

An Analysis of Spawner Biomass and Recruitment of Cod (*Gadus morhua*) in Divisions 2J and 3KL

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Abstract

Replacement of the spawner stock is necessary for a population to persist. The risk of not achieving replacement will depend on weight-at-age, proportion mature-at-age and weight specific fecundity, and may be expected to increase as fishing mortality increases. Weights-at-age and proportion mature-at-age are routinely measured for many fish stocks and have been shown to vary over time. Using average values may give a false impression of whether replacement was met or not, particularly when there are trends in the values. Data for cod (*Gadus morhua*) in Div. 2J and 3KL were analyzed to demonstrate this and introduce an alternative biological reference point, "annual replacement", that is sensitive to annual changes in these values. It is shown that recruitment has been below annual replacement from 1983 to 1989, primarily as the result of high levels of fishing mortality. It is demonstrated that recruitment probabilities estimated from a nonparametric analysis can be used to assess the probability of failing to achieve replacement at a specific spawner biomass. Following this approach, it can be predicted that recruitment is below annual replacement in 1990 and 1991 as well.

Key words: Biological reference points, cumulative probability, non-parametric, recruit per spawner, recruitment, replacement, spawner stock

Introduction

For a fish population to persist, recruitment (R) must, on average, be sufficient to replace the spawner stock biomass (SSB) that gave rise to it. The amount of recruitment required to replace the spawner biomass is determined by the spawner per recruit (SPR) ratio, the per capita lifetime production of SSB by a single recruit. The SPR ratio is influenced by the survival rate, body growth rate and maturity-at-age schedule. The survival rate is a function of both fishing mortality (F) and natural mortality (M). If the probability distribution of R varies with SSB as a result of an underlying stock-recruit (S–R) relationship, or as a result of changes in the environmental influences on recruitment, then the amount of recruitment obtained will vary and may not be sufficient to meet replacement at the prevailing levels of fishing mortality, natural mortality, weights-at-age and maturity-at-age. Typically, recruit per spawner (RPS) is considered to be some decreasing function of SSB as a result of density dependence in egg production, fertilization or pre-recruit survival, so that at high SSB, R falls to the replacement level and the population does not grow infinitely.

Singly or in combination, SSB, S–R, SPR and RPS can be used to provide insight into the status of a fish stock. These quantities and relationships can be used to define conservation and overfishing and

to determine biological reference points and management targets. For example, Sissenwine and Shepherd (1987) proposed a biological reference point related to recruitment overfishing termed F_{rep} , the fishing mortality rate that corresponds to average replacement, i.e. that on average reduces the spawning biomass produced by a year-class over its lifetime to the spawning biomass of its parents. The present work introduces a reference point based on annual values of fishing mortality, weights and proportions mature-at-age and demonstrates the potential usefulness of determining the risk of failing to meet this reference point at different levels of fishing mortality (see also Shelton and Morgan MS 1993). The term 'risk' is used here to denote the 'chance of bad consequences', following Fowler and Fowler (1934).

Methods and Results

Spawner stock biomass

The approximate spawner biomass of both males and females in the Div. 2J and 3KL cod (*Gadus morhua*) population is frequently calculated by summing the age 7+ biomass estimated from an ADAPT formulation (e.g. Baird *et al.*, MS 1992). While this is a useful first approximation, it would seem more appropriate to use year-specific proportions mature-by-age and sex to calculate mature biomass where such data are available. Because maturity-at-age differs between the sexes (Morgan *et al.*, 1994,),

and because the female biomass is of primary importance with respect to egg production and subsequent recruitment, it may also be useful to use an estimate of the sex ratio to obtain mature female biomass. In the case of cod in Div. 2J and 3KL the overall sex ratio does not appear to differ significantly from 1:1, and, for comparability with ADAPT estimates, we treated spawner biomass as the biomass of both males and females, even though the proportions mature used to obtain it in this study were derived only from females.

Prior to 1971, groundfish trawl surveys in Div. 2J and 3KL were carried out using mainly a line transect sampling design. From 1971 onwards a stratified random sampling design was implemented, giving better spatial distribution of samples. Maturity data from autumn surveys in Div. 2J and 3K for 1978–91, autumn surveys in Div. 3L for 1981–91 (with the exception of 1984 because in that year the survey ended 2 months before the autumn survey started in any other year), and spring surveys for Div. 3L for 1973 to 1992 were used in the analysis. Spring surveys in Div. 3L were carried out in 1971 and 1972 but the maturity data have not yet been fully analyzed.

For the period 1978–92 sexed length frequencies were used to estimate catch numbers-at-length from the research surveys for use in correcting the length stratified sampling of age (see below). Sexed length frequency data do not exist before 1978. For the 1978–92 period the overall sex ratio did not differ from 1:1. Therefore, prior to 1978, a sex ratio of 1:1 was assumed in determining catch-at-length by sex from the length frequency data.

Fish were assigned to the category 'mature' or 'immature' based on the scheme of Templeman *et al.* (1978). In this scheme there are nine maturity stages for females. The first stage is immature and all other stages show some evidence of maturing to spawn or of having spawned and are therefore classified as mature in this study.

Otoliths were collected by the Gadoids Section of the Department of Fisheries and Oceans in St John's for age determination from fish caught in stratified random research trawl surveys using a length stratified sampling scheme. In this scheme 25 fish per 3 cm length-class were sampled for each Division. A given age can straddle several length-classes. Further, the possibility of being mature at a given age is influenced by length. This can result in inaccuracies in the estimation of proportion mature-at-age if length and catch-at-length are not taken into account. A formula for correcting for this sample scheme developed by Morgan and Hoenig (MS 1993) was used:

$$p_j^{m'} = \frac{\sum_{i=1}^n (C_i p_{ij} p_{ij}^m)}{\sum_{i=1}^n (C_i p_{ij})} \quad (1)$$

where

- C_i = catch in length-class i ,
- p_{ij} = proportion of length-class i that is age j ,
- p_{ij}^m = the proportion of length-class i that is age j and that is mature,
- $p_j^{m'}$ = the corrected proportion of age j that is mature, and
- n = the number of length-classes.

The catch in length-class i (C_i) was calculated from research vessel survey length frequencies using stratified analysis programs (STRAP, Smith and Somerton, 1981) which weight the catch from a stratum by the size of the stratum.

In order to produce annual estimates of overall Div. 2J and 3KL proportion mature-at-age in the autumn for the period 1973–91, the proportions mature were analyzed using PROBIT analysis with a logit link function (SAS Institute Inc. 1989) such that

$$\hat{p}_{jkl}^{m'} = \frac{1}{(1 + \exp(-x))} \quad (2)$$

and

$$E(x) = \tau + \alpha \text{ age } j + \beta_k \text{ year } k + \gamma_l \text{ season } l,$$

- where $\hat{p}_{jkl}^{m'}$ = predicted proportion mature at age j in year k and season l ,
- α = age effect,
- β = year effect,
- γ = season effect, and
- τ = intercept.

All terms in the model were significant ($p \leq 0.001$). From the parametrised model, the proportion mature at age $j = 3$ to 14 in autumn for year $k = 1973$ to 1991 were predicted (Fig. 1).

