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The Propagation of Cod Gadus morhua L.

THE MANAGEMENT OF COD STOCKS WITH SPECIAL REFERENCE TO GROWTH AND RECRUITMENT OVERFISHING AND THE QUESTION WHETHER ARTIFICIAL PROPAGATION CAN HELP TO SOLVE MANAGEMENT PROBLEMS
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ABSTRACT

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The terms growth overfishing and recruitment overfishing are defined. The exploitation and management of two of the major cod stocks in the North-East Atlantic, North-East Arctic cod and North sea cod, are briefly reviewed with special reference to the two forms of overfishing. Possible density-dependent factors limiting stock size and yield are discussed, and it is suggested that density-dependent growth and especially cannibalism of young by adults might be important regulatory mechanisms in cod stocks.

Potential effects on yield of artificial propagation are then considered, making different assumptions about the form of the yield curve of the natural population. It is concluded that veral factors should be further studied before starting laiye scale releases of artificially produced recruits on a regular basis.

## INTRODUCTION

When discussing management of cod stocks and potential effects on yield from releasing artificially produced re-
cruits, it is important to know the factors which limit the yield from a natural population. These could be grouped as follows:
(i) Limitations in yield arising from the way the fishery is conducted and its overall intensity.
(ii) Biological factors limiting the maximum sustainable yield or surplus production.

The simplest case to deal with is the situation where the yield is limited by the fishing effort. The stock is underexploited, and an increase in both short and long term yield could be achieved by simply increasing the effort or catching capacity of the fleet.

A more complicated case to handle from a fishery management point of view is the situation where the yield has been reduced below the maximum sustainable one by overfishing. It is more complicated since increase in yield can only be achieved by putting constraints on fishing activity. This increase will only be achieved some time after a period with decreased yield, and unsufficient knowledge of the biological factors limiting the surplus production makes it difficult to estimate with any precision the size of the long term gain.

GROWTH AND RECRUITMENT OVERFISHING

Definitions

In line with Cushing (1972) and Ulltang (1975) two forms of overfishing will be distinguished - growth overfishing and recruitment overfishing.

A fish stock is growth overfished if yield per recruit ( $Y / R$ ) could be increased by decreasing fishing mortality on all or some parts of the fishable stock.

A fish stock is recruitment overfished if overall recruitment level and thereby yield have decreased due to small spawning size as a result of too heavy fishing.

Yield per recruit is dependent on both the overall exploitation rate and the exploitation pattern (exploitation pattern $=$ distribution of fishing mortalities by age). Growth overfishing may result from a bad exploitation pattern (age of first capture too low) or too high an overall fishing effort, or a combination of these factors (Fig. 1). The term growth overfishing is used because too many fish are caught before their growth potential has been utilized.


Fig. 1. Yield per recruit curves. Weight at age as for North-East Arctic cod. M=0.2. Knife-edged recruitment to the fishery at 3 years (a) and 5 years (b).

Recruitment overfishing may very rapidly cause total collapse in stock if management actions are not taken immediately since a reduced recruitment will cause a further decline in spawning stock which in turn will further reduce the recruitment. In practice it is very difficult to detect
when a stock becomes subject to recruitment overfishing because of the large variations in year class strength which are independent of spawning stock.

Case studies

For both illustrating the general problems in cod stock management and the magnitudes of potential gains by changing the exploitation rate and pattern, the exploitation and management of two of the major cod stocks in North-East Atlantic, the North-East Arctic cod and the North sea cod, will be briefly reviewed.

## North-East Arctic cod

Total fishing effort has, since the mid 1950's, been above the level giving maximum $Y / R$, and in addition an unfavourable fishing pattern has contributed to reducing the yield. The cod recruit to the fishery as 3 years old and spawn for the first time at an age of about 8 years old. In particular exploitation of $3-4$ years old fish reduces $Y / R$ (Fig. 1). It is therefore clear that the stock has been in a strongly growth-overfished state for a long time.

