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Declining Weight-at-age in Northern Cod and the Potential Importance of the Early Years and Size-selective Fishing Mortality

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Abstract

Weight-at-age of northern cod (*Gadus morhua*) declined between 1979 and 1993 for all age-classes, with the greatest reduction in size-specific growth evident at ages 3, 4 and 5. The extent to which the declines in weights at these young ages have been responsible for smaller weights in older age-classes was determined. On average 68% of the decline in weight of 4- to 8-year-olds was attributable to a decline in weight-at-age in previous years. Differences in weight-at-age among cohorts suggested that cohorts that are small early in life tend to remain small, and that size in early years greatly influences future production. These findings suggest that the environment for growth may have worsened specifically for these young ages, highlighting the importance of studying what is affecting growth processes in the early years. These results also point to the possibility that size-selective fishing on the 3- to 5-year-olds may have played an important role in the decline in weight-at-age.

Key words: Atlantic cod, growth, size-specific growth, weight-at-age

Introduction

The weight-at-age of northern cod (*Gadus morhua*) has been declining over the last 15 years on the Labrador and Newfoundland shelves (Div. 2J and 3K) (Bishop *et al.*, MS 1995). On average, a cod of a given age in 1979 weighed almost twice as much as a cod of the same age in 1993 (Fig.1). Fish growth rates exhibit a high degree of plasticity depending largely on temperature and food availability. Weight-at-age of Atlantic cod can vary up to 12-fold among stocks (Brander, 1995) and up to 2- to 3-fold among years within a given stock (Sinclair *et al.*, MS 1995). These variations in growth rate affect current production as well as future production because larger fish are more fecund.

The low weights-at-age in Div. 2J and 3K are not unprecedented; they were also low through the early- and mid-1970s. However, the recent low weights-at-age are particularly of concern because these have been concurrent with very low stock biomass. This decline in weight-at-age also coincided with declines in temperature. Water temperature and capelin biomass have been found to be correlated with both northern cod condition factor and northern cod growth (Millar and Myers, MS 1990; Bishop and Baird, MS 1993; de Cárdenas, MS 1994; Shelton and Lilly, MS 1995; Krohn *et al.*, 1997) and temperature is correlated with size-at-age of cod on the Scotian shelf (Campana *et al.*, 1995).

For the same size-specific growth rate, smaller fish have smaller growth increments; therefore, smaller growth increments in a given year may not indicate slower size-specific growth, but may be due to smaller size of the fish at the beginning of that year. In this paper we ask whether weight-at-age of northern cod on the Labrador and Newfoundland Shelves (Div. 2J and 3K) has declined across age-classes because of decreased size-specific growth rate in all the age-classes, or has a decrease in size-specific growth been restricted to young ages and the smaller size carried on through to the older age-classes? Identifying the ages for which specific growth rate has declined may help point to the reasons for the decline in weight-at-age.

During this period of declining weight-at-age, fishing mortality increased (Baird *et al.*, MS 1992; Myers *et al.*, 1997). It is therefore possible that some of the reduction in weight-at-age was not due to reduced growth rates at all but was due to the selective removal of larger fish by the fishery. For age-classes that are not fully recruited to the fishing gear, the slower growers of a given age-class have a higher chance of escaping through the nets. Because growth rates are measured as differences in weight-at-age of the same cohort in two different years, an increase in size selective fishing pressure could make growth rates appear to increase or decrease depending on which age-classes are most affected. Reduced weight-at-age may be expected to persist through the older age-classes even if size