Weights-at-age on 1 January determined from sampling the commercial fishery (Fig. 2) were used together with the PROBIT estimates of proportion mature-at-age and ADAPT estimates of numbers-at-age (Bishop *et al.*, MS 1993) to calculate spawner biomass for each year between 1973 and 1992. Weights-at-age on 1 January were obtained by calculating the geometric mean of the June weights from the commercial fishery in the year before and

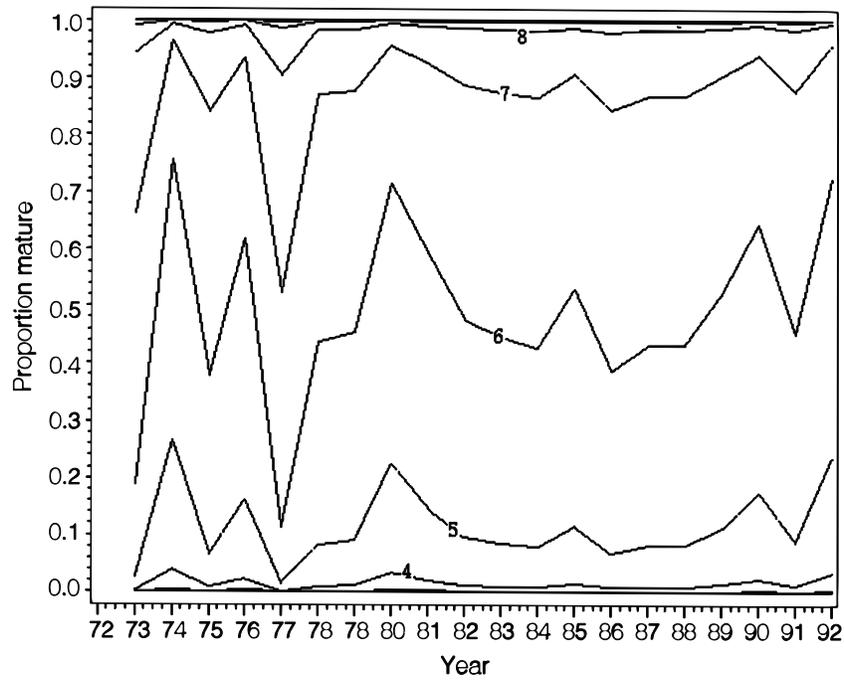


Fig. 1. PROBIT estimates of proportion mature-at-age for the NAFO Div. 2J and 3KL cod stock for the period 1973–92 based on survey data.

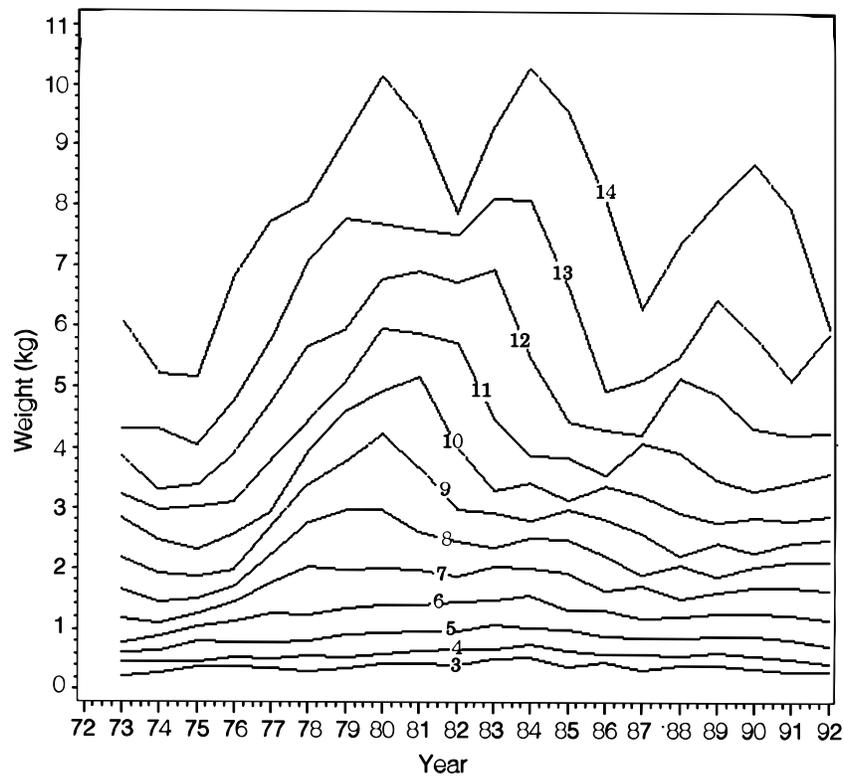


Fig. 2. Weights-at-age of cod in Div. 2J and 3KL on 1 January in each year estimated from the commercial fishery.

the year after (Rivard 1982). The estimated spawner biomass using the proportion mature-at-age was generally higher than that estimated using age 7+ (Fig. 3), although both showed a similar pattern. SSB reached lows in 1977 and 1991–92. The estimate of SSB for 1992 was 60 000 tons greater using the proportion mature-at-age than for the age 7+ estimate.

Replacement and spawner per recruit

For a population to persist, each year-class must, on average, replace the spawner biomass that gave rise to it. The risk of not achieving replacement may be expected to increase as fishing and natural mortality increase and as weight-at-age, proportion mature-at-age and weight specific fecundity decrease. Weights-at-age and proportion mature-at-age are routinely measured for many fish stocks and have been shown to vary over time. In the case of Div. 2J and 3KL cod stock, proportions mature-at-age were quite variable in the 1970s; values for 5, 6 and 7 year olds declined in the early-1980s while in more recent years this trend has reversed (Fig.

1). Weights-at-age for the Div. 2J and 3KL cod stock demonstrate strong cohort effects as well as non-random year effects (Fig. 2). ADAPT estimates of fishing mortality-at-age demonstrate a declining trend in the late-1970s after extension of jurisdiction by Canada to 200 nautical miles, followed by an increasing trend throughout the 1980s and early-1990s, and a sharp decline coinciding with the introduction of the moratorium on the fishery in 1992 (Fig. 4). In this study we demonstrate that the calculation of replacement recruitment based on an average of these values is misleading because of these patterns in the data.

As a cohort ages, it makes annual contributions to the spawner biomass over its lifetime, the magnitude of which depends on natural and fishing mortality rates, weights-at-age and proportion mature-at-age. The spawner biomass resulting from a cohort can be calculated as:

$$S' = \sum_{i=r}^l (N_i w_i p_i) \quad (3)$$

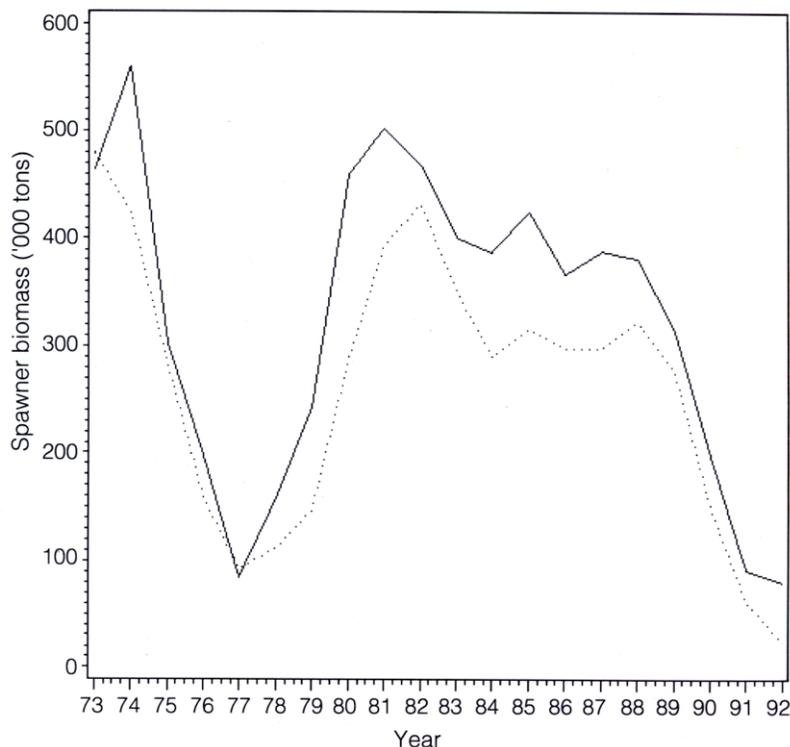


Fig. 3. Spawner biomass from ADAPT estimates of numbers-at-age and weights-at-age on January 1, calculated using estimated proportions mature-at-age from survey data (solid line) and by assuming all fish 7+ are mature (dotted line).

