carlo simulation technique is used to study the influence of variations in recruitment to the North Sea fish stocks on the yield predictions of the MSFOR model. Recruitment is drawn at random from a lognormal distribution and the average long-term yield is estimated. In an attempt to include interactions not accounted for by the model, a principal components analysis is used to preserve the observed correlation between recruitment to the various stocks in the forecast. The results show that the long-term predictions of yield of the MSFOR model are largely insensitive to random variation in recruitment. They are, however, sensitive to the level around which this variation occurs. Taking the correlation of recruitment into account does not change this conclusion.

Henrik Gislason: Danish Institute for Fisheries and Marine Research, Charlottenlund Castle, DK-2900 Charlottenlund, Denmark.

Introduction

In the classical single-species model of Beverton and Holt (1957) the yield is directly proportional to recruitment. This is not the case when species interactions are taken into account. In the multispecies VPA (MSVPA) and corresponding forecast (MSFOR) used by the Multispecies Working Group (Gislason and Sparre, 1987; Anon., 1988) predation mortality is proportional to the number of predators and inversely proportional to the total amount of food available to the predators. This implies that the total natural mortality will change as the stock sizes of predators and prey change. The change in natural mortality with stock size makes long- and medium-term predictions from the MSFOR model dependent on recruitment. As shown in Anon. (1987) the long-term yield is highly sensitive to changes in recruitment. Long-term yield was in fact found to be more sensitive to recruitment than to predator rations, to residual mortality, and to the amount of other food.

This paper is an attempt to study how the level of recruitment and fluctuations around this level affect yield and biomass predictions from the MSFOR model. The literature on fisheries biology is full of attempts to explain variation in recruitment by the size of the spawning stock, biological interaction, and environmental influences. Instead of constructing a recruitment model based on postulated causal links between recruitment and spawning-stock size, abiotic factors, and biological interactions, recruitment is here assumed to be constant, to be randomly fluctuating around a constant level, or to be fluctuating around a constant level in a way which takes interspecific correlations into account.

The MSVPA and MSFOR models

The MSVPA is used by the ICES Multispecies Assessment Working Group to provide estimates of the stock size, predation mortality, and fishing mortality of commercially exploited fish stocks in the North Sea (Pope, 1991).

The MSVPA model is an extension of the single species VPA (Gulland, 1965). The only difference is that the natural mortality is split into a mortality, M2, due to predation and a constant residual mortality, M1, due to all other natural causes. The predation mortality, M2, is accounted for by adding one more equation to the usual VPA equations:

\[ C_{i,t} = F_{i,t} \times N_{i,t+1} \times (e^{Z_{i,t}} - 1)/Z_{i,t} \]

\[ N_{i,t} = N_{i,t+1} \times e^{Z_{i,t}} \]

\[ M2_{i,t} = \sum_p S_{p,i} \times R_p \times \bar{N}_{p,i} / (\bar{N}_{i,t+1} \times W_i) \]
where the summation runs over all predator species age groups, \( p \), and
\[
\bar{N}_{i,t} = N_{i,t+1}(e^{Z_{i,t}} - 1)/Z_{i,t}
\]
\[
Z_{i,t} = F_{i,t} + M_{1i} + M_{2i,t}
\]

where: \( N_{i,t} \) = stock size of prey species age group \( i \) at time \( t \); \( C_{i,t} \) = catch of \( i \) during the time interval from \( t \) to \( t + 1 \); \( Z_{i,t} \) = total mortality; \( F_{i,t} \) = fishing mortality; \( S_{p,i} \) = fraction of the food of predator species age group \( p \) which constitutes prey species age group \( i \); \( R_p \) = total food intake (per individual) of \( p \) in time interval from \( t \) to \( t + 1 \); \( \bar{N}_{i,t} \) = average stock size of \( i \) in time interval from \( t \) to \( t + 1 \); and \( W_i \) = body weight of species age group \( i \).

If estimates of food intake and food composition are available for each time interval these equations can be solved without having to make any more assumptions than required for solving the single species VPA. However, as this is seldom the case additional assumptions are required. The first of these is that the food intake, \( R_p \), is constant over time, the second is that the food composition can be described as a function of the available prey by an equation from Andersen and Ursin (1977):
\[
S_{p,i} = \frac{G_{p,i} \times \bar{N}_{i,t} \times W_i}{\sum_j G_{p,j} \times \bar{N}_{j,t} \times W_j + G_{p,0} \times B_o}
\]

where the summation runs over all prey species age groups, \( G_{p,i} \) is a constant which reflects the suitability of a particular prey species age group, \( i \), to predation by a particular predator species age group, \( p \), and \( B_o \) is the biomass of "other food", i.e. food consisting of species not included directly in the model. Assuming suitability and other food to be constant over time makes it possible to estimate the suitabilities, \( G_{p,i} \), within the model provided food composition data is available for one or several time intervals (Gislason and Sparre, 1987).