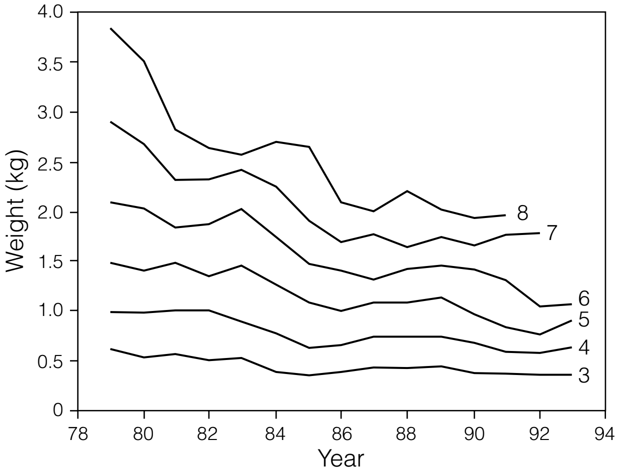

Fig. 1. Time series of weight-at-age of Div. 2J and 3K cod (3- to 8-year-olds).

selection is limited to the first few age-classes that are recruited to the fishing gear, because for the same size-specific growth rate, smaller fish grow by smaller increments.

The objective was to identify age-classes in which size-specific growth had decreased the most, and to establish whether those were the same age-classes that experienced the greatest size-selective fishing mortality. By tracking the cohorts we also aimed to determine to what extent decreases in weight-at-age of cod early in life could lead to an observed decrease in weight-at-age later in life.

Methods

General approach

Weights-at-age for this study were obtained from the Department of Fisheries and Oceans, Canada, annual autumn groundfish surveys as reported by Bishop *et al.*, MS 1995. Weights-at-age from Div. 2J and 3K were analyzed noting their reported declines. In the more southerly Division (Div. 3L), on the northern Grand Bank, weight-at-age had not declined and was therefore not included in the analysis.

After identifying the age-classes in which size-specific growth rates declined to the greatest extent, the objectives were to:

1) determine the proportion of variance in weight-at-age that can be explained by weight-at-age of the corresponding cohorts in the previous year.
2) examine the difference in weight-at-age among cohorts to determine whether differences in weight-at-age track through the life of a given cohort.
3) assess, by using a simulation model, the proportion of the decline in weight-at-age of older age-classes that can be attributed to weight-at-age in previous years.

Weight-at-age and size-specific growth

Mean annual weight-at-age from the annual autumn groundfish surveys, as reported by Bishop *et al.*, MS 1995, were used for the analysis. They calculated weight-at-age from length-at-age using the same length-weight relationship in all years. The annual changes in weight-at-age therefore directly reflect changes in length, not weight.

In the present analyses mean weight-at-age and size-specific growth rates were averaged for Div. 2J and Div. 3K. Size-specific growth (G) was estimated using weight-at-age (W_1 and W_2 in kg) in two consecutive years (t_1 and t_2 in days):

$$G = \frac{(\ln W_2 - \ln W_1)}{t_2 - t_1} \times 100 \qquad (1)$$

The analyses were limited to the period 1979 to 1993 (the period over which the recent decline in weight-at-age was observed) and age-classes 3 to 8. The analyses included weight-at-age of northern cod in Div. 2J and 3K, but not Div. 3L where weight-at-age had not declined. The weight-at-age of the 7- and 8-year-olds in 1992 and 1993 was eliminated from the analyses because of low sample sizes (see Tables 20 and 21, Bishop *et al.*, MS 1995).

Corrected size-specific growth rate

Because size-specific growth decreases with increasing weight (Jobling, 1983), size-specific growth were corrected for weight. This correction allowed the comparison of size-specific growth of cod among years for cod of the same age but different weights. Size-specific growth was corrected by dividing it by $0.1021 \times weight^{-0.441}$. The weight exponent was taken from Jobling (1983), and the slope was calculated by fitting the size-specific growth rates with the weight exponent of -0.441. We chose not to use the exponent calculated from the size-specific growth rates used in this study (as described below) because it was high compared to other estimates (see Jobling, 1983 and 1993 for reviews). The exponent calculated from the data may be an overestimate because of size-selective mortality in some or all age-classes.