Based on $Y / R$ curves for different trawl mesh sizes given in Anon. (1980), a gain in $Y / R$ of about $35 \%$ could be achieved by a) increasing the trawl mesh size from 120 mm to 150 mm and b) decreasing fishing mortality to the level giving maximum $Y / R$ for the exploitation pattern corresponding to the new mesh size.

Although ICES has repeatedly recommended increase in mesh size and decrease in fishing effort, little has been achieved due to both unability by the management bodies to agree on proper regulatory measures and lack of proper enforcement of the measures which could be agreed. The potential increase in $Y / R$ referred to above corresponds to an average increase in annual yield of about 250000 tonnes, assuming a recruitment of $700 \times 10^{6} 3$ years old fish which is about the average

VPA-estimated level during the period 1960-1975 (Anon., 1983a).

The question whether, this cod stock has also been recruit-ment-overfished is difficult to answer, because of both the large annual variations in recruitment and problems with calculating the size of the spawning stock backwards in time (ICES, 1983).

North Sea cod

From yield per recruit studies (Anon., 1982) and assessments of exploitation rate and pattern both during the most recent years (Anon., 1982) and during earlier periods (Daan, 1978), it is clear that this stock has been heavily growthoverfished at least since the 1920's.

It has repeatedly been recommended by ICES that the trawl mesh size should be increased from 75 mm to at least 90 mm and to decrease the fishing effort. The mesh size has been increased to 90 mm in parts of the North Sea (Norwegian EEZ), although it is not clear to the author what the enforced minimum mesh size is at present in the rest of the North Sea. From $Y / R$ considerations, even 90 mm is a much too low a mesh size in the cod fishery. Concerning fishing effort, no decrease has been observed.

The $Y / R$ studies given in Anon. (1982) indicate that an increase in mesh size from 75 to 140 mm (which still would be below the optimum), and a decrease in fishing effort to the level giving maximum $Y / R$ for the new mesh size, would increase $Y / R$ by about $100 \%$. Assuming an average recruitment of $236 \times 10^{6} 1$ year old fish (Anon., 1982) this would correspond to an increase in annual catch of about 250000 tonnes.

By increasing the mesh size to only 90 mm but decreasing fishing mortality to $F_{\text {max }}$ for that mesh size, the annual yield would increase by $70 \%$ or 170.000 tonnes.

For this stock, there are no signs at all of recruitment overfishing. A plot of recruitment against spawning stock size for the period 1963-1980, based on figures given in
(Anon., 1983b), show no correlation. If the three outstanding year classes 1969, 1970 and 1979, which fall outside the main cluster of points, are disregarded, there is even an indication of an inverse relationship between spawning stock and recruitment.

Possible density dependent factors limiting yield

The calculated gains from reduced growth overfishing given above are based upon certain basic assumptions which need some careful examination before judging whether the calculations are realistic.

In traditional $Y / R$ calculations it is assumed that growth and natural mortality are independent of stock size, and when multiplying $Y / R$ by an average recruitment figure to get average annual yield it is also assumed that recruitment is independent of stock size.

When comparing yield under different exploitation strategies, it is of course only necessary to assume that the basic parameters are independent of stock size within the range covered by the calculations. However, this range can be very wide. For example, when going from the present exploitation rate to $\mathrm{F}_{\text {max }}$ for North Sea cod, equilibrium spawning stock is, according to the $Y / R$ model, increased from about 200000 tonnes to 1500000 tonnes. The question is then whether the stock would ever reach such a level, or would density-dependent changes occur in one or more of the basic parameters and thereby put a ceiling on stock size at a lower level? Unfortunately, it is not possible to investigate this from past data since very little is known about stock size and other parameters during periods before the hard exploitation started. This would probably be the case for most of the exploited cod stocks.

It is, however, suggested that two factors may limit the yield of a cod population below that predicted by the yield per recruit model when going from a growth overfishing situation to a more optimum exploitation strategy (according
to that model). Firstly, limited food supply may reduce the growth rate when stock is increased to a much higher level. Secondly, and perhaps more important, heavy predation from the large cod on juvenile cod may reduce the recruitment to the fishable stock when the stock of larger cod is increased. Such heavy cannibalism have been demonstrated for North Sea cod by Daan (1975).