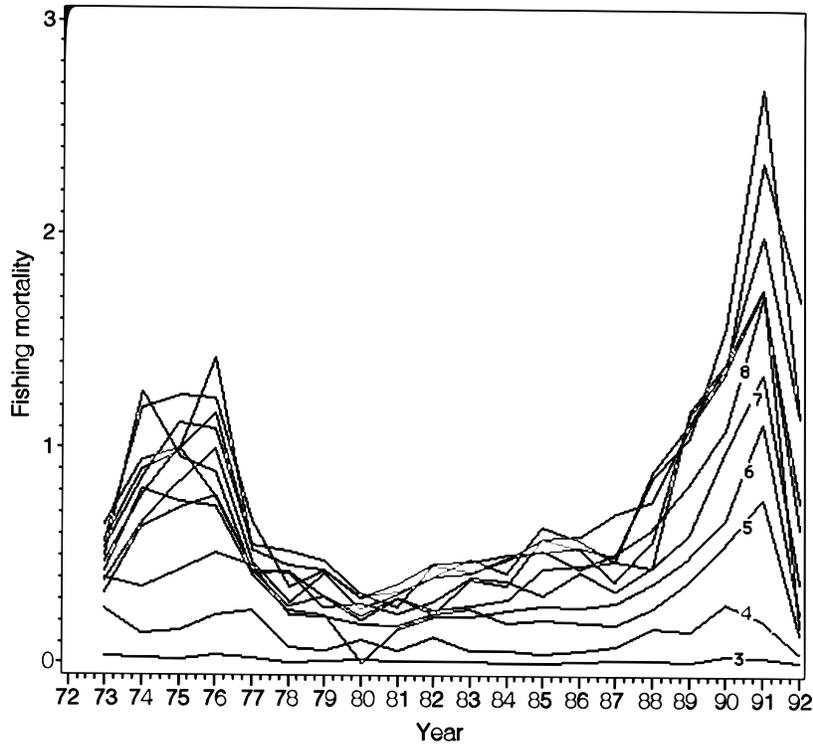


Fig. 4. ADAPT estimates of fishing mortality-at-age by year for the period 1973-92.

where

$$N_{i+1} = N_i e^{-(F_i+M)} \quad (4)$$

and where S' = the cumulative contribution to spawning biomass by a cohort over its lifespan,

N_i = the number alive in a cohort at age i ($N_i = R$ when $i = r$),

w_i = the weight of an individual fish at age i ,

P_i = the proportion mature at age i ,

r = the age at recruitment,

L = terminal age-class (alternatively a 'plus' age-class could be used),

F_i = the annual instantaneous fishing mortality rate on age i , and

M = the annual instantaneous natural mortality rate.

In contrast to the spawner biomass that accumulates over the lifespan of a cohort, the spawner biomass in a particular year j , S_j can be calculated

by summing the product of numbers-at-age, weights-at-age and proportion mature-at-age in year j , so that:

$$S_j = \sum_{i=r}^L (N_{ij} W_{ij} p_{ij}) \quad (5)$$

For a cohort to replace the spawner biomass that gave rise to it, and so doing ensure persistence, S' would have to equal S_j , where j is the year in which the cohort arose. "Cohort replacement" is the underlying process assumed in most age structured models, but it does not in itself, lead easily to a useful heuristic on which to base a biological reference point. Having determined S_j , it may be more useful to calculate the amount of recruitment, R^*_j , required to obtain this spawner biomass for particular values of fishing mortality, weights and proportions mature-at-age, making the assumption that replacement occurs in year j , rather than over the lifespan of the cohort. It is common practise in these kinds of calculations to use average vectors of w and p , and a variety of values of fishing mortality (e.g. Sissenwine and Shepherd, 1987; Gabriel *et al.*, 1989; Mace and Sissenwine, 1993).

R^*_j can be computed as:

$$R_j^* = \frac{S_j}{\sum_{i=r}^j (\gamma_i w_i p_i)} \quad (6)$$

where $\gamma_i = 1$ for $i = r$

and

$$\gamma_i = \prod_{i=r}^i (e^{-(F_{k-1} + M)}) \text{ for } i > r \quad (7)$$

We refer to replacement recruitment using average values for the vectors w and p as “average replacement recruitment”. Average replacement recruitment has the advantage that it is easy to display because it is a straight line passing through the origin in a stock-recruitment (S - R) plot. In an historic analysis, for which annual vectors of w and p are available, and particularly where these values are varying non-randomly, we favour a calculation in which the replacement recruitment in year j , R_j^* , corresponding to S_j , is calculated from the w_j and p_j vectors. It may also be of interest to calculate R_j^* using the fishing mortality-at-age estimated to have pertained in year j . We refer to R_j^* calculated in this manner as “annual replacement recruitment”. The two approaches are compared below for cod in Div. 2J and 3KL for the period 1973–88.

Average replacement recruitment for the period 1973–88 calculated using weights, maturities and fishing mortalities-at-age averaged over the period 1984–88 (from data in Baird *et al.*, MS 1992) is, in this instance, equivalent to F_{med} , a commonly used estimator of F_{rep} or replacement fishing mortality (Mace and Sissenwine 1993 (Fig. 5)). The implication is that fishing mortality was not excessive over this period. However, the trajectory of annual replacement revealed that the level of recruitment required to meet replacement increased sharply over the period 1980–88. The different perspectives obtained from examining average replacement and annual replacement, and the causes for these differences, are considered further below, using data from the 1993 assessment of the Div. 2J and 3KL cod stock (Bishop *et al.*, MS 1993).

Average replacement recruitment was calculated using average values over the period 1973–92 for the vectors of fishing mortality, weights and proportions mature-at-age from the data in Bishop *et al.* (MS 1993) and estimates of proportions mature presented above. By plotting average replacement and annual replacement recruitment against year, together with annual recruitment values, it can be seen that, although recruitment from 1983 onwards appeared to have been below both annual and average replacement levels, the trends in these levels differed (Fig. 6). Annual replacement appeared to have increased steadily over the period 1978–

89, whereas average replacement declined fairly steadily from 1981 onwards. By removing the SSB effect in the calculation of replacement, and plotting annual replacement per spawner and average replacement per spawner, it can be seen that the trend in the annual replacement recruitment persisted, indicating that it had become progressively harder for recruitment to exceed replacement in recent years (Fig. 7) as a result of trends in fishing mortality, weights-at-age and proportions mature-at-age.

The dramatic decline in annual replacement per spawner in 1992 is a result of reduced fishing mortality brought about by the moratorium imposed in that year on the commercial fishery within the 200 nautical mile zone. Annual replacement per spawner for $F = 0$ (Fig. 8) removes the direct effect of fishing (possible indirect effects of fishing on weights or proportions mature-at-age persist) and shows that the replacement level stopped increasing after 1987. The only two variables in this calculation were weights-at-age and proportion mature-at-age. Although weights-at-age had been declining over the 1980s, proportions mature at the lower ages increased in the late-1980s (Fig. 9), arresting the decline in annual replacement per spawner level. A plot of annual replacement recruitment per spawner at $F = 0$ together with the estimated recruit per spawner data points, indicates that recruitment in the late-1980s had come close to the replacement level below which the stock will continue to decline even in the absence of fishing (Fig. 10).