Relative weights-at-age

In order to include weight-at-age of 3- to 8-year-old cod in the same analyses, weights-at-age were corrected for age. Relative weights-at-age were calculated by dividing weight-at-age for a given age-class in a given year by the mean weight-at-age of the age-class over the period 1979–93. For example, if the weight-at-age of 3-year-olds in 1979 was 0.65 kg, and the mean weight of age 3 cod over the period 1979–93 was 0.5 kg, the relative weight of age 3 in 1979 would be 1.3. Each age-class, therefore, had a mean relative weight-at-age equal to 1.

Detrended weight-at-age

The weights-at-age were detrended, or corrected for "year", to remove environmental effects that could be confounded with cohort effects. The mean was taken of the relative weight-at-age of all age-classes in a given year, and then each relative weight-at-age was divided by the mean for the year. For example, if the mean relative weight of all age-classes in 1979 was 1.4 kg (i.e., if in 1979 across age-classes, cod were 40% larger than average), then the weight-at-age for each age-class in 1979 would be divided by 1.4.

Differences in weights-at-age among cohorts

To determine whether differences in weight-at-age persist through cohorts, a bootstrapping program was used to compare relative weights-at-age among cohorts (for details see Krohn and Boisclair, 1994).

Proportion of the decline in weight-at-age due to the decline in weight-at-age of the same cohorts in previous years

Simulations were run to determine the proportion of the decline in weight-at-age of older age-classes that could be due simply to smaller weights at an earlier age, specifically at age 3, 4 and 5. For all pairs of years over which there was a reduction in weight-at-age in a given age-class, the expected difference in growth was simulated from the earlier observed weights of the same two cohorts at age 3, 4 and 5 . Size-specific growth rates were used from the appropriate Division, Div. 2J or Div. 3K (Fig. 2; and see below). The expected decline (from the two modelled weights-at-age) was then divided by the observed decline in the two weights-at-age to obtain a proportion of the observed reduction in weights-at-age that, given equal growth rates, could have been due solely to smaller weights at ages 3, 4 or 5.

To simulate appropriate growth rates for cod in the Div. 2J and 3K area, size-specific growth (G) was modelled as an function of weight (W_2) Fig. 2:

$$G = aW_2^b \tag{2}$$

The modelled growth was used as a function of weight at the end of the growth interval (W_2) rather than at the beginning (W_1) to avoid creating a

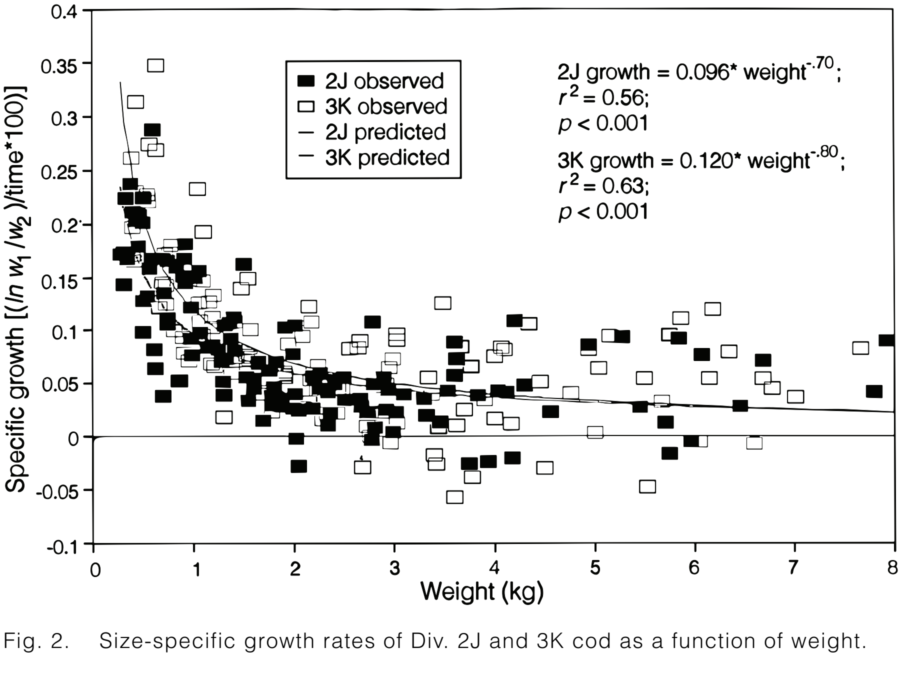

Fig. 2. Size-specific growth rates of Div. 2J and 3K cod as a function of weight.