If one or both of these factors are present, Y/R calculations would overestimate the gains in yield which could be achieved by decreasing the exploitation rate or improving the exploitation pattern.

POTENTIAL EFFECTS OF ARTIFICIAL PROPAGATION OF COD

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In this section the potential effect on yield from a cod stock, if artificially produced recruits are released into the population, are considered. It is assumed that the artificially produced recruits will mix with the natural population and have the same growth and mortality rates as cod of the same age in the natural population. Also in all other respects (age of maturity, fecundity etc.) they are assumed to have the same characteristics.
The accumulated juvenile natural mortality is defined as
```

$$
M_{\text {juv }}=\int_{t_{\text {rel }}^{t_{\text {rekr }}}} M(t) d t
$$

where
$t_{\text {rel }}=$ age at release
$t_{\text {rekr }}=$ age of recruitment to fishable stock
$M(t)=i n s t a n t a n e o u s$ natural mortality at age $t$

If $N_{r e l}$ artificially produced recruits are released into the population, this will increase recruitment to the fishable stock by $N_{r e l} e^{-M}$ juv.

It will be assumed that $M(t)$ and thereby $M_{j u v}$ is independent of $N(t)$, where $N(t)$ is total stock of juveniles of age $t$. However, in a simulation model outlined later, $M(t)$ is made dependent on the size of the recruited stock through cannibalism.

For illustrative purposes, a cod population has been constructed with about the same biological characteristics as the North Sea cod but with a recruitment level and stock size of about $1 / 10$ of the North Sea stock. This will be our local coastal cod stock, and we will look into the possibility of increasing the yield by releasing 0-group fish.

Population parameters independent of stock size

Let us first look on the simplest case where there is no density dependency in growth, mortality or recruitment in the natural population. The yield curve, assuming recruitment at age $1\left(N_{1}\right)$ and mean weights at age equal to the equilibrium values at $F=1.0$ in the simulation model (see Appendix), is shown in Fig. 2 for three different exploitation patterns. The fishing mortality at age of recruitment to the fishery ( $t_{c}$ ) is assumed to be $15 \%$ of the fishing mortality on older cod. $t_{c}=1$ corresponds approximately to the present exploitation pattern on North Sea cod.

Putting
$M_{\text {juv }}=\int_{t_{\text {rel }}}^{1} M(t) d t$
the long term yield (Y') if releasing annually $N_{r e l} 0$-group cod but not changing the exploitation rate or pattern is

$$
Y^{\prime}=Y\left(1+\frac{N_{r e l} e^{-M} j u v}{N_{1}}\right)
$$

where $Y$ is the yield with no release $\left(N_{1}\right.$ recruits at age 1). The additional yield per 1 million released 0 -group cod are shown below for various values of $\mathrm{M}_{\mathrm{juv}}$ and fishing mortality $F\left(t_{C}=1\right)$ (Table 1).


Fig. 2. Yield curves for the natural cod population, assuming constant growth and recruitment.

The additional yield is thus dependent both on the juvenile natural mortality and the exploitation rate.

The figures given in Table 1 should be compared with potential gains by improving the exploitation rate or pattern. For example, long term yield could be increased by about 19000 tonnes by decreasing $F$ from 1.0 to $F_{\max }(F i g .2)$. To achieve the same by releasing 0 -group cod but not changing the exploitation rate, one would annually have to release about 36 million fish if $M_{j u v}=0.6$. If both decreasing the

TABLE 1.

Additional yield (Y' - Y) per million released 0-group cod.

| $M_{\text {juv }}$ | $Y^{\prime}$ - Y (tonnes) |  |  |  |
| :---: | :---: | :---: | :---: | :---: |
|  | F |  |  |  |
|  | 0.2 | 0.6 | 1.0 | 1.5 |
| 0.2 | 1366 | 1050 | 803 | 656 |
| 0.4 | 1119 | 860 | 658 | 537 |
| 0.6 | 916 | 704 | 539 | 440 |
| 0.8 | 750 | 576 | 441 | 360 |
| 1.0 | 614 | 472 | 361 | 295 |
| 1.5 | 372 | 286 | 219 | 179 |
| 2.0 | 226 | 174 | 133 | 108 |

exploitation rate and improving the exploitation pattern by increasing age of first capture by 2 years, the yield from the natural population could be increased by about 37000 tonnes. This could alternatively be achieved by releasing annually 69 million 0 -group cod, still assuming $M_{j u v}=0.6$.