Thus, although both average replacement and annual replacement attempt to simplify the actual replacement of parent spawner biomass by a cohort over its lifespan, only annual replacement gives an indication of how temporal trends in values have affected the ability of a cohort to replace the spawner biomass. Further, we suggest that analyses of properties such as stability, and depensation below replacement are unlikely to be informative if they are based on an S - R analysis using average replacement rather than annual replacement, or cohort replacement within an age structured model. However, cohort replacement cannot readily be used as a basis for developing biological reference points relevant to the current year. This is because, for a long-lived species, it provides information on whether or not a cohort replaced its parent spawner biomass which existed, for example, 14 years ago, based on fishing mortality, weights, and proportions mature-at-age over the past 14 years. Further, for cohorts that have not yet reached terminal age (i.e. in order to say something useful about the replacement of recent spawner biomass), some assumption regarding the future (e.g. annual replacement) will have to be made to complete the calculation.

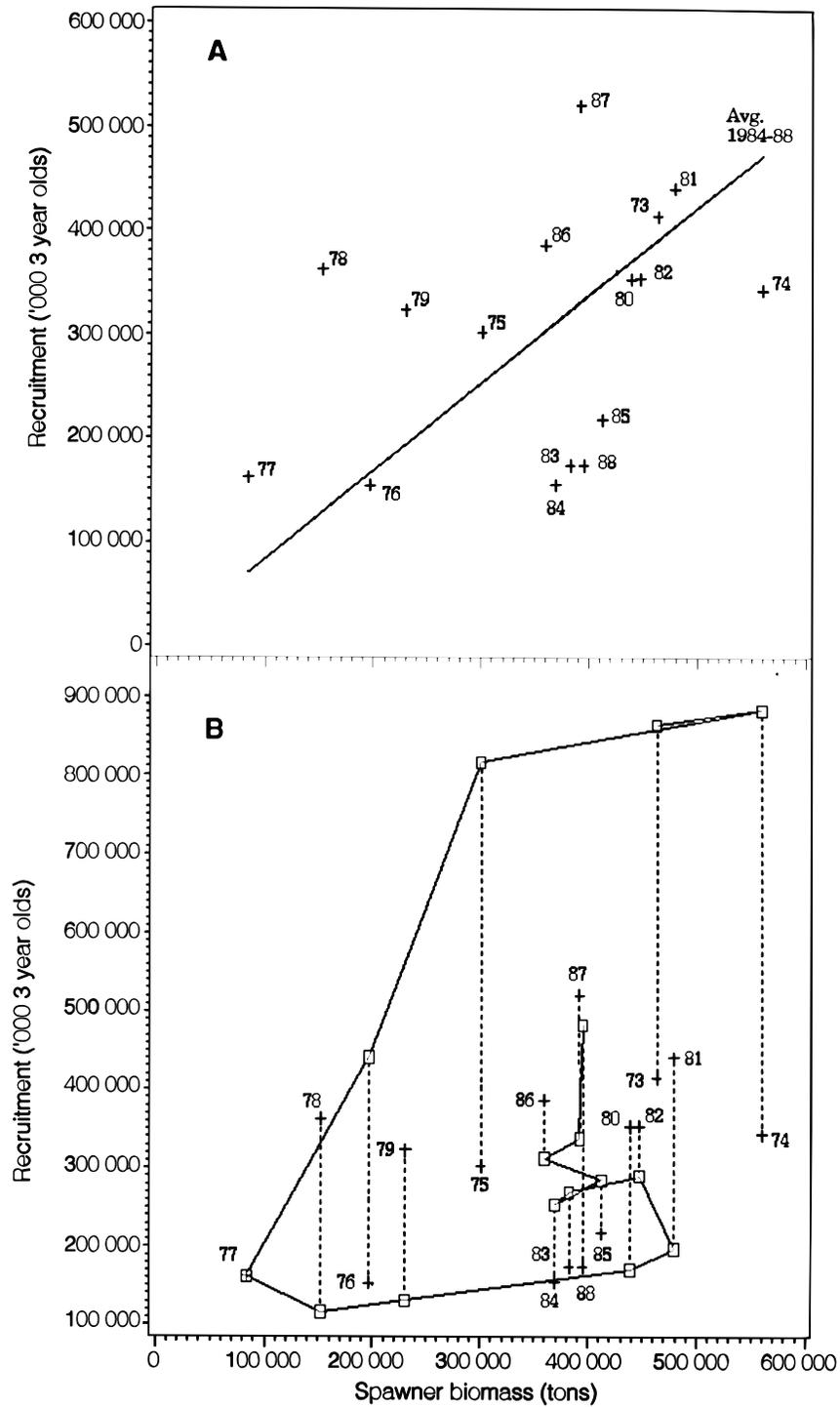


Fig. 5. (A) Stock-recruit data from ADAPT estimates for the period 1973-91 together with replacement calculated using average weights, maturities and fishing mortalities for the period 1984-88. (B) Including an annual replacement trajectory. The relative position of recruitment data points with respect to annual level of replacement is indicated by a vertical broken line.

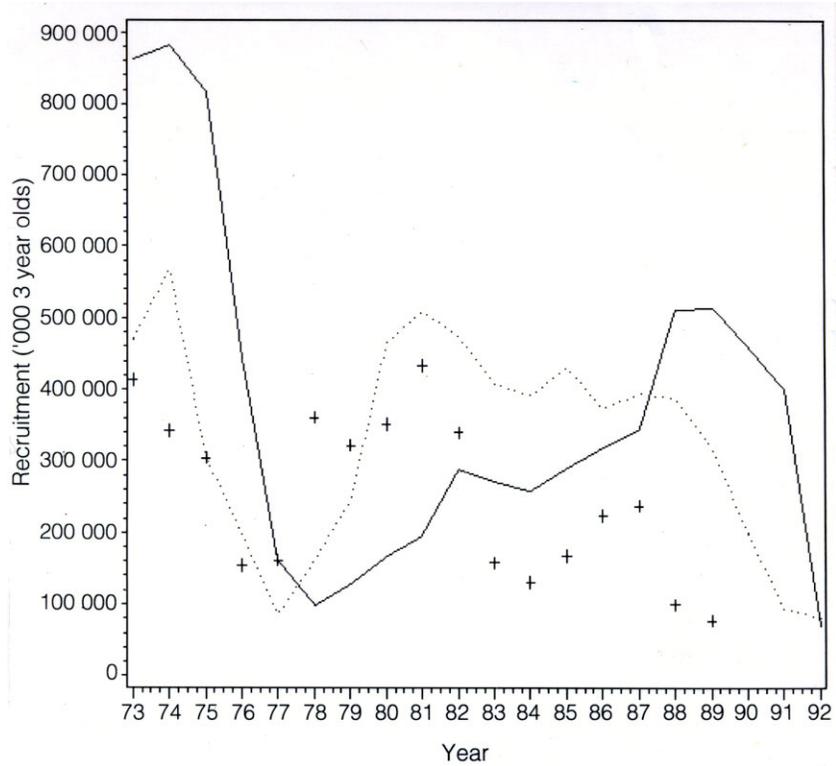


Fig. 6. Average (dotted line) and annual (solid line) replacement recruitment levels together with estimates of annual recruitment (+) for the period 1973–92.