spurious negative correlation between size-specific growth from equation (1) and initial weight (W_1), because size-specific growth decreases with weight. The age 3 through age 12 cod were included to extend the weight range.

For the simulation of growth rates starting from observed weights-at-age, the weight exponent was used directly from the survey data rather than the exponent from Jobling (1983). As mentioned previously, the exponent calculated from the survey data include any effects of size-selective mortality, as the effects needed to be included in the modelled weights-at-age so they can be compared to the observed weights-at-age.

Results

Size-specific growth rates

Size-specific growth rates declined significantly for 3-, 4- and 5-year-olds ($p<0.0005$, 0.01, 0.02, respectively), the first three years that cod are recruited to the fishery (Fig.3a; Table 1). Size-specific growth rates did not decline significantly for the 6-, 7- and 8-year-olds (Fig. 3b; Table 1). Growth rates were estimated from changes in weight between consecutive years, so the more pronounced decline in growth rate for the 3-year-olds represents a large decrease in the difference in weight-at-age of 2- and 3-year-olds through time or, more specifically, reflects a decrease in the weight at age 3 relative to a more stable weight at age 2. It is possible, however, that weight at age 2 had also decreased but that the sampling gear only caught the largest 2-year-olds. Therefore, size-specific growth rate declined sometime before age 3, not necessarily between age 2 and 3.

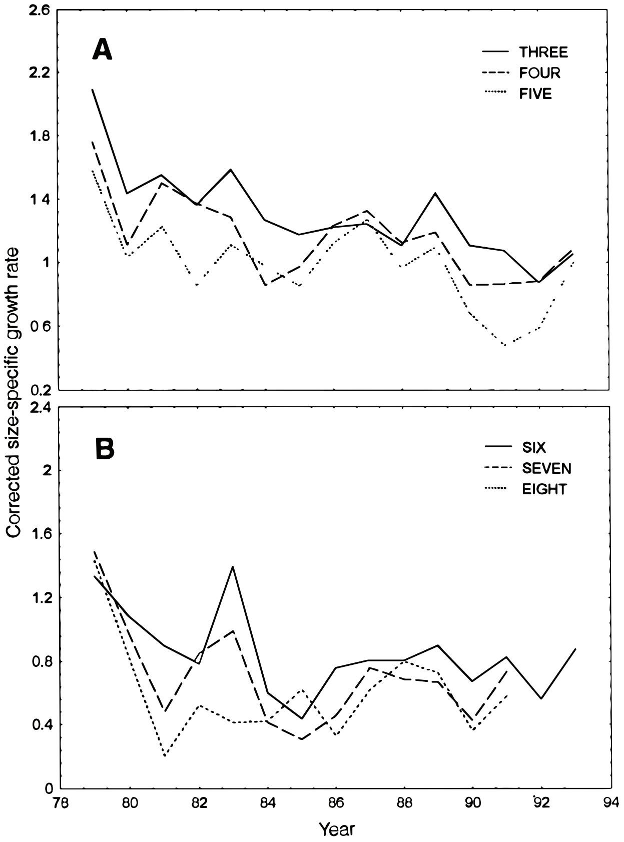

Fig. 3. Time series of corrected size-specific growth rates of Div. 2J and 3K cod: (**A**) 3- to 5-year-olds and (**B**) 6- to 8-year-olds.

TABLE 1. Regression coefficients for the change in size-specific growth rate from 1979 to 1993.

