

# Effect of changes in reproductive potential on perceived productivity of three Northwest Atlantic cod (*Gadus morhua*) stocks

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Variation in maturity-at-age, sex ratio, and potential egg production (through changes in length at age) were examined for northern cod (NAFO Division 2J + 3KL), southern Grand Bank cod (3NO), and southern Newfoundland cod (3Ps). All showed significant interannual variability in each stock. Estimates of reproductive potential were produced by sequentially incorporating estimates of proportion mature at age, sex ratio at age, and potential egg production. The estimates of reproductive potential produced by each method were broadly similar, but there were important differences. This leads to differing perceptions of stock productivity, as measured by relative rate of recruitment of a stock and in the spawning stock produced per recruit. These differing perceptions can have a major impact on expectations for the recovery of depleted stocks and the sustainability of various levels of fishing. Efforts should be made to improve estimates of reproductive potential by further exploring the impacts of changes in the spawning characteristics of populations, and by collecting such basic information as fecundity data.

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## Introduction

Several factors contribute to the number of recruits produced by a fish population. The composition of the spawning stock, particularly the age structure, is important and may affect the spawning success of the population (Lambert, 1990; Kjesbu *et al.*, 1996; Marteinsdottir and Thorarinnsson, 1998; Trippel, 1998). Variation in condition of the spawners can result in changes in fecundity and/or viability of eggs and larvae, or even in failure to spawn (Marshall *et al.*, 1998; Marteinsdottir and Steinarsson, 1998; Lambert and Dutil, 2000; Rideout *et al.*, 2000). The sex ratio of the spawning stock can also vary, leading to changes in egg production (Marshall *et al.*, 1998; Kraus *et al.*, 2002). Moreover, the proportion of fish that are mature at each age can change substantially over time (Rijnsdorp, 1989; Jørgensen, 1990; Hunt, 1996; Morgan and Colbourne, 1999). The combination of these factors will determine a population's reproductive potential (Trippel, 1999).

The relationship between spawning stock biomass (SSB) and recruitment is the basis for determining biological reference points under the precautionary approach. Limit reference points are generally chosen as the SSB below which recruitment is seriously impaired (Mace and Sissenwine, 1993; Shelton and Rivard, 2003). Additionally, predictions about the potential for depleted stocks to rebuild will depend on the underlying assumptions about the stock-recruit relationship. Use of SSB assumes that it is a good estimate of stock reproductive potential. If it is not a good predictor of recruitment, then our ability to set limit reference points and predict stock recovery will be seriously impaired (Murawski *et al.*, 2001).

Three cod (*Gadus morhua*) populations in the Northwest Atlantic, northern cod (NAFO Divisions 2J + 3KL), southern Grand Bank cod (Divisions 3NO), and southern Newfoundland cod (Subdivision 3Ps; Figure 1), have undergone major declines in population size in the past decades (Lilly *et al.*, 2001; Brattey *et al.*, 2002; Healey

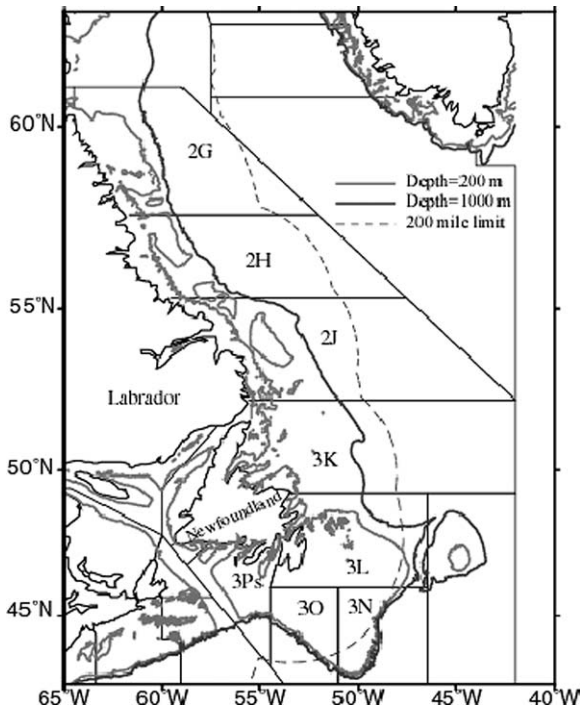


Figure 1. The study area, showing the Northwest Atlantic Fisheries Organization Divisions. The 200 and 1000-m depth contours, and Canada's 200 mile limit are shown.

*et al.*, 2003). Each supported commercial fisheries until the early 1990s, but only the southern Newfoundland cod population has recovered to a size capable of sustaining a commercial fishery. Despite the potential for a number of the factors affecting stock reproductive potential to vary with population size (Trippel, 1995; Marshall *et al.*, 1998; Jakobsen and Ajiad, 1999; Morgan and Colbourne, 1999), there has been little examination of these factors for these commercially important cod populations. In particular, there has been little study of changes in maturation, sex ratio, or potential egg production (though see Olsen *et al.*, 2004, for some analyses of changes in maturation).

The purposes of this study were to quantify the extent and variability of changes in maturity, sex ratio, and potential egg production at age in northern cod, southern Grand Bank cod, and southern Newfoundland cod, and to determine the impact of any changes in these factors on estimates of reproductive potential. We also explored the impact of variability in these factors on perceived stock productivity, by examining differences in the rate of recruitment and in the spawning stock produced per recruit.