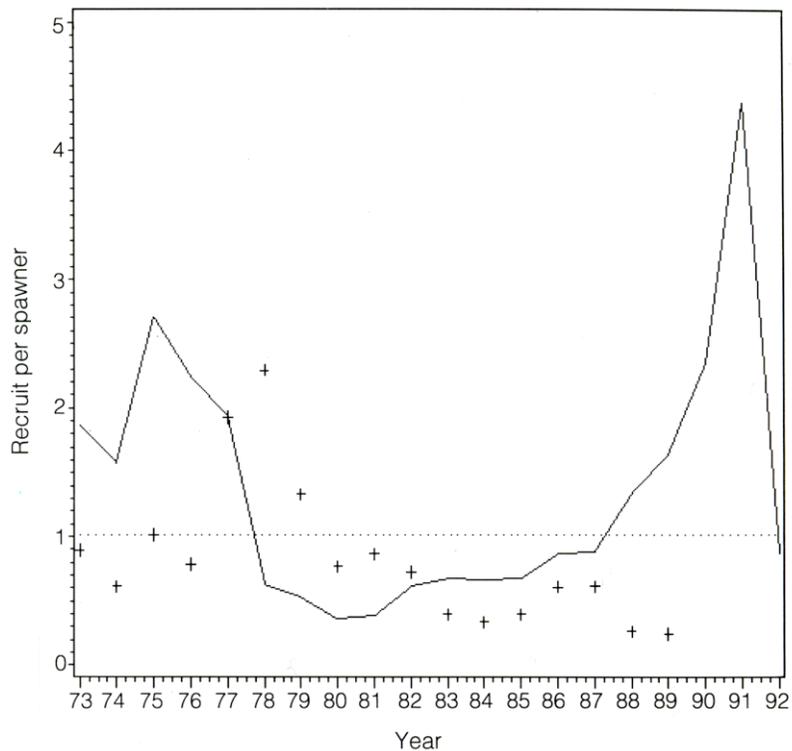


Fig. 7. Average (dotted line) and annual (solid line) replacement recruitment per spawner together with estimates of annual recruitment (+) for the period 1973–92.

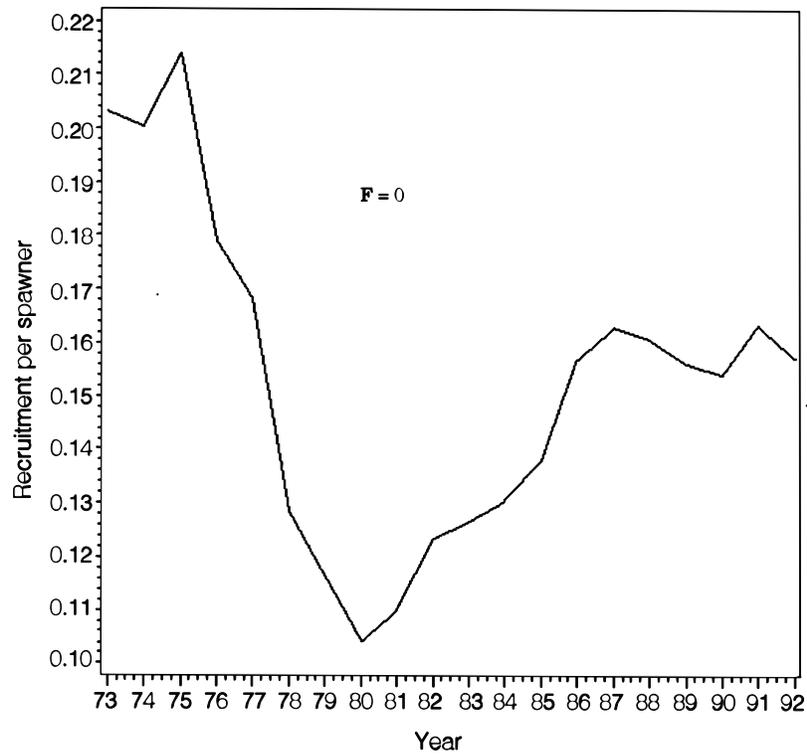


Fig. 8. Annual replacement recruitment per spawner at $F = 0$ for the period 1973–92.

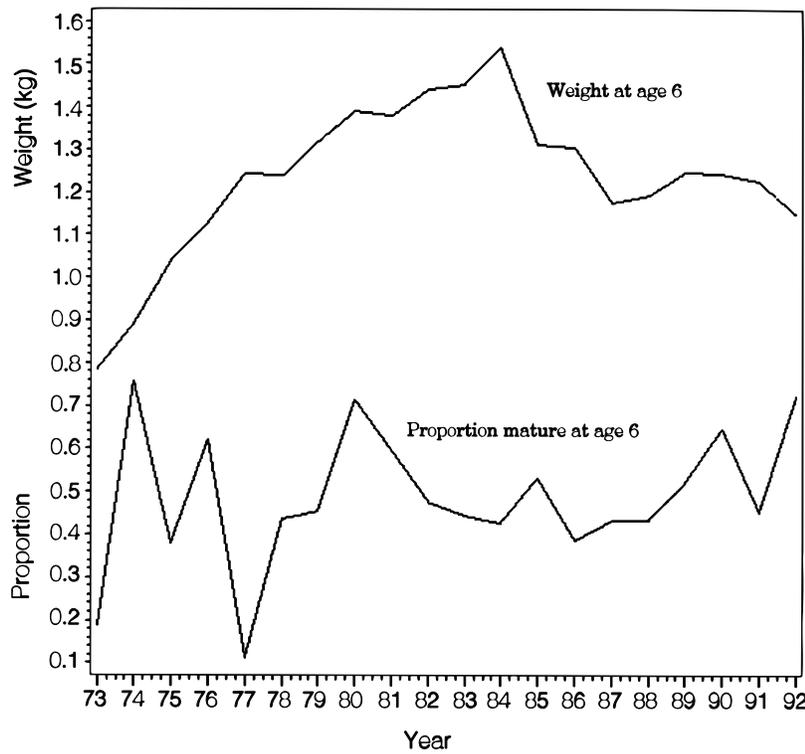


Fig. 9. Trends in weight and proportion mature at age 6 extracted from Fig. 1 and 2.

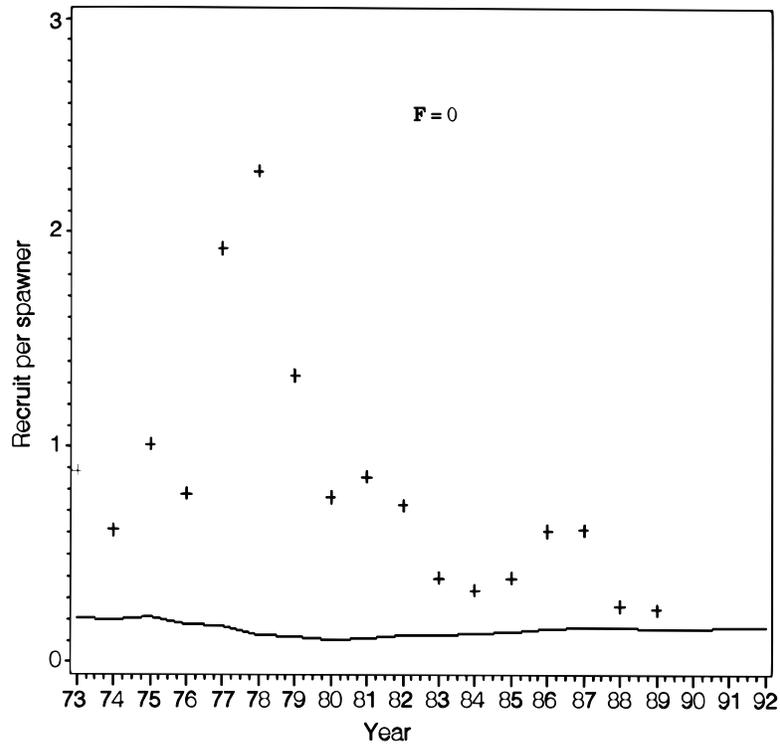


Fig. 10. Annual replacement recruitment per spawner at $F = 0$ together with estimates of annual recruitment per spawner.