Age	r^2	p	n
3	0.62	<0.001	15
4	0.43	<0.01	15
5	0.39	<0.02	15
6	0.23	>0.05	15
7	0.24	>0.05	13
8	0.08	>0.05	13

Relationship between weight-at-age of the same cohort in two consecutive years

To quantify the importance of size of fish in one year on size of the same fish in the following year, relative weights-at-age in year X were regressed against relative weights-at-age of the same cohort in year $X + 1$. It was found that 70% of the among-year variability in weight-at-age can be explained by weight in the previous year, suggesting that if the fish are small, they stay small (Fig. 4). This relationship was weaker, but was still significant with the detrended relative weights-at-age ($r^2 = 0.35$, $p<0.001$, Fig. 5).

Differences in weight-at-age among cohorts

Relative weights-at-age differed significantly among cohorts; the largest-bodied cohorts being as much as 84% larger than the smallest ones in Div. 2J ($p<0.001$; Fig. 6), and 50% bigger in Div. 3K ($p<0.001$; Fig. 7) with the earlier cohorts being larger than the more recent ones. After detrending the weights-at-age, the range in relative weights among cohorts was greatly reduced, but the differences in relative weights among cohorts were significant ($p<0.004$; and $p<0.02$ in Div. 2J (Fig. 8) and 3K (Fig. 9), respectively). Therefore, even after removing most of the variability in weights-at-age among cohorts, cohort effects were still detectable in both divisions.

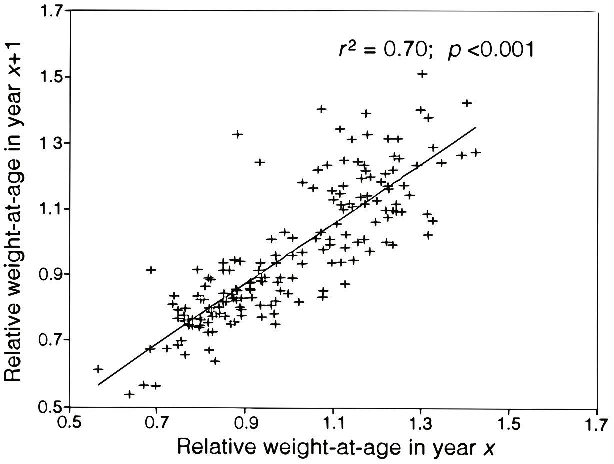

Fig. 4. Effect of weight-at-age of Div. 2J and 3K cod on weight-at-age in the following year.

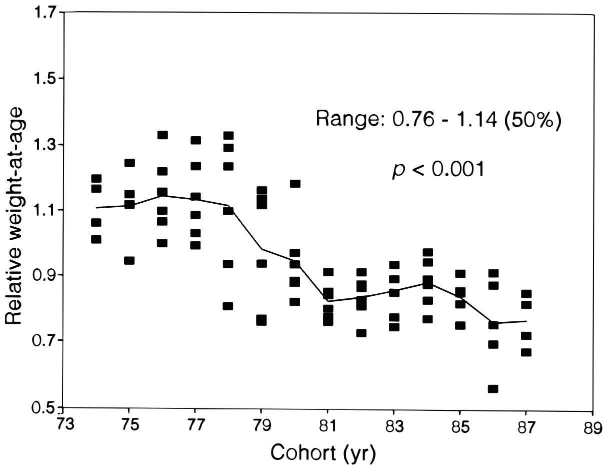

Fig. 7. Relative weight-at-age of cohorts (3- to 8-year-old cod in Div. 3K).