Thus, with growth overfishing, for example fishing at $\mathrm{F}=1.0, \mathrm{t}_{\mathrm{C}}=1$, in Fig. 2, releasing a few million 0-group cod would only marginally increase the yield compared to what could be achieved by exploiting the natural population in a more rational way. Instead of solving the management problems one would just produce some extra recruits suffering the same overfishing as the natural population!

Changing the exploitation rate and pattern would increase the yield from both the naturally and artificially produced recruits. For example, from the table above it can be seen that the return from 1 million released 0 -group cod is 539 tonnes at $F=1.0$ and 916 tonnes at $F=0.2$ ( $M_{j u v}=0.6$ ). By
decreasing $F$ to 0.4 but increasing $t_{c}$ by two years the return could be increased to 1262 tonnes.

Instead of asking whether artificially produced recruits can help solve the management problems one should therefore rather ask whether proper management of the fishery can make artificial production of recruits profitable.

It may of course be doubted whether the yield curves in Fig. 2 and the figures given above for gains in yield are realistic at all, since growth and recruitment in the natural population have been assumed constant and independent of stock size.

Stock size dependent growth and recruitment

In order to study the effects of stock size dependent growth and recruitment, a simulation model was constructed.

Concerning growth, it was decided to assume a linear relationship between $L_{\infty}$ and biomass.

The initial number of 0 -group cod was assumed to be related to the spawning stock by a Beverton-Holt curve. Daan (1975) has documented a heavy predation on 0 -group cod by larger cod in the North Sea. Combining this cannibalism mortality with the Beverton-Holt curve results in
$N_{1}=\frac{1}{\alpha+\beta / S} \quad a e^{-b B}$
where $N_{1}$ is the number of 1 -group cod, $S$ the parent spawning stock and $B$ the stock of cod predators on the year class as 0-group.

Further details about the model and the underlying assumptions are given in the appendix.

Equilibrium situations for various values of the parameters defining the stock size dependent growth and recruitment were studied by running the model for a period of 40 years for different constant $F$-values.

The data reported by Daan (1975) indicated a cannibalism mortality of about 2.4 during the years $1967-1970$ if all
consumed cod was 0 -group. Some of them were l-group, but for the calculation of yield and stock size it would not make a noticeable difference if a part of the mortality was placed on early 1 -group instead of placing all on 0-group. The F-level during 1967-70 was about 0.6 (Anon., 1983b).

Although the cannibalism mortality of 2.4 reported above is the best estimate which can be made from published data, it was decided to chose values for the predation parameters which resulted in appreciable lower cannibalism mortality at $\mathrm{F}=0.6$.

In Fig. 3a-3d are given results of the simulations for the set of parameter values listed in the appendix. Maximum yield (Fig. 3d) is obtained at an F of about 0.75. Predation mortality at $F=0.6$ (Fig. 3c), subtracting the "rest" mortality $M_{o}$ of 0.2 , is about 0.9 , i.e. appreciably lower than indicated by Daan's data.

In Fig. 3d are also shown the yield curves if 10 or 30 million 0-group cod are released anually. In contrast to the constant parameter case, where maximum additional yield occurs when the yield from the natural population is maximized, the additional yield in Fig. 3d increases with increasing $F$. This is mainly a result of decreasing $M_{j u v}$ with decreasing stock size (increasing $F$ )

In Table 2 is shown the maximum yield (MSY) for the three yield curves in Fig. 3d.

TABLE 2.

Maximum yield (MSY) and additional yield per million released 0 -group cod.

| Number released | MSY <br> (tonnes) | Additional yield <br> per mill. released <br> 0-group cod |
| :---: | :---: | :---: |
| 0 | 28200 |  |
| $10 \times 10^{6}$ | 30500 | 230 |
| $30 \times 10^{6}$ | 34600 | 210 |



Fig. 3a. Recruitment as 0-group ( $N$ ) and resulting number of 1 -group $\left(N_{1}\right)$ plotted against spawning stock size.