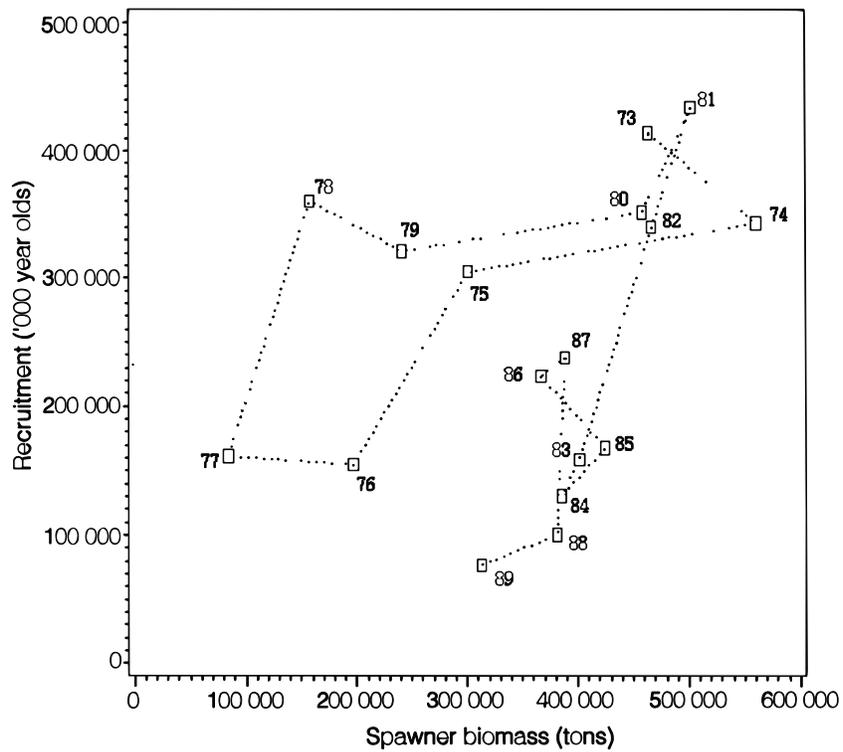


Fig. 11. Stock-recruit scatter for the period 1973–89. Data points are connected to show temporal sequence.

Annual replacement per spawner can be calculated for the most recent year for which there are data on weights and proportions mature-at-age. This can be useful for determining the appropriate level of F for the current year. If estimates of spawner biomass are available for the most recent years and an S - R relationship has been demonstrated, then recruitment can be predicted for the most recent years and compared with the replacement level. We now demonstrate the usefulness of non-parametric S - R analysis in estimating the probability of failing to achieve replacement of the spawner stock.

Spawner-recruit relationship

The stock-recruit scatter for Div. 2J and 3KL cod for the period 1973–89 (Fig. 11) shows considerable variability in recruitment with spawner stock size, particularly at intermediate spawner biomass. A non-linear fit of the Ricker (1954) model assuming normal error ϵ_j

$$R_j = S_j e^{(a-bS_j)} + \epsilon_j \quad (8)$$

gives estimates of a and b with wide confidence limits ($a = 0.1366$, lower $(1-a)\% = -1.458$, upper $(1-a)\% = 1.216$; $b = 0.132E-5$, lower $(1-a)\% = -0.23E-5$, upper $(1-a)\% = 0.419E-5$; $\alpha = 0.05$). A non-parametric analysis of recruitment, following the general approach of Evans and Rice (1988), Noakes (1989) and, Rice and Evans (MS 1986, 1988) may be more useful. This approach benefits from not requiring the assumption of a specific model. Ignoring SSB for the time being, the recruitment data can be plotted as a frequency distribution, and as a cumulative plot of the probability of recruitment (ordinate) being less than or equal to a specified value (abscissa) (Fig. 12). It is noted that because the frequency distribution and the cumulative probability plots reflect only the 17 estimated recruitments between 1973 and 1989, they are irregular in appearance. In the absence of further information, we can predict from the cumulative frequency distribution that, based on past data, there is a probability of 0.5 that recruitment in the next year will be approximately 230 million or less 3 year old fish. The question can now be asked 'can we make a better prediction if we pay more attention to previous recruitment that occurred at biomass levels similar to that biomass at which we wish to predict recruitment, rather than treating recruitment at all biomass levels as equally probable?'

In order to examine this, we can weight a recruitment data point that corresponds to a spawner biomass that is close in magnitude to the spawner biomass at which we want to make the prediction, more than a recruitment data point that corresponds

to a spawner biomass that is not as close. Following Rice and Evans (1988) we used a Cauchy probability density function to weight the contribution of surrounding data to the estimate at the point of interest. We used a jackknife-like approach (more correctly, cross-validation, for example, as in Rice and Evans 1988) to estimate the scale parameter (b) which minimised the prediction sums of squares (ss) for the probability density function applied to the 17 S - R pairs. The estimator using Cauchy weighting performed better (jackknifed prediction $ss = 18.23E10$) than both unweighted mean recruitment ($ss = 23.35E10$) and the commonly used geometric mean recruitment ($ss = 24.64E10$), with a minimum ss at $b = 36.53E3$ tons (Fig. 13).

The improvement in predictive ability using Cauchy weighting over the unweighted mean indicates that there is information in the spawner stock size with respect to recruitment. The probability that the resulting reduction in the prediction ss was obtained due to chance alone, can be estimated by an appropriate randomization test. The estimator using Cauchy weighting was applied 500 times on randomly shuffled recruitment data (i.e. each recruitment value randomly assigned to each spawner stock value for the 17 years). In only 17 cases the jackknifed prediction ss from the randomly shuffled data was less than or equal to that obtained from the correctly sequenced recruitment data. This implies that there is only a small probability ($p = 0.034$) that the prediction ss value obtained using the unshuffled data is due to chance alone.

Using the estimated minimum prediction ss value of b for the Cauchy weighting, the cumulative probability of recruitment at different spawner stock sizes can be computed (Fig. 14). This can be used to determine the probability of obtaining a recruitment of less than or equal to some specified value at different spawner stock sizes. Although there is a substantial shift to the right in the cumulative probability for a SSB of 500 000 tons compared to 100 000 tons, the cumulative curve for a SSB of 300 000 tons crosses over the cumulative curve for 100 000 tons as a result of several low recruitment values at intermediate SSB.

The low recruitment values at intermediate SSB are of considerable interest, particularly when the time sequence of the data are examined (Fig. 11). During the decline in SSB in the mid-1970s and the subsequent recovery in the late-1970s and early-1980s recruitment was substantially higher than that estimated for the period over the mid- to late-1980s. This change in RPS with time (non-stationarity in the S - R relationship) may invalidate the application of estimators that do not take the temporal pattern of