## Methods

### Maturity

Female maturity data were collected during research vessel bottom-trawl surveys. For 2J + 3KL cod, data were

available from 1963 to 2002, the number of females examined for maturity ranging annually from 55 to 1472. In only 5 years were fewer than 100 females sampled. Data from 1960 to 2002 were available for 3NO cod, and sample size ranged from 18 to 810, only 3 years yielding fewer than 100 fish. For 3Ps cod, data were available continuously from 1972 to 2002 and for 8 years in the 1960s. Sample size ranged from 94 to 664, and there was just 1 year when fewer than 100 fish were examined. For the three cod stocks combined, only three cohorts had a sample size of <100. Stratified random surveys were used where possible (1978–2002 for 2J + 3KL cod, 1971–2002 for 3NO cod, 1972–2002 for 3Ps cod). Data from earlier years came from surveys that were conducted mainly as line transects, during which the coverage of a stock area would generally not be as complete as in stratified random surveys. For 3NO cod, spring survey information was used (mainly May and June), for 2J + 3KL cod, data were from autumn (October–December), and for 3Ps cod, the timing of the surveys varied from February to June, though most data came from spring (February–April). Females were classed as immature (juvenile) or mature (adult) according to the classification of Templeman *et al.* (1978), following macroscopic examination of the gonad. In this classification, the earliest stage is immature, and all other stages show some evidence of maturing to spawn, spawning, or having spawned in the past, so were classed as mature. For the period of the stratified random surveys, the observed proportion mature at age was calculated according to the method of Morgan and Hoening (1997), to account for the length-stratified means of sampling. Prior to this, only data from the aged fish were used, without weighting by the length frequencies, but this should not have had a large impact on model estimates (Morgan and Hoening, 1997).

Maturities were modelled by cohort using a generalized linear model with a logit link function and binomial error (McCullagh and Nelder, 1983; SAS Institute Inc., 1993). Age was modelled as a continuous variable. For the logit link function,

$$\eta = \log\left(\frac{\mu}{1 - \mu}\right)$$

and

$$\eta^{-1} = \left(\frac{1}{1 + \exp(-x)}\right) = \text{proportion mature}$$

where  $x = \tau + \gamma A + \psi_i$ ,  $\tau$  is an intercept,  $\gamma$  an age cohort interaction effect,  $A$  the age ranging from 1 to the maximum age observed in a cohort, and  $\psi_i$  is the cohort effect for each cohort.

Only cohorts with both a significant slope and a significant intercept in single cohort model fits were included in the overall model. For 2J + 3KL cod the 1961, 1963, 1968, and 1970 cohorts were excluded, for 3NO cod the 1991 cohort was excluded, and for 3Ps cod the 1963 cohort was

excluded. For excluded cohorts, the average of the two adjacent cohorts was used. For the earliest and latest cohorts for which maturities could not be estimated, the average of the three closest cohorts was used. Age at 50% maturity ( $A_{50}$ ) was calculated for each cohort to illustrate trends. In addition, the data were tested for a significant cohort effect, using generalized linear models where the effect of age was first removed and cohort was considered to be a class variable.

### Sex ratio

Observed sex ratio was calculated as the proportion female at age calculated from estimates of population numbers at age by sex, from stratified analysis programs applied to stratified random research vessel data (Smith and Somerton, 1981). These proportions were examined for significant cohort and age effects, using generalized linear models with a logit link function and binomial error. Cohort and age were modelled as class variables. In this case age was treated as a class variable, because there was no *a priori* reason to believe that sex ratio would change continuously across age. The fitted models were used to produce estimates of sex ratio at age for each cohort.

### Fecundity

Time-invariant relationships between fecundity and cod length were used to estimate the number of eggs produced at each age. The relationships were taken from May (1967) and Pinhorn (1984), and they estimate the total number of eggs produced. The relationships were:

$$\begin{aligned} 2J + 3KL \text{ Log fecundity} &= 3.63 \times \log \text{ length} - 0.64 \\ 3NO \text{ Log fecundity} &= 3.97 \times \log \text{ length} - 1.45 \\ 3Ps \text{ Log fecundity} &= 3.37 \times \log \text{ length} - 0.38 \end{aligned}$$

Mean lengths at age from the commercial fishery were examined for significant differences across cohort, by examining residuals from regressions of length on age for cohort effects. Yearly length-at-age data were not available prior to 1971 for 2J + 3KL and 3NO cod, or prior to 1976 for 3Ps cod. To extend the time-series to the period before collection of length data began, all lengths at age in that period were set as equal to the mean lengths at age in the first year of the length-at-age data series. The fecundity-length equations were then applied to the mean lengths at age to produce a time-series of fecundity at age. For the time period prior to the availability of annual length data, the fecundity at age would be the same in each year.

### Indices of reproductive potential

To examine the possible impact of changes in maturity, sex ratio, and fecundity (through changes in length), several different indices of reproductive potential (RP) were calculated. The basis for all calculations was the number

at age from sequential population analysis (SPA) and the mean weight at age for each stock, both from the beginning of the year (Shelton and Lilly, 2000; Brattey *et al.*, 2002; Healey *et al.*, 2003).