Given catch in numbers at age, food composition, food intake, weight-at-age, and fishing mortality for the oldest age group in each cohort the equations are solved simultaneously for all predator and prey stocks within a given time interval. As in the single species VPA the estimated stock numbers are then used as input to the calculations for the preceding time interval. For each cohort the calculations are only carried back to 1 July for the 0-group; therefore MSVPA does not account for predation on eggs, larvae, and small juveniles.

The output from the MSVPA consists of estimates of stock sizes, fishing mortalities, predation mortalities, and suitability coefficients.

The MSFOR model is the predictive counterpart of the MSVPA and is based on the same set of equations. The predation parameters and terminal stock sizes are transferred from the MSVPA, but as the traditional single species forecast, the MSFOR requires estimates of the future recruitment and fishing mortalities.

The MSFOR program and database used in this paper is the same as was used at the 1988 meeting of the ICES Multispecies Assessment Working Group (Anon., 1988). The database includes cod, whiting, saithe, mackerel, and haddock as predators and cod, whiting, haddock, herring, sprat, Norway pout, and sandeel as prey. In the predictions the status quo level of fishing mortality is defined as the average (1980–1985) fishing mortality at age estimated from the MSVPA and recruitment as the number of 0-group fish at 1 July from the MSVPA for the period 1974 to 1985 (Table 1).

Changing the level of recruitment

The MSFOR model was run until an equilibrium situation was obtained in which the change in stock size in numbers at age was less than 0.01% over a 9-year period. This usually required predicting approximately 50 years ahead. The predictions were repeated with recruitment changed for one stock at a time from 20% to 200% of the average of the period 1974 to 1985. At each level of recruitment the Y/R was calculated in the equilibrium situation. For each stock the calculations were repeated for three values of average fishing mortality, a 50% reduction, status quo, and a 50% increase. Figure 1 shows Y/R versus recruitment for cod, whiting, haddock, herring, sprat, Norway pout, and sandeel. No results are presented for saithe and mackerel, which are not predated upon and therefore behave in accordance with the traditional single-species model in which Y/R is independent of recruitment.

As seen in Figure 1, Y/R changes in a non-linear way as a function of recruitment. As recruitment increases Y/R declines for cod and whiting and increases for haddock, herring, sprat, Norway pout, and sandeel. The decline for cod and whiting is an effect of cannibalism. When recruitment increases the total stock size will increase. This leads to an increase in the mortality due to cannibalism, to a decrease in the survival of the recruits, and to a subsequent reduction in Y/R. The increase in the Y/R of the prey species is a result of predator satiation. As prey biomass increases the predators will eat a decreasing proportion of the prey biomass, natural mortality will decrease, and Y/R will increase.

With the exception of cod, the Y/R changes in the same way irrespective of the level of fishing mortality. The curves are close to parallel. This signifies that the shape of the Y/R curve in this range of fishing mortality is unaffected by recruitment to the stock itself. For cod, however, the three curves intersect. At the present level of recruitment a small gain in yield is to be expected by increasing the fishing mortality by 50%, but if the level...
of recruitment is reduced to 20% of the present the conclusion is the opposite. The highest Y/R is now obtained when the fishing mortality is reduced. The explanation for this somewhat surprising result is that cannibalism is insignificant when the stock size of cod is low (low recruitment), but increases in significance as the stock size increases (high recruitment). If cannibalism is of minor importance the yield will increase as fishing mortality is reduced and cod is allowed to reach a larger size before it is caught. If cannibalism is important the highest yield is obtained by increasing the fishing mortality in order to reduce the adult stock and protect the juveniles. In terms of the usual Y/R curve this means that the shape of the curve will change and F_{MSY} will shift from the right to the left of the present level.

Remembering that the outcome of Y/R calculations reflects the balance between natural mortality, fishing mortality, and rate of growth it is not surprising that the three curves do not intersect for whiting even though the rate of growth is much lower. For this reason and as shown by Figure 2 the yield curve of whiting does not exhibit a maximum as it does for cod. Decreasing mortality due to cannibalism by reducing recruitment to 20% of the present level does not reduce the total natural mortality sufficiently to produce a Y/R curve with a maximum to the left of the present level of fishing mortality. In terms of Figure 1 this means that the three curves do not intersect when recruitment is reduced.