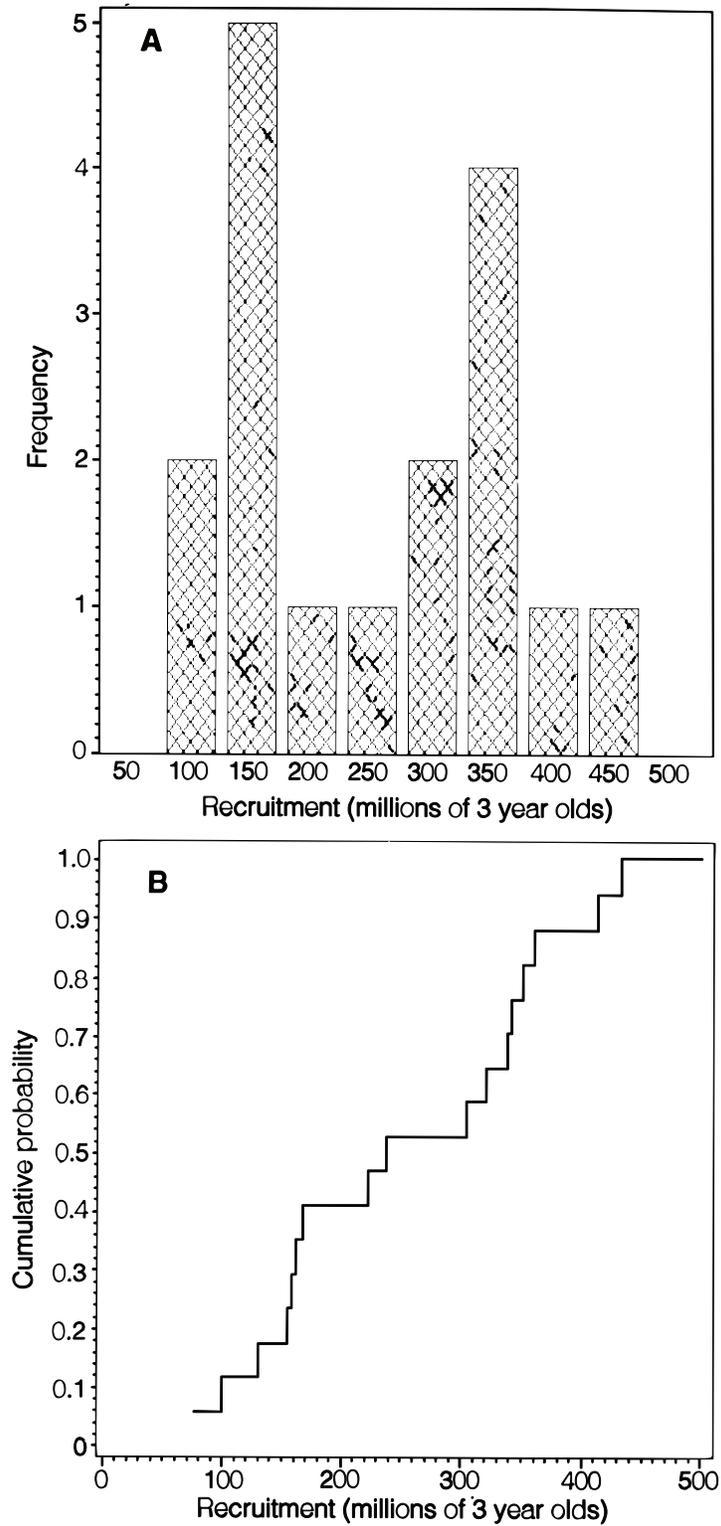


Fig. 12. (A) Frequency distribution and (B) cumulative probability plot for recruitment (millions of 3 year old fish) for the period 1973-89.

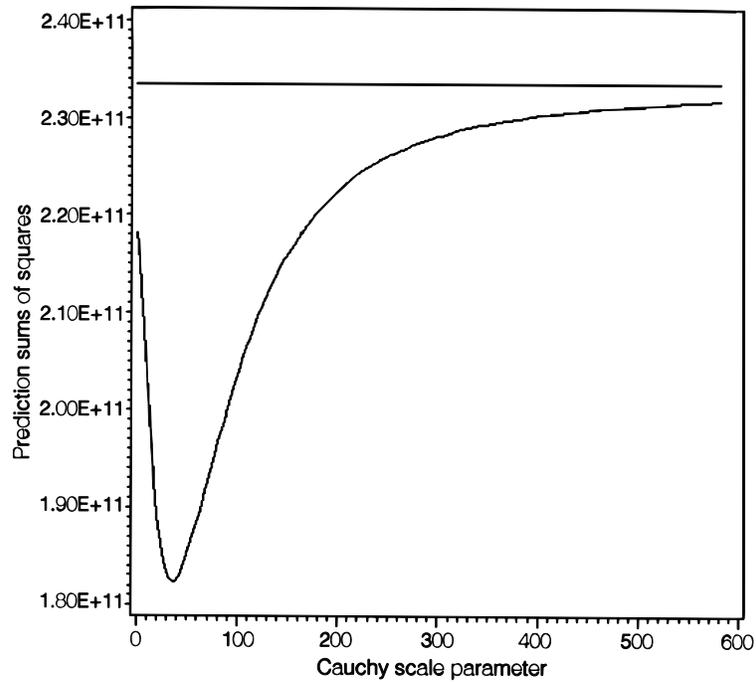


Fig. 13. Jackknifed prediction sums of squares using Cauchy weighting at different values of the scale parameter b . The horizontal line gives the jackknifed prediction sums of squares for the unweighted data.

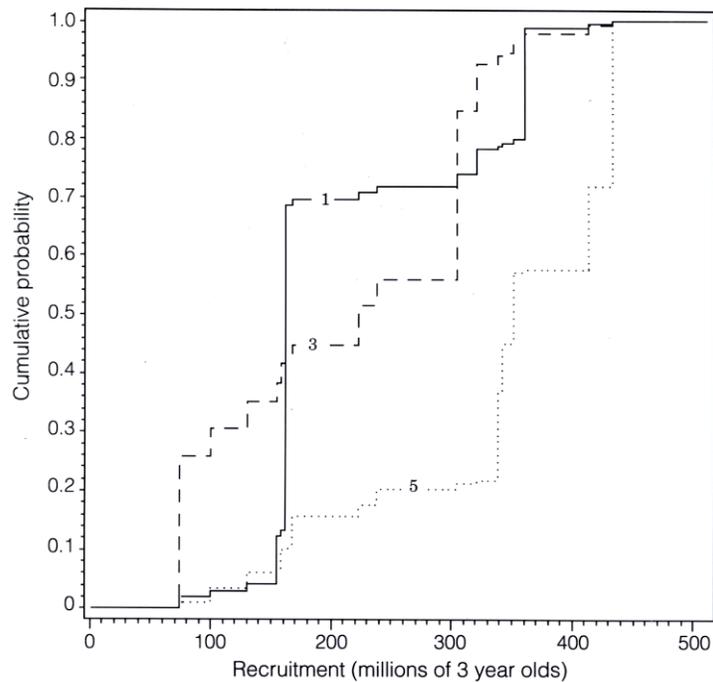


Fig. 14. The cumulative probability of recruitment at different spawner stock biomass levels (1 = 100 000 tons spawner biomass, 3 = 300 000 tons, 5 = 500 000 tons).

the data into account.

Because the time series is relatively short, complicated time series models may not be warranted. With this in mind, the simplest possible time series model was examined,

$$\hat{R}_j = R_{j-1} \quad (9)$$

The jackknifed prediction ss for the period 1974–89 using the unweighted mean recruitment was $20.39E10$. Using Cauchy weighting only, the prediction ss was lowered to $16.60E10$ ($b = 45.49E3$ tons). Using recruitment in the year before to predict recruitment in the current year using equation (9), gave a prediction ss of $14.41E10$, a substantially better prediction than using either the unweighted mean or the Cauchy weighted mean (Fig. 15). Using the value of recruitment in the year before as a predictor of recruitment in the current year is unlikely to be robust with respect to a decline in spawner biomass, and a predictor incorporating both spawner biomass and temporal pattern in recruitment may be more reliable. An estimator consisting of a weighted mean of the predictions from

Cauchy weighted recruitment and the value of recruitment in the year before was investigated,

$$\hat{R}_j = w \bar{R}^c + (1 - w)R_{j-1} \quad (10)$$

where w is the relative weight given to the two predictions and \bar{R}^c is the Cauchy weighted mean recruitment. Values of the two parameters, the relative weight w and the Cauchy scale parameter b , which minimised the jackknifed prediction ss were found using a grid search, illustrated by the noisy arc in Fig. 15. The prediction ss was minimized with parameter values $w = 0.43$ and $b = 44.20E3$ tons, with $ss = 11.72E10$. This combined model was promising, however its significance has yet to be examined using a randomization test.