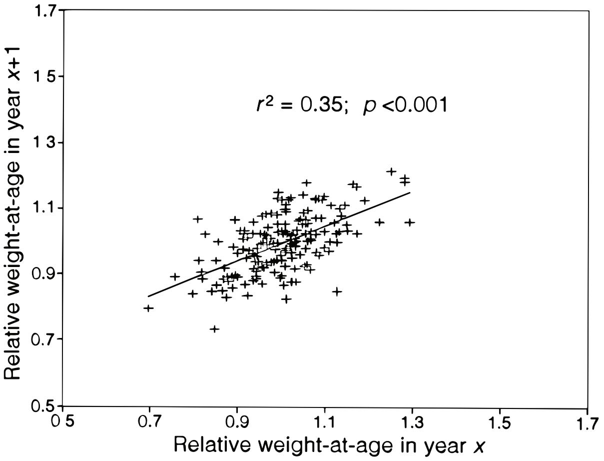

Fig. 5. Effect of weight-at-age of Div. 2J and 3K cod on weight-at-age in the following year, detrended for annual environmental effects.

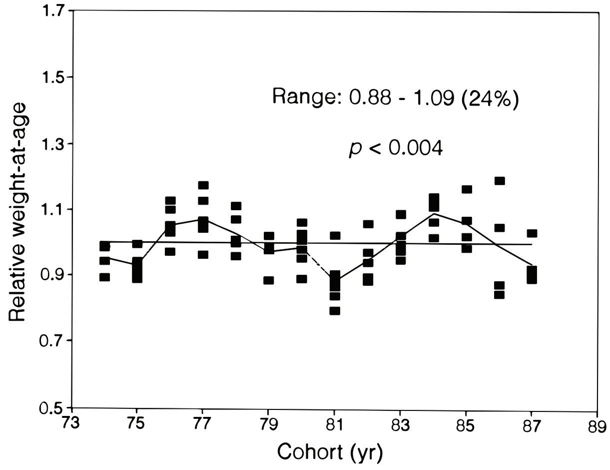

Fig. 8. Relative weight-at-age of cohorts, detrended for annual environmental effects. (3- to 8-year-old cod in Div. 2J).

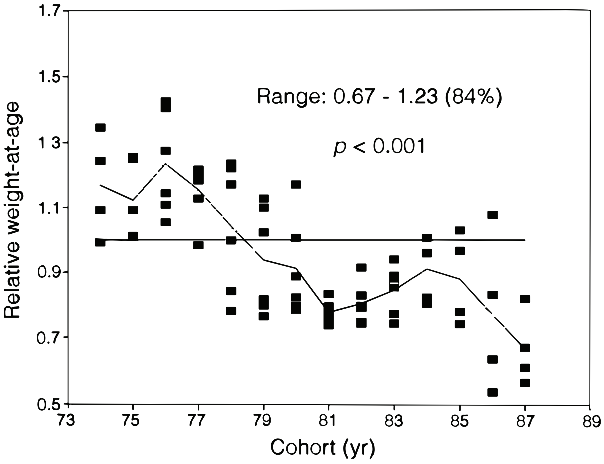

Fig. 6. Relative weight-at-age of cohorts (3- to 8-year-old cod in Div. 2J).

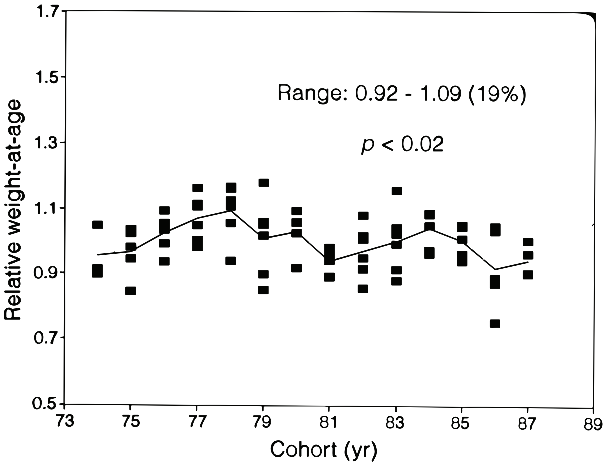

Fig. 9. Relative weight-at-age of cohorts, detrended for annual environmental effects. (3- to 8-year-old cod in Div. 3K).