Fig. 3b. Juvenile mortality (M, juv) plotted against annual mean biomass ( $\vec{B}_{1+}$ ).


Fig. 3c. Juvenile mortality ( $M_{j u v}$ ) plotted against fishing
mortality (F).


Fig. 3d. Yield plotted against fishing mortality (F).

The additional yield per million released is much lower than the corresponding figures in the constant parameter case. If parameter values which, gave cannibalism mortalities more consistent with Daan's (1975) data had been chosen, the additional yield would have been even lower. The additional yield is increasing when the natural stock is over-exploited. However, from a rational resource utilization point of view, it would not be an interesting strategy to over-exploit the natural population and trying to compensate for this by artificially producing recruits.

However, the larger returns from the released recruits when the stock is over-exploited could indicate that in a situation where the stock is strongly depleted, a combination of releasing recruits and reducing fishing mortality might significantly speed up the recovery process compared with the alternative of only reducing fishing mortality.

This was in fact studied by starting with the equilibrium population at $F=2.4$ and running the model for 10 years applying $\mathrm{F}=0.75$. Three alternatives were run, and in Fig. 3e $\overline{\mathrm{B}}_{1+}$ is plotted against time. The simulated stock recovered very rapidly without any release of recruits, and an annual release of 10 million recruits over a 3 year period, or the whole period, did not speed up the process to an extent which was likely to justify a large release programme.

The difference between the yield curves in Fig. 3d and Fig. 2 is mainly created by the assumed stock-recruitment relationship and the cannibalism. However, density-dependent growth was also introduced, and in order to illustrate how much the growth varied the relationship between $W_{\infty}$ and $\bar{B}_{1+}$ is shown in Fig. 3f. Some corresponding F-values are also shown. In Fig. $3 g$ the growth curves at two extreme F-values, $F=0$ and $F=2.5$, are shown.

The yield curve assuming constant growth $\left(W_{\infty}\right.$ corresponding to $F=1.0$ in Fig. 3f) was also calculated. The difference between this yield curve and the curve in Fig. 3d was very moderate. The MSY point was moved a little to the left, the yield at high $F$-values decreased somewhat while it increased at low F-values.


Fig. 3e. Rebuilding stock. Annual mean biomass ( $\overline{\mathrm{B}}_{1+}$ ) plotted against year when (a) releasing 10 million recruits ${ }^{+}$each year, (b) releasing 10 millions recruits in year 1, 2 and 3, and (c) no release.


Fig. 3f. $W_{\infty}$ plotted against annual mean biomass ( $\overline{\mathrm{B}}_{1+}$ ).


Fig. 3g. Mean weight plotted against age.

DISCUSSION AND CONCLUSIONS

The yield curves presented above were meant only to illustrate various possibilities. The yield curve of a fish stock is seldom known with any accuracy. Further, different cod stocks, as for example the North-East Arctic cod and North Sea cod, may have very different yield curves.

By assuming stock size independent natural mortality, growth and recruitment, the increase in yield by releasing a number of recruits will be a certain percentage of the yield from the natural population, the percentage being independent of fishing mortality $F$. The increase in yield will therefore be largest when fishing at $F_{\text {max }}$. For estimating the increase, the natural mortality on juveniles has to be known.

However, by assuming constant population parameters, most of the commercially important cod stocks are at present heavily growth-overfished, and much larger gains could be achieved by simply reducing the overfishing instead of artificially producing some millions recruits which in turn would also be growth-overfished.

When juvenile mortality is made dependent on recruited stock biomass by cannibalism, the increase in yield by releasing artificially produced recruits will increase by decreasing stock size or increasing $F$. Stock size dependent growth will strengthen this trend. However, by increasing F beyond the MSY point of the natural population we may soon lose more yield than we gain from artificially produced recruits, and it was demonstrated that the MSY can only be increased marginally even by releasing substantial number of recruits.