Based on the analysis with spawner biomass only, the probability of achieving replacement recruitment was examined for 1990–92, the years for which no recruitment estimate currently exists from ADAPT (Fig 16). At the values of F estimated in Bishop *et al.* (MS 1993), it was estimated that there was a $p = 1$ that recruitment was less than that required to meet replacement in 1990 and only a slightly lower

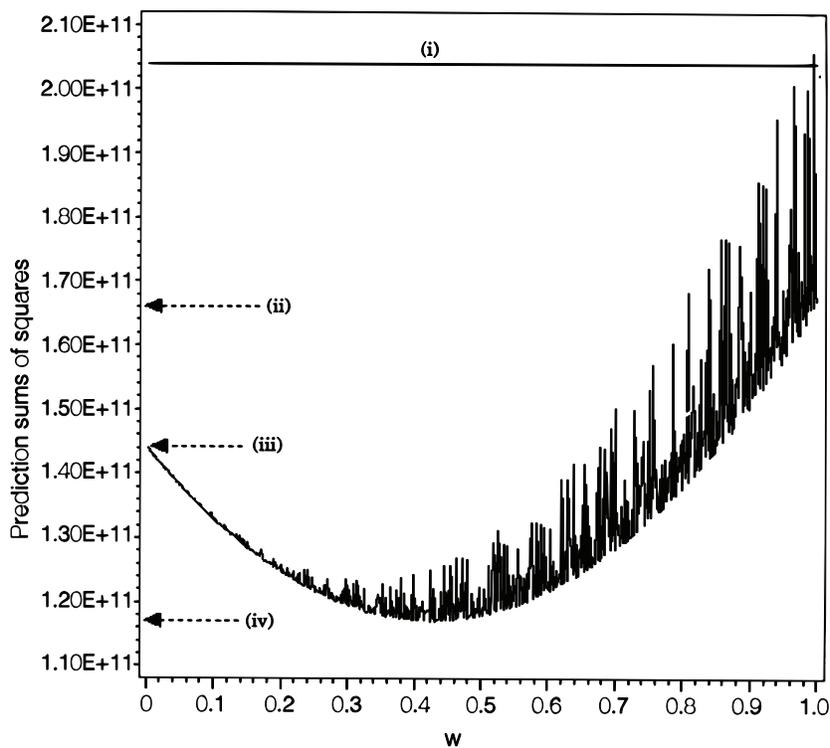


Fig. 15. Jackknifed prediction sums of squares for the 1974–89 using different estimators: (i) unweighted mean, (ii) Cauchy weighting, (iii) recruitment in the year before, and (iv) a combination of (ii) and (iii). The results of the grid search for parameters w and b for the combined estimator are shown by plotting the jackknifed prediction sums of squares against w .

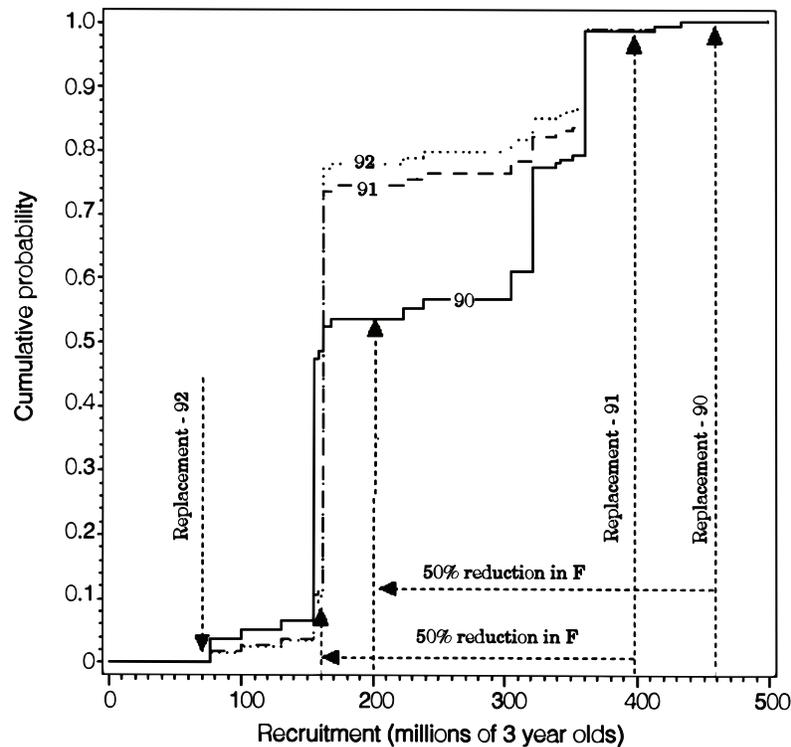


Fig. 16. The cumulative probability of recruitment corresponding to the biomass levels in 1990–92. Vertical broken lines indicate the position of the 1990, 1991 and 1992 replacement levels. The horizontal broken lines indicate the decreased probability of failing to meet replacement which could have been expected with a 50% reduction in fishing mortality in 1990 and 1991.

probability in 1991, whereas, as a consequence of the moratorium, this dropped to $p = 0$ in 1992. The decreased probability of good recruitment with the decline in the spawner biomass over the period 1990–92 was indicated by the shift in the cumulative frequency for recruitment values between 200 and 400 million. There is a considerable improvement in the probability of achieving replacement with a 50% reduction in F for both 1991 and 1992, indicating that lower fishing mortality in these years might have begun to arrest the decline in spawner biomass. Because annual replacement is an approximation to cohort replacement, the effect would of course not be immediate and would depend on F in subsequent years.

Discussion

Both annual replacement and average replacement are quantities calculated by simplifying true replacement by a cohort in an attempt to provide biological reference points which indicate whether a population is likely to grow or decline under different levels of F . The disadvantage of average replacement recruitment and associated reference

points such as F_{rep} is that they do not reflect important year-to-year changes in weights and proportions mature-at-age. Annual replacement is sensitive to these changes. Calculation of R^*_j per spawner or annual SPR at $F = 0$ are also useful steps in the assessment of stock status because they clarify the causes for changes in the level of recruitment required to meet replacement. Calculations of annual R^*_j per spawner at $F = 0$ demonstrated that the time trends in weights and maturities-at-age in the Div. 2J and 3KL cod stock have resulted in an increase in the recruitment per spawner required to meet replacement over the period 1980–87, as a consequence of changes in weights and maturities-at-age.

Non-parametric analysis of S–R data can provide a probabilistic prediction of recruitment in the most recent years for which recruitment estimates are not available. These predictions can be used, together with calculations of replacement levels at current weights and maturities-at-age to determine the probability of meeting replacement at different values of F .

The analyses conducted in this paper suggest that biological reference points and management targets for the northern cod stock, and perhaps for other groundfish stocks, should incorporate annual estimates of weights-at-age and proportions mature-at-age, particularly where trends in these values are found to occur. The use of averages to calculate quantities such as replacement for such stocks is likely to be misleading. Application of this approach to the northern cod shows that recruitment was below annual replacement from 1983 onwards, precipitating the stock decline. Predicted recruitment from the non-parameteric analysis suggests that the 1990 and 1991 year-classes were also below annual replacement. However, reduction in fishing mortality in 1992 as a result of the moratorium suggests that, even though the probability of good recruitment is low at low spawner biomass, there is a low probability that it will have failed to meet the 1992 replacement level.

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