The first estimate of RP (knife-edge maturity) assumed no change in the maturity schedule of the fish and that the spawning stock was simply the sum of the biomass above a certain age. Biomass was calculated by multiplying the weights at age described above by half the estimate of the population number at age. This biomass was summed over the ages that were used historically in the calculation of RP for these stocks; these were age 7+ for 2J + 3KL, and age 6+ for 3NO and 3Ps cod. This method of calculating RP assumes that the sex ratio is unity for all ages and cohorts. Thus,

$$RP_{\text{knife edge}} = 0.5 \sum_{a=i}^j N_{ay} W_{ay} \tag{1}$$

where  $N_{ay}$  is the population number at age  $a$  in year  $y$ ,  $W_{ay}$  the weight at age  $a$  in year  $y$ , and  $a$  is the age from  $i$  to  $j$ :

$$\begin{cases} 2J + 3KL & i=7, \quad j=20 \\ 3NO & i=6, \quad j=12 \\ 3Ps & i=6, \quad j=14 \end{cases}$$

The second estimate of RP (variable maturity) incorporates the estimated proportion mature at age for each cohort, by multiplying half the population number at age by the weight at age and estimated proportion mature at age. This estimate will show the impact of any changes in maturation over time:

$$RP_{\text{variable maturity}} = 0.5 \sum_{a=i}^j N_{ay} W_{ay} M_{ay} \tag{2}$$

where  $M_{ay}$  is the proportion mature at age  $a$  in year  $y$ , a the age  $i$  to  $j$ :

$$\begin{cases} 2J + 3KL & i=2, \quad j=20 \\ 3NO & i=2, \quad j=12 \\ 3Ps & i=2, \quad j=14 \end{cases}$$

and the other symbols are as defined above, except that the age range was as described for  $M_{ay}$ .

In the third estimate of RP (sex ratio), we applied the variable sex ratios estimated along with the estimates of proportion mature at age:

$$RP_{\text{sex ratio}} = \sum_{a=i}^j N_{ay} W_{ay} M_{ay} R_{ay} \tag{3}$$

where  $R_{ay}$  is the proportion female at age  $a$  in year  $y$ , and the other symbols are as defined above.

The fourth estimate of RP incorporated estimates of fecundity (egg production). The series of fecundity at age derived from the fecundity-length relationships and the

mean length at age as described above was multiplied by the population number at age times the proportion mature at age times the sex ratio at age:

$$RP_{\text{egg production}} = \sum_{a=i}^j N_{ay} M_{ay} R_{ay} E_{ay} \quad (4)$$

where  $E_{ay}$  is the number of eggs produced per female at age  $a$  in year  $y$ , and the other symbols are as defined above.

### Stock productivity

The number of recruits was taken to be the number of 2-year olds derived from SPA. The recruitment rate ( $RPS = \text{recruits}/RP$ ) was calculated for each index of reproductive potential for each population. The RPS from each index was then standardized to the mean rate for the index to facilitate comparison. The biomass of spawners (or number of eggs) produced per recruit (SPR) was also calculated for each stock, using each method of estimating the RP of the stock. This was calculated starting with one recruit at age 0, so that

$$N_{j+1} = N_j e^{-Z} \quad (5)$$

where  $Z = F + M$ , and  $M = 0.2$ .

For each age from 0 to the maximum age in the SPA (see above), the biomass of spawners (or number of eggs) produced was calculated according to the equations for reproductive potential given above, and inserting the number at age from Equation (5). The result was then summed across all ages to give the SPR for each index. This was done assuming that fishing mortality was zero ( $F = 0$ ), and the fishing mortality estimated in the SPA ( $F$ ). Each series of SPR was standardized to its mean for comparison.

## Results

There was a significant effect of cohort on the proportion mature at age in all three stocks (2J + 3KL:  $\chi^2 = 435$ , d.f. = 37,  $p < 0.0001$ ; 3NO:  $\chi^2 = 641$ , d.f. = 43,  $p < 0.0001$ ; 3Ps:  $\chi^2 = 1045$ , d.f. = 42,  $p < 0.0001$ ). Age at 50% maturity has declined in all stocks (Figure 2); fish now mature younger. The  $A_{50}$  in all stocks has declined by at least a year, from  $>6.5$  years to 5.5 years or less. The largest decrease was in 3Ps, where the  $A_{50}$  declined from about 7 years at the beginning of the time-series to 5.0 years for the most recent cohorts.

Sex ratio varied significantly across age and cohort. For 2J + 3KL, there was a higher proportion female among older ages and among more recent cohorts (Figure 3; age:  $\chi^2 = 25$ , d.f. = 12,  $p = 0.02$ ; cohort:  $\chi^2 = 37$ , d.f. = 19,  $p = 0.007$ ). For 3NO cod, older ages also had a higher