There is one situation where artificially produced recruits could theoretically contribute significantly to solve management problems. If the stock is heavily recruitmentoverfished, i.e., is at such a low level that even without fishing rebuilding will be very slow because of recruitment failure, then artificially produced recruits could significantly speed up the recovery process. It would, however, depend critically on whether the artificially produced recruits and their progency will join the natural population. Further, the author is not aware of an example of such a heavily recruitment-overfished cod stock.

Before starting large scale releases of artificially produced recruits on a regular basis several factors should be further studied. Some of them can only be studied by carrying out a rather large scale release.

First of all it should be clarified whether the purpose is to restock a defined natural population or just to release juveniles in an area in order to fish them later on. To what extent artificially produced recruits will mix with a natural population, and for management purposes be treated as part of that population, could be investigated by large scale tagging
(combined with biological studies) of both released juveniles and naturally produced fish.

Secondly, the level of juvenile mortality and its causes should be further investigated. Again, tagging may be an appropriate method for estimating the mortality. Concerning its causes, a fish stomach sampling programme could clarify whether there is intensive cannibalism or whether predators from other species is an important factor. It is also important to know at what time high mortalities are generated. For example, if a high predation mortality on 0-group occurs in August-September, then much higher survival could be expected if the release of 0 -group was delayed until October.

Thirdly, if the purpose is to restock a natural population, one should have some ideas about the form of the yield curve of that population. To clarify whether $M_{j u v}$ is mainly caused by cannibalism or predation from other species would of course be a part of what is needed for establishing the yield curve. One should also know the present level of fishing mortality $F$ in order to evaluate whether much larger increases in yield could be achieved by simply changing $F$ than releasing recruits.

Finally, if 0 -group cod are released in a rather closed area wi.th its own established ecosystem, an important question not yet discussed is to what extent an increased cod stock, far above its "natural" level, will affect the productivity of other stocks and change the whole system. A pilot project is probably the only way of trying to answer that question. One should start with describing as accurately as possible the existing system (i.e. species composition, yield and stock size of each main species, growth and mortality parameters) and preferably also have information about past fluctuations. Then the changes should be monitored year for year when significant numbers of juvenile cod are released into the area.

APPENDIX

BASIC ASSUMPTIONS AND EQUATIONS IN THE SIMULATION MODEL

Concerning growth, the von Bertalanffy growth equation

$$
w_{a}=w_{\infty}\left(1-e^{-K\left(a-a_{0}\right)}\right)^{3}
$$

where $a$ is age of fish, was used for calculating a mean weight for each age group. Based on empirical data, Beverton and Holt (1957) were led to propose a linear relationship between the growth parameter $\mathrm{L}_{\infty}$ and stock biomass for North Sea plaice, and between $L_{\infty}$ and population numbers in haddock. For this study, it was decided to assume a linear relationship between $\mathrm{L}_{\infty}$ and biomass. With $\mathrm{W}_{\infty}=\mathrm{qL} \mathrm{L}_{\infty}^{3}$, this would mean that the relationship between $W_{\infty}$ and biomass has the following form:

$$
W_{\infty}=(b+c B)^{3}
$$

where $b$ and $c$ are constants and $B$ is the stock biomass. In the calculations, it was further decided to relate $W_{\infty}$ in year $t, W_{\infty, t}$, to biomass in year $t-1$, i.e.

$$
\begin{equation*}
w_{\infty, t}=\left(b+c B_{t-1}\right)^{3} \tag{1}