In the present formulation of the food selection model, i.e. with a constant amount of other food, reducing recruitment for all species at the same time will lower the level of predation mortality. When the stock sizes of prey are low predation mortality will be roughly proportional to the stock size of the predators. As the predator stocks are reduced the Y/R curves will change towards the single species Y/R curves with a constant natural mortality equal to the constant other mortality, M1. This means that the single species Y/R curve will function as an upper limit to the multispecies predictions.
The effect of random fluctuations in recruitment

As shown in Figure 1, yield per recruit is a non-linear function of recruitment. Year-to-year variations in recruitment will thus produce non-linear responses which, if important, may change the average long-term predictions, e.g. by reducing large year classes less than small.

It is generally believed that recruitment fluctuations are lognormally distributed (Hennemuth et al., 1980). Recruitment was therefore modelled as a stochastic process by random selection from a lognormal distribution with a mean and variance equal to the arithmetic mean and variance of the historic recruitment estimates from the MSVPA (0-group, 1 July) in the period 1974–1985 (Table 1).

Table 1. Estimates of recruitment (0-group, 1 July) from MSVPA (in millions). Data from Anon. (1988).

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Cod</td>
<td>1479</td>
<td>693</td>
<td>2449</td>
<td>1306</td>
<td>1330</td>
<td>2470</td>
<td>988</td>
<td>1534</td>
<td>732</td>
<td>1313</td>
<td>267</td>
<td>1180</td>
</tr>
<tr>
<td>Whiting</td>
<td>17388</td>
<td>16124</td>
<td>15595</td>
<td>17541</td>
<td>18589</td>
<td>19802</td>
<td>14049</td>
<td>8624</td>
<td>7213</td>
<td>7913</td>
<td>7579</td>
<td>11851</td>
</tr>
<tr>
<td>Saithe</td>
<td>210</td>
<td>133</td>
<td>144</td>
<td>130</td>
<td>296</td>
<td>190</td>
<td>235</td>
<td>386</td>
<td>571</td>
<td>528</td>
<td>175</td>
<td>246</td>
</tr>
<tr>
<td>Mackerel</td>
<td>590</td>
<td>316</td>
<td>190</td>
<td>34</td>
<td>113</td>
<td>160</td>
<td>238</td>
<td>254</td>
<td>30</td>
<td>8</td>
<td>550</td>
<td>118</td>
</tr>
<tr>
<td>Haddock</td>
<td>82749</td>
<td>10148</td>
<td>12935</td>
<td>24893</td>
<td>28548</td>
<td>44215</td>
<td>20040</td>
<td>30690</td>
<td>732</td>
<td>17876</td>
<td>46555</td>
<td>25723</td>
</tr>
<tr>
<td>Herring</td>
<td>16659</td>
<td>3355</td>
<td>3097</td>
<td>4461</td>
<td>4681</td>
<td>12824</td>
<td>18711</td>
<td>30423</td>
<td>40913</td>
<td>34054</td>
<td>34776</td>
<td>3424</td>
</tr>
<tr>
<td>Sprat</td>
<td>38673</td>
<td>530123</td>
<td>29387</td>
<td>276389</td>
<td>464121</td>
<td>197196</td>
<td>124377</td>
<td>60983</td>
<td>31599</td>
<td>104758</td>
<td>223011</td>
<td>20659</td>
</tr>
<tr>
<td>Norway pout</td>
<td>336486</td>
<td>466621</td>
<td>343641</td>
<td>178131</td>
<td>231383</td>
<td>241322</td>
<td>124003</td>
<td>376187</td>
<td>277541</td>
<td>220317</td>
<td>222510</td>
<td>278608</td>
</tr>
<tr>
<td>Sandeel</td>
<td>1376701</td>
<td>842078</td>
<td>825973</td>
<td>823558</td>
<td>596900</td>
<td>674895</td>
<td>345929</td>
<td>832013</td>
<td>252674</td>
<td>643445</td>
<td>199935</td>
<td>885688</td>
</tr>
</tbody>
</table>
The recruitment distributions were generated from lognormal distributions in which the parameters $\mu$ and $\sigma^2$ (the mean and variance of the normally distributed log recruitment) were estimated by the method of moments:

$$\mu = \log \bar{R} - \frac{1}{2} \log \left( \frac{V(R)}{R^2} + 1 \right)$$
$$\sigma^2 = \log \left( \frac{V(R)}{R^2} + 1 \right)$$

where $\bar{R}$ is the arithmetic mean and $V(R)$ the variance of the recruitment series (Aitchison and Brown, 1957). The method of moments provides unbiased estimates of $\mu$ and $\sigma^2$ which are less efficient than the maximum likelihood estimators. They were nevertheless preferred because they generate simulated values with an arithmetic mean and variance identical to the observations and hence render the stochastic and constant recruitment runs directly comparable.