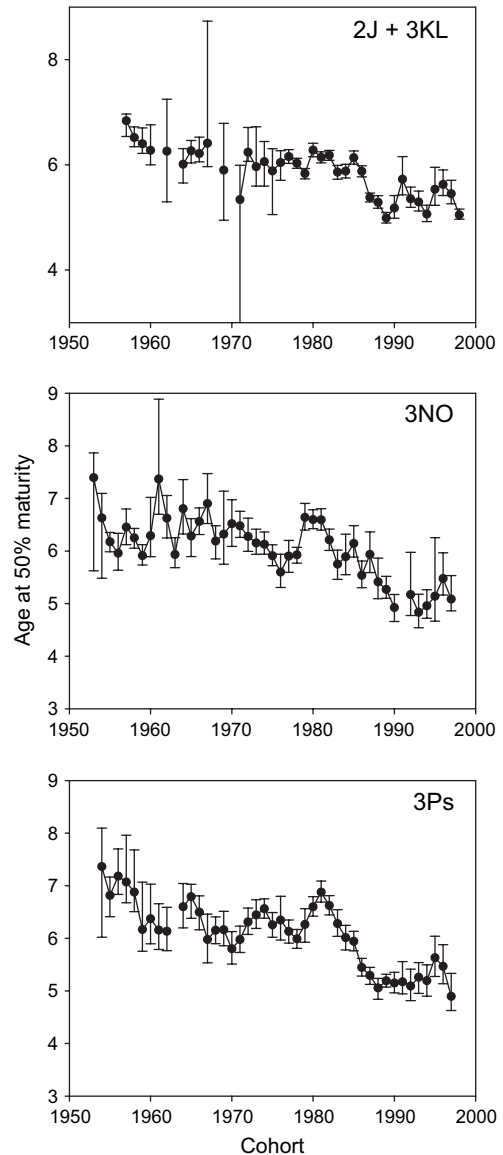


Figure 2. Estimated age at 50% maturity ( $\pm 95\%$  fiducial limits) by cohort for female cod in 2J + 3KL, 3NO, and 3Ps.

proportion female ( $\chi^2 = 27$ , d.f. = 9,  $p = 0.001$ ), though cohorts from 1970 to about 1987 had a lower proportion female (Figure 3;  $\chi^2 = 91$ , d.f. = 30,  $p < 0.0001$ ). For 3Ps there was also a tendency for the proportion female to increase at older ages, at least to age 12, although the significance was marginal ( $\chi^2 = 19$ , d.f. = 11,  $p = 0.06$ ). There was a significant cohort effect for 3Ps ( $\chi^2 = 60$ , d.f. = 33,  $p = 0.0002$ ), but no clear trend. All populations showed a tendency for the proportion female to increase with age from age 3 to age 5 or 6, then a decline to age 9 or 10. 2J + 3KL and 3NO proportion female increased after age 10, but for 3Ps, sex ratio increased to age 12 and then declined, the lowest sex ratios being at the oldest ages.

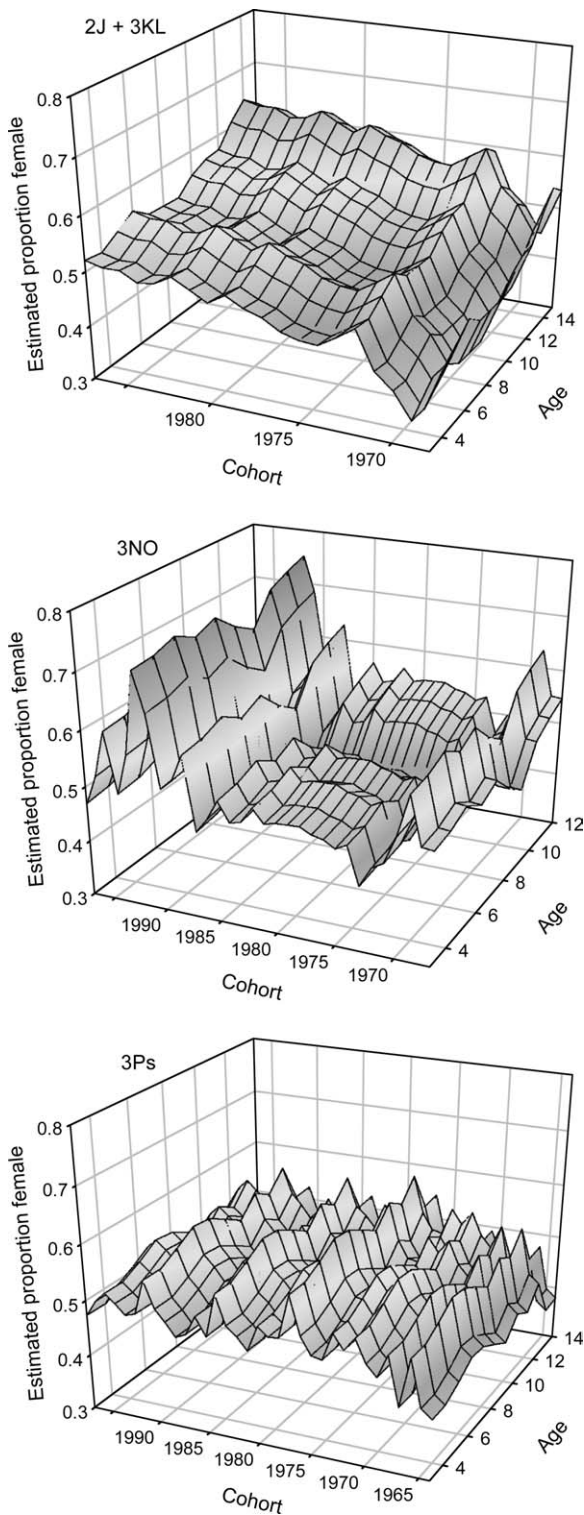


Figure 3. Estimated proportion female by age and cohort for cod in 2J + 3KL, 3NO, and 3Ps.