\end{equation*}
$$

It can of course be questioned whether it is biological meaningful at all to define a $W_{\infty}$ for each year common for all year classes instead of defining a $W_{\infty}$ for each year class. However, since in most applications of the model the primary interest was in the final equilibrium state and not in what happened in each specific year, this distinction was not regarded critical.

Concerning the relation between stock and recruitment, Ricker (1975) points out that of the two curves most used, the Ricker type

$$
R=a P e^{-b P}
$$

is more appropriate when cannibalism of young by adults is an important regulatory mechanism, while the Beverton-Holt curve

$$
R=\frac{1}{\alpha+\beta / P}
$$

is likely to be appropriate when there for example is a ceiling of abundance imposed by available food or habitat.

It was decided to combine the two curves. Firstly, it was assumed that the numbers surviving to the 0 -group stage ( $N_{0}$ ) was related to spawning stock (S) by

$$
N_{0}=\frac{1}{\alpha+\beta / S}
$$

i.e. a Beverton-Holt curve.

Secondly, it was assumed that the accumulated natural mortality on juveniles until recruitment to the fishable stock at age $a_{r}$ in year $t$ was given by

$$
M_{j u v, t}=M_{0}+{\underset{a}{\sum_{r-1}} k_{a} B_{t-a_{r}}+a}
$$

where $M_{o}$ is a "rest" mortality and the second term is the cannibalism mortality generated by the predator biomass $B$ in each year, assuming that for each age group a the cannibalism mortality is equal to the biomass $B$ multiplied by a proportionality constant $k_{a}$. Thus

$$
N_{a_{r, t}}=\left(\frac{1}{\alpha+\beta / s_{t-a_{r}}}\right) e^{-\left(m_{0}+\sum_{a=0}^{a_{r-1}} k_{a} B_{t-a_{r}}+a^{\prime}\right)}
$$

In our local stock, which was assumed to be of a North Sea cod type, $a_{r}=1$ and therefore

$$
\begin{equation*}
N_{l, t}=\frac{1}{\alpha+\beta / S_{t-1}} e^{-\left(M_{0}+k_{o} B_{t-1}\right)} \tag{2}
\end{equation*}
$$

The second factor in (2) corresponds to Ricker's survival function from spawning to recruitment to the fishable stock $\left(R / P=a e^{-b P}\right)$, the difference being that in Ricker's expression $P$ is the parent spawning stock while in the expression above $B$ is the biomass of the stock feeding on juveniles. This survival factor is then applied on the initial number of 0 -group generated by the Beverton-Holt curve. Equation (2) could of course be refined by splitting $B$ on age groups, defining different constants $k_{o}$ for each group.

In the simulations, $B_{t}$ was defined as the mean biomass during year $t$ of age groups 1 year old and older, calculated from annual mean stock in number as defined by Beverton and Holt and the mean weight for each age group.

In the simulation runs underlying Figs. 3a-3f, the following values of growth paramters and $\alpha, \beta$ and $k_{o}$ were chosen:

$$
\begin{aligned}
& \mathrm{K}=0.333 \\
& \mathrm{a}_{\mathrm{o}}=0.77 \text { years } \\
& \mathrm{b}=2.567 \\
& \mathrm{c}=-3.111 \times 10^{-6} \\
& \alpha=1.29 \times 10^{-5} \\
& \mathrm{~B}=0.0829 \\
& \mathrm{k}_{\mathrm{o}}=1.6810^{-5}
\end{aligned}
$$

This resulted in the following equilibrium situation at $\mathrm{F}_{2+}=1.0 \quad\left(\mathrm{~F}_{1}=0.15 \mathrm{x} \mathrm{F}_{2+}\right.$ ) .

Predation mortality on juveniles $=0.6$.
$\mathrm{N}_{\mathrm{o}}=62.0 \times 10^{6}$
$N_{1}=27.9 \times 10^{6}\left(M_{o}=0.2\right.$ giving $\left.M_{j u v}=0.8\right)$
$W_{\infty}=14.82 \mathrm{~kg}$
Annual mean biomass of $1-g r o u p$ and older $\operatorname{cod}\left(\bar{B}_{1+}\right)=$ 35700 tonnes

Annual catch $=27400$ tonnes

Other equilibrium situations were studied by running the model for a period of 40 years for diferent constant $\mathrm{F}-$ values, starting with the equilibrium stock in number by age and mean weights by age at $F=1.0$ (which itself was estimated by a similar procedure starting with guessed values). Natural mortality on 1 year old and older cod was assumed to be 0.2.

In order to get mean weights comparable with those of North Sea cod, correction factors had to be applied when calculating weight at age 1 and 2 from the growth equation, and it is the corrected values which have been used in all calculations.

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