The MSFOR was then run for 1000 years in each of which a new set of recruitment estimates was drawn at random. At the end of the 1000 year period the average and standard deviation of the catch and spawning-stock biomass (SSB) was estimated.

The results are compared with those from a constant recruitment run in Figure 2, which shows the yield curves in the constant recruitment case and the average $\pm$ the standard deviation in the stochastic case. In general, only insignificant differences appear between the averages in the constant and stochastic case. For prey species which are important as food items and show large fluctuations in recruitment, such as haddock, Norway pout, and sandeel, a slight increase in average yield is found, but the general shape of the yield curves remains unchanged. The slight increase in average yield may be explained as a result of predator satiation. In the MSFOR (and MSVPA) the predators have a fixed total ration which sets an upper limit on the amount predated. When a large year class occurs the predation mortality will be reduced and $Y/R$ will increase.

**Including interspecific correlations**

The above predictions were based on preserving the mean and the variance of the observed recruitment in the period from 1974 to 1985. At best this is an oversimplified representation of the recruitment process. Be-
cause of interactions among the juveniles and common responses to environmental changes it is likely that recruitment to one stock will be related to recruitment to other stocks. A high recruitment to one stock may thus be more likely if recruitment to another stock is low, etc. This interdependence could change the results. It may therefore be of interest to make predictions in which these between species links are preserved.

The correlation matrix of the logged recruitment estimates from the MSVPA is given in Table 2. Out of 32 correlations seven are significant, i.e. larger than 0.576 (p = 0.05 on 10 d.f.). Of these, three are significant at the p = 0.01 level. Recruitments of herring and sprat, herring and whiting, and sprat and saithe are negatively correlated, while cod and sandeel, whiting and sprat, whiting and saithe, and herring and saithe are positively correlated.

The correlations were preserved in the predictions by Principal Components Analysis (PCA), which is a technique used for similar problems in models of weather and climate (Preisendorfer, 1988).

A PCA may be considered as a transformation of coordinates. In this case a PCA transforms the nine time series of logged recruitment data into a new coordinate system in which they are represented by nine new uncorrelated time series (the principal components scores). The idea is then to draw values at random from the uncorrelated principal components scores and to back-transform them to correlated estimates of recruitment.

With y years and n species the transformation may be written

\[ \text{PCS} = \mathbf{A} \mathbf{LR} \quad \text{or} \quad \mathbf{LR} = \mathbf{A}^T \text{PCS} \]

where \( \mathbf{LR} \) is a \((y \times n)\) matrix of log recruitment values, \( \mathbf{A} \) is the \((n \times n)\) matrix of eigenvectors, PCS is a \((y \times n)\) matrix of uncorrelated principal components scores, and \( \mathbf{T} \) denotes matrix transpose.

The transformation matrix, \( \mathbf{A} \), is used to go from one set of coordinates to the other. Given a vector of principal component scores pertaining to a particular year the corresponding log recruitment values can be found by multiplication with \( \mathbf{A}^T \). If (as assumed) the log recruitment values are normally distributed, the corresponding principal component scores will also be normally distributed.
The results of a PCA of the nine logged time series of recruitment from the MSVPA are shown in Table 2. The first principal component explains 48% of the total variance, the second an additional 26%. Only the first of these series of principal component scores (the one associated with the highest variance) shows a significant decline with time, the others remain stable (Fig. 3).

In the simple stochastic recruitment case \( \mu \) and \( \sigma^2 \) were used to create the distributions. This complicates our analysis somewhat. We may, however, use \( A \) to transform the original vectors \( \mu \) and \( \sigma^2 \) into the new system of coordinates. Thus:

\[
\mu' = A\mu \quad \text{and} \quad \sigma'^2 = B\sigma^2
\]

where \( B \) is a \((n \times n)\) matrix containing the elements of \( A \) squared. The two formulas are only approximative because the covariances have been ignored in estimating \( \sigma'^2 \) and because \( A \) has been estimated directly from the log recruitment series and not from the variances, \( \sigma^2 \), and covariances of the normal distributions of log recruitment. In practice, however, the use of \( \mu' \) and \( \sigma'^2 \) produced only minor differences between the original arithmetic mean and variance and the simulated.

The MSFOR was then used to predict 1000 years ahead. In each of the years the PCA scores were drawn from normal distributions with parameters \((\mu',\sigma'^2)\). The scores were then transformed to estimates of log recruitment by \( A^T \) and backtransformed to recruitment values. The results in terms of average yield are shown in Figure 4.