Each population showed significant variation across cohort in the residuals from a model accounting for the effect of age on length. This indicates a significant difference among cohorts in mean length at age (2J + 3KL:  $F = 5.7$ ,  $d.f. = 41$ ,  $p < 0.0001$ ; 3NO:  $F = 6.4$ ,  $d.f. = 38$ ,  $p < 0.0001$ ; 3Ps:  $F = 6.3$ ,  $d.f. = 35$ ,  $p < 0.0001$ ). As an example, mean length at age 8 is shown in Figure 4: it generally declined for all three stocks in the cohorts subsequent to the early to mid-1970s, but then increased after the 1985 or 1986 cohort. Assuming a constant fecundity-length relationship across time for each population, this would result in substantial differences in the number of eggs produced (Figure 4). For example, for

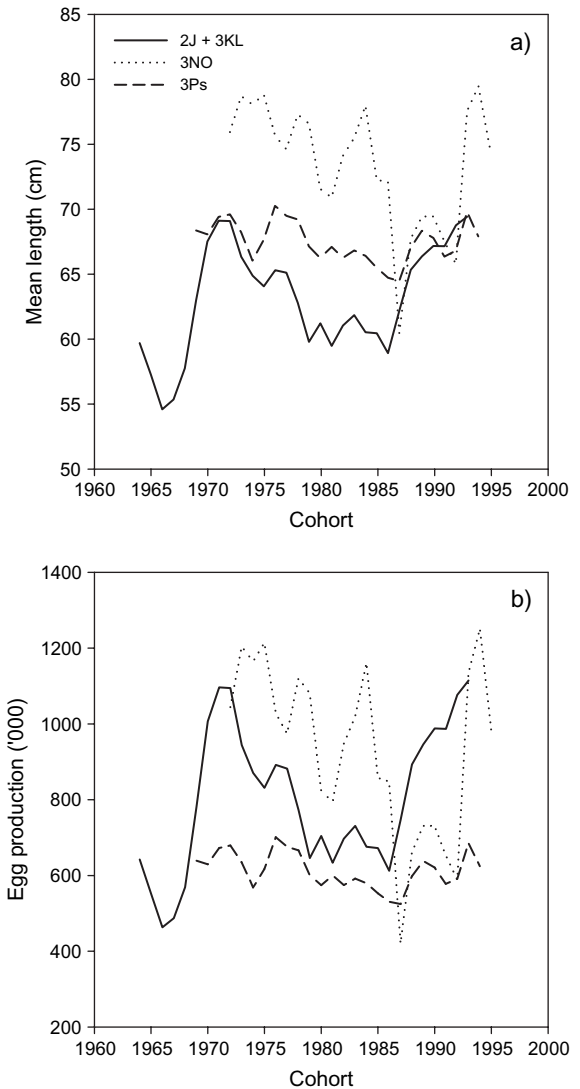


Figure 4. (a) Mean length at age 8 by cohort from the commercial fishery for cod in 2J + 3KL, 3NO, and 3Ps. (b) Predicted egg production at age 8 using stock-specific relationships between fecundity and length.

2J + 3KL and 3NO cod, the range in mean length at age 8 was sufficient to produce a 2.5–3-fold range in egg production. The range in length at age 8 in 3Ps was narrower, resulting in egg production varying by a factor of 1.3.

For all stocks, the overall trends in RP are similar regardless of the method of estimation (Figure 5). However, there are some important differences. For example, egg production was greatest in 3Ps in 1985, whereas the highest

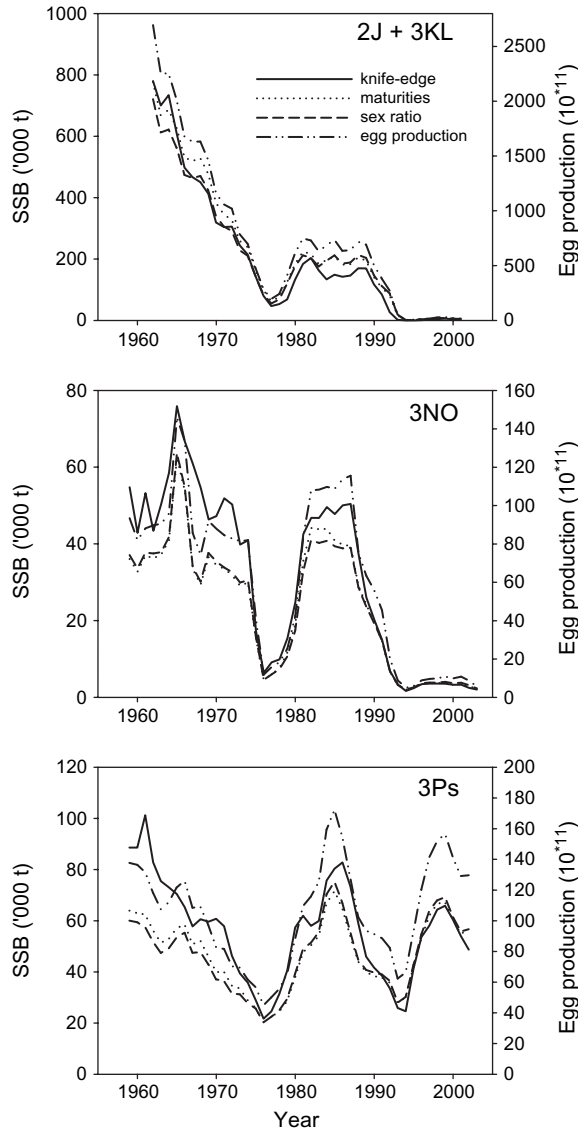


Figure 5. Estimates of reproductive potential as biomass or egg production for 2J + 3KL, 3NO, and 3Ps cod. Estimates are produced using the biomass of all fish greater than a specific age (knife edge), using estimates of proportion mature at age (maturities), using maturities and estimated sex ratio (sex ratio), and by calculating egg production using variable maturity, sex ratio, and estimated fecundity at age.

RP with knife-edge maturity was in 1961. The peak in RP for egg production, variable maturity, and sex ratio in 3Ps in the mid-1980s occurs 1 year before the peak in knife-edge RP. In the last year of RP using knife-edge maturity declined, whereas all other indices increased slightly. For 3NO, RP decreased through the 1980s when calculated using variable maturity at age and sex ratio, whereas estimates using knife-edge maturity and potential egg production both increased over the same period. For 2J + 3KL cod, the trends in RP were similar across the indices, but small differences are apparent. For example, in the early part of the time-series, the index using knife-edge maturity declined continuously from 1964 to 1971, whereas all other indices showed a slight increase between 1967 and 1968. In the early 1980s, the index using knife-edge maturity peaked 1 year later than the other indices of RP. The level of variability was highest in all stocks using knife-edge maturity to estimate RP, but for each stock the CVs varied by <15% across indices.

The absolute level of difference between the indices can be compared for knife-edge maturity, variable maturity, and sex ratio. The maximum difference between knife-edge maturity and the other two indices was large in all cases, ranging from 27 000 to 112 000 t for the three stocks. For 3NO and 3Ps, the maximum difference between the index using variable maturity and the one incorporating sex ratio was small at 4000 and 5000 t, respectively. For 2J + 3KL, the maximum difference between the same two indices was 64 000 t.

Trends in the standardized rate of recruitment for each index also show the same overall patterns within each population (Figure 6). However, depending on the index used, there is a different impression of the relative productivity of a population across time. The clearest example is for 2J + 3KL cod. RPS for that stock, calculated using knife-edge maturity as RP, was below average at the beginning of the time period, and peaked recently at more than twice the average. In contrast, the index using egg production was above average at the beginning of the time period, and in the same year (1994) that the RPS for the index using knife-edge maturity was more than twice its average, that for the egg production index was only 1.3 times its average. From 1993 to 1996, RPS using the index based on knife-edge maturity would give the impression of a much higher relative productivity than the other indices of RP. There is little difference in the RPS for the four indices across the time period for 3NO cod, except for a divergence in indices in the late 1960s. For 3Ps cod there are some differences between indices. For example, the RPS for knife-edge maturity is the lowest at the beginning of the time-series and highest at the end of the series. However, the differences tend not to be as large as for 2J + 3KL cod. The extent of difference in the indices of RP for a population provides an indication of the difference in the stock-recruit relationship between the various indices. Although the stock-recruit relationships do differ to some extent, it is not

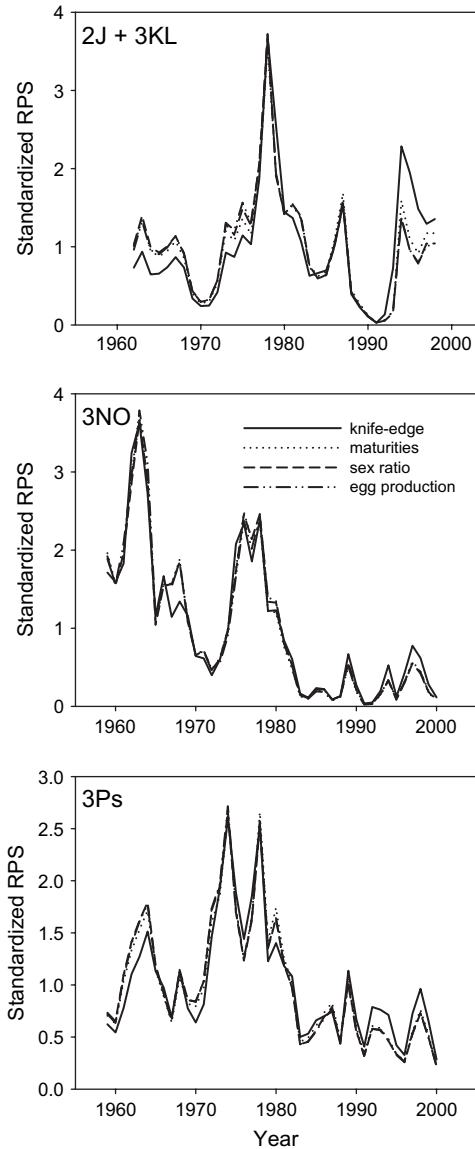


Figure 6. Standardized recruitment rate (recruits/spawner; RPS) from each estimate of reproductive potential for 2J + 3KL, 3NO, and 3Ps cod.