As in the simple stochastic case no major difference is seen between the constant recruitment runs and the simulations.
Discussion

The results show that yield predictions from the MSFOR for the North Sea depend on the level of recruitment in a non-linear way. This dependency is, however, mainly important in a management context if the shape of the Y/R curve changes. With cod as an exception this change does not seem to be of importance if the level of recruitment remains between 20 and 200% of the present level. This signifies that fishing strategies can be defined which will be robust to changes in recruitment provided these changes take place within reasonable limits.

As shown by the change in F_MSY of cod, gains and losses of a change in fishing strategy should in practice be evaluated for different levels of recruitment to ensure that gains are not converted to losses if the level of recruitment changes. This evaluation should not (as in this paper) only consider the effect of changing the level of recruitment for a particular species to the yield of the species itself, but should also consider interactions of a higher order, e.g. how changes in the recruitment of whiting affect the Y/R curve of cod at various levels of cod recruitment.

Adding stochastic noise to the recruitment does not significantly change the average long-term yield predicted by the MSFOR, except for species which show large year-to-year fluctuations in recruitment and/or are important prey. For all species the shape of the yield curve remains the same as in the constant recruitment case.

Throughout this exercise it has been assumed (as in the single species Y/R model) that the size of the spawning stock does not influence subsequent recruitment. Several models have been proposed in order to link recruitment to the size of the spawning stock, but usually these models have not explained much of the observed variation. Daan et al. (1989) concluded that no correlation could be observed between spawning-stock size and subsequent recruitment for the North Sea stocks, with herring and mackerel as two possible exceptions. As long as the predictions do not fall outside the historic range of spawning-stock biomasses, the stock recruitment relationship may thus be ignored.

Environmental changes and biological interactions have also been used to explain both short- and long-term variations in recruitment. Taking the covariance of the recruitment into account by the use of a principal components analysis is an attempt to include shared responses to these variables in the predictions. The observed correlation is thought to be due to shared interactions between older fish and the 0-groups prior to 1 July, interactions among the 0-groups themselves, shared responses to environmental factors, and of course to chance. Preserving the correlation in the predictions is based on the assumption that these interactions will not change over time, i.e. that the effects will operate in the same way in the future as in the past.

Whether this is a reasonable assumption remains to be seen. Shepherd et al. (1984) found that the first principal component of recruitment data for North Sea cod, haddock, saithe, sole, plaice, whiting, and herring correlated significantly with the average March temperature in the central North Sea. Thompson and Hilden (1987) extended their analysis by including more recent data points and found that the correlation became weaker. From 1962 to 1973 temperature seems to have been important, but later on some other factor or combination of factors appears to have taken over. It is
unlikely that there is a simple explanation for the decrease in the first principal component over time in this exercise.

Preserving the correlations in the predictions does not seem to change the shape of the yield curve. This conclusion, however, is based on an approximative formula and should be rechecked when an exact formula which relates the covariances of the recruitment and logged recruitment series has been found.

It has also been observed that recruitment data may show a significant amount of autocorrelation (Cook and Armstrong, 1984; Rothschild, 1986). Preserving the autocorrelations in the predictions would be interesting. Even though the total variance of the simulated recruitment data would be the same, a positive correlation between recruitment in year y and year y - 1 would increase the amplitude of the fluctuations in stock size and yield, due to the increased probability of having several large or poor year classes in succession. Most likely this would increase the effects of the non-linear description of predation mortality, leading to a larger discrepancy between the predicted yield in the constant and stochastic recruitment case. A negative autocorrelation would work the other way around, decrease the amplitude and the importance of non-linear interactions, and therefore lead to an even greater correspondence between the constant and stochastic case.

Thus it is difficult to say whether including autocorrelations would change the conclusion that variations in recruitment are of minor importance. It would depend very much on the magnitude of the estimated autocorrelations and on whether they were positive or negative.

With only 12 years of data at hand it seems premature to fit a time-series model including both correlations and autocorrelations. With such a short series, estimates of covariance and autocovariance would be highly correlated, and little confidence could be given to the actual outcome. However, given a longer time series of MSVPA recruitment estimates, such an approach should certainly be pursued.
Figure 4. Yield predictions for constant (curve) and stochastic recruitment. □: Average yield plus minus standard deviation in stochastic simulation in which the between-species correlation has been preserved. (a) Cod, (b) haddock, (c) whiting, (d) herring, (e) sprat, (f) Norway pout, (g) sandeel.

References