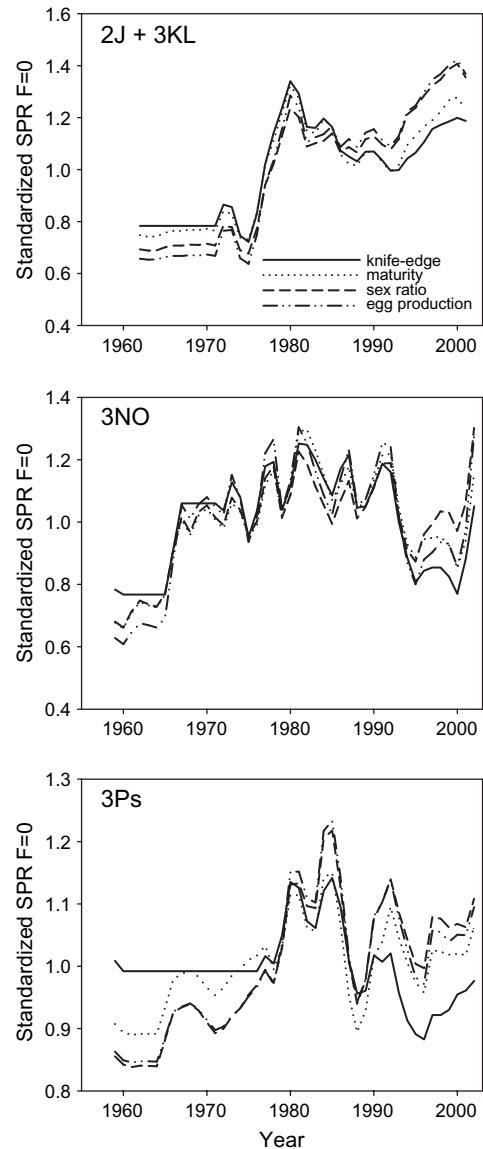


Figure 7. Standardized spawner per recruit (SPR) at  $F = 0$  from each method of calculating reproductive potential for 2J + 3KL, 3NO, and 3Ps cod.

clear at this stage that any one of them provides a “better” relationship between RP and recruitment.

At an assumed  $F = 0$ , there are differences in the trends in standardized SPR between the different indices of RP, particularly for 3Ps (Figure 7). For 2J + 3KL cod, the standardized SPR for all indices was below average through the 1960s and 1970s. The SPR calculated as egg production was the lowest of the indices during that period, while knife-edge SPR was the highest. In 1986 this switched, and from then on knife-edge SPR was the lowest of the indices and egg production the highest. All show the same general increase since 1992, but the rate of increase has been lower

(19%) for knife-edge maturity than for the other indices (25%). The different indices of SPR at  $F = 0$  were similar over most of the time period for 3NO cod. As with 2J + 3KL, standardized knife-edge SPR began as the highest of the indices, but in the mid-1980s became the lowest. The largest divergence in standardized SPR began in the mid-1990s. For 3Ps cod, standardized SPR using knife-edge maturity again was the highest of the indices at the beginning of the time-series, dropping to the lowest in 1990. While the other indices of SPR have been above average for most of the period since 1990, knife-edge SPR has been below average.

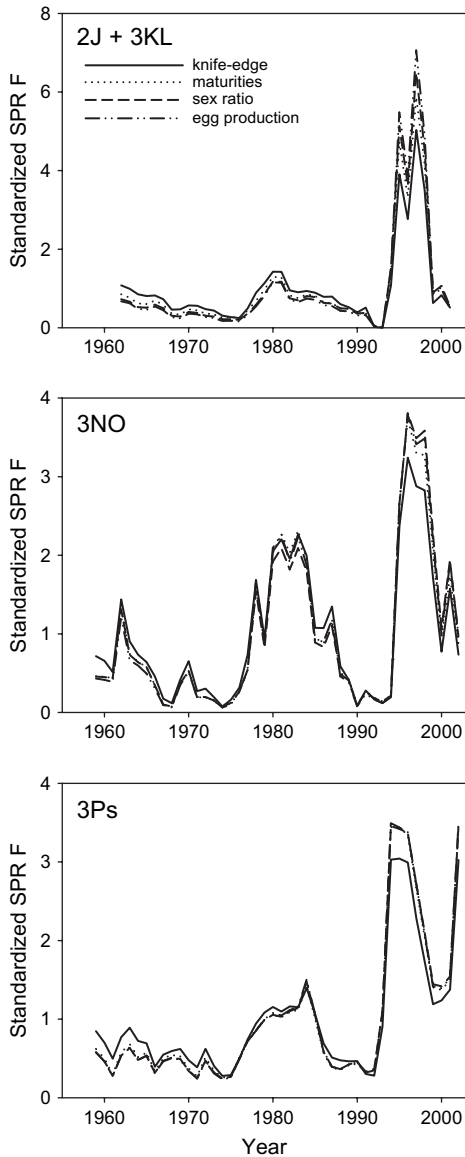


Figure 8. Standardized spawner per recruit (SPR) at actual  $F$  from each method of calculating reproductive potential for 2J + 3KL, 3NO, and 3Ps cod.

When SPR is calculated incorporating the actual  $F$  estimated in the SPA, the standardized SPR is similar using all methods, except when  $F$  is low (Figure 8). For 2J + 3KL cod, the greatest difference between indices was from 1995 to 1998, when the average SPR for egg production was 5.3 times the average of the entire series, while the other indices were from 3.8 to 4.9 times the average. The greatest difference in 3NO cod was in the period 1995–1999, when the standardized SPR for variable maturity, sex ratio, and egg production were all above 3, whereas that for knife-edge maturity was 2.5. In 3Ps during the period 1994–1997, the average standardized SPR for

knife-edge maturity was 2.8, whereas those for variable maturity, sex ratio, and egg production were all above 3.2. For each stock, the largest difference between indices of SPR was during the period when average  $F$  was the lowest in the time-series. The deviation of SPR from the mean during these periods was much greater than any deviation seen in the estimates of SPR for  $F = 0$ . The CV was highest for SPR as egg production, and lowest for knife-edge maturity in all stocks at both  $F$  and  $F = 0$ . However, the difference in variability in the indices was much greater at  $F$  (20–50%), than at  $F = 0$  (5–8%).

## Discussion

The northern cod, southern Grand Bank cod, and southern Newfoundland cod stocks have all shown major changes in population size over the past 40 years. During this period, variables fundamental to stock reproductive potential, i.e. maturity, sex ratio, and potential egg production, have also changed significantly. Incorporation of this information into estimates of reproductive potential leads to different perceptions of the size of the spawning stock and levels of stock productivity.

All three populations varied substantially in the proportion mature at age, with a trend towards maturing younger. Such variability in maturation is not uncommon (Rijnsdorp, 1989; Jørgensen, 1990; Hunt, 1996; Morgan and Colbourne, 1999). Maturation at a younger age is often associated with declines in population size (Trippel, 1995), and may be a genetic response to increased mortality (Olsen *et al.*, 2004). Both 2J + 3KL and 3NO cod populations have declined to and remained at low levels, but the cod population in 3Ps declined and then recovered, though  $A_{50}$  remains low. The reasons for this are not known, and it will be of interest to see whether age at maturity changes for this population in the near future.

Changes in the proportion mature at age have direct impacts on estimates of reproductive potential. Any assumption of constant rates of maturity rates (either knife-edge maturity, or a single maturity ogive) over extended time periods will fail to account for this important, and common aspect of life history variation. Decreases in the actual proportion mature at age relative to an assumed constant rate of maturation will result in an overestimate of RP, whereas increases will result in RP being underestimated.

Sex ratio was also variable within each stock. There were temporal trends, as well as trends across age. Other cod populations exhibit variability in sex ratio (Hunt, 1996; Marshall *et al.*, 1998; Jakobsen and Ajiad, 1999; Kraus *et al.*, 2002). Differences in sex ratio could be a combined result of differential spawning mortality between sexes, and changes in fishing mortality on the sexes (Jakobsen and Ajiad, 1999). For calculations of RP not including sex ratio, there is an implicit assumption that sex ratio is 50:50, or at



least that it is invariant over time. If sex ratio does vary temporally, then an inconsistent bias will be introduced to the estimate of the RP.

Changes in estimated length at age resulted in substantial variation in estimated egg production, even with the use of constant fecundity–length relationships. Condition and/or growth, as well as temperature, are likely correlated with fecundity, so fecundity at length is unlikely to have been constant over this time period (Rijnsdorp, 1991; Kjesbu *et al.*, 1998; Kraus *et al.*, 2002; Blanchard *et al.*, 2003; Lambert *et al.*, 2003). Clearly, including variability in fecundity would be a preferred method to that used here. Studies of interannual variation in fecundity have found that relative fecundity can vary by 30–40% (Kjesbu *et al.*, 1998; Kraus *et al.*, 2000). Pinhorn (1984) found that fish of the same length could have a twofold difference in fecundity between years. In a study of RP in northeast Arctic cod, Marshall *et al.* (1998) were able to use the relationship between condition and fecundity to incorporate interannual variation in fecundity into estimates of egg production. However, no proxies for fecundity exist for these populations, so updated fecundity estimates are not available. Fecundity data are fundamental to estimating stock reproductive potential, but such data have not been collected routinely for most fish stocks (Tomkiewicz *et al.*, 2003).

All indices of RP calculated for a given stock showed broadly similar trends for that stock. There were, however, differences in the relative size and timing of some of the peaks and troughs in RP. Differences between indices of RP are a result of variation in maturity, sex ratio, and fecundity (through length-at-age), but also a result of changes in age composition of the spawning stock. The different trends in RP lead to variation in the stock-recruit relationships derived from the indices, as evidenced by the differences in RPS. Therefore, the limit reference points derived from these relationships, as well as information on current stock status relative to these reference points, may vary. The extent of this variation has not been examined in this study, but our results do highlight the importance of deriving estimates of RP that can be used to predict recruitment accurately.

The divergence between the indices of RP produced differences in the perception of recruitment rate of a stock over time. The largest differences in RPS were for 2J + 3KL cod where, in the mid-1990s, RPS ranged from slightly above average to more than two times the average, depending on the estimate of RP. Expectations for recovery of that stock would be very different depending on the recruitment rate used in stock projections.

Another indicator of stock productivity is SPR. An assumption of  $F = 0$  gives insight into the potential productivity of a stock under no exploitation. The trends in these metrics were quite different using different methods to calculate the spawning stock. For example, for 2J + 3KL cod, the knife-edge index of RP showed a <20% increase in stock productivity since 1992, whereas the other indices

increased by 25%. In 3Ps cod, knife-edge RP gave recent stock productivity as less than average, though the other indices were above average. These different perceptions of stock productivity would lead to different estimates of recovery time or sustainable harvest rate for these stocks.

When SPR was calculated using actual  $F$ , the trends were similar for the different indices, but there were large differences in the magnitude of the standardized SPR during periods of low  $F$ . These results indicate that trends in SPR may be associated with trends in  $F$ , except when  $F$  is low. At low  $F$ , the perceived level of productivity will differ, depending on the method used to calculate the spawning stock. These results are consistent with those of a modelling study conducted by Scott *et al.* (1999), who showed only a small effect of different measures of RP on recruitment when populations were subjected to fishing mortality.

Estimates of RP that include more information on variability in the biology of the spawning fish lead to different perceptions of trends in stock productivity over time. It is not clear at this stage whether the predictability of recruitment will be improved for those populations by use of more realistic estimates of RP. Efforts should continue to explore the impact of this variability on estimates of RP, and the implications for stock-recruit relationships and reference points.

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