Proportion of the decline in weight-at-age due to the decline in weight at ages 3–5

According to the simulations, the decline in weight at ages 3, 4 and 5 explained, on average across age-classes, 67%, 65% and 75%, respectively, of the declines in weight-at-age in the older age-classes (Fig. 10).

Discussion

The analyses point to the importance of the decline in size-specific growth rate of young fish, 5 years old or less. They have experienced the greatest decline in growth rate, and this small size has been propagated through the older age-classes. The 6- to 8-year-olds did not experience a significant decline in size-specific growth, but were smaller because they were smaller at an earlier age.

To establish whether an increase in size-selective fishing mortality at young ages could be responsible for small sizes in older age-classes, it is important to determine whether cohorts that are small early in life remain small through their lives. Differences in weight-at-age among cohorts may, however, not reflect cohort differences *per se*; for example, cohorts in recent years may be much smaller than cohorts 15 years ago, not because of anything inherent in the cohort, but because of a concomitant change in the environment over the same period. It was, therefore, necessary to detrend the weights-at-age to remove environmental effects that could be confounded with cohort effects. One can partition the influences on growth into two categories; one category that includes environmental influences, which vary annually (such as food supply or temperature) and the second category that includes cohort effects, most importantly the size of the fish at the beginning of the year. To remove annual environmental effects that act on all age-classes at once, weight-at-age were detrended, or corrected weight-at-age for year. The correction for annual environmental effects corrects only for those annual effects that act across the age-classes.

Weight-at-age in a given year had a strong effect on weight-at-age of the same cohort in the very next year, both before and after weight-at-age was detrended, suggesting that small-bodied cohorts in one year are still small the next year. This implies that the most important determinant of weight-at-age is weight-at-age in the previous year. By tracking the relative weight-at-age of cohorts through their lives, we saw that this effect of weight-at-age in one year on weight-at-age in the next year does translate into significant differences in relative weight-at-age among whole cohorts, both before and after detrending the data for annual environmental effects. Detrending the weight-at-age gives a conservative estimate of the effect of weight in a given year on weight in following years. It is not possible to separate the effects of environment and cohorts and, in detrending data to remove the effects of annual environmental conditions, most of the range in the weights-at-age and possibly much of the cohort weight effect were removed.

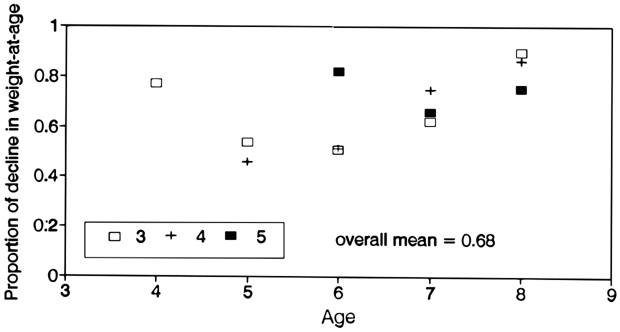

Fig. 10. Proportion of decline in weight-at-age due to weight-at-age of the same cohorts in previous years.

Given the importance of weight-at-age on future growth, what proportion of the observed decline in weight-at-age in older ages can be attributed to a decline in weight at ages 3, 4 and 5, the ages which experienced the decline in size-specific growth? The simulations suggest that, on average, 68% of the observed declines in weight-at-age can be attributed to reduced weights at ages 3, 4 and 5. A mean of 100% across the age-classes would have suggested that all of the reduction in weight-at-age of older age-classes could have been explained entirely by reduced weight at age 5 or earlier, and that after age 5, cod have not experienced reduced growth rates but were smaller only because of smaller initial sizes. The mean of 68% suggests that lower weight at age 5 and earlier was not entirely responsible for the decline in weight-at-age in later age-classes. The size-specific growth rates themselves may have also declined somewhat, but it does suggest that most of the decline in weight-at-age may be a direct result of smaller sizes at or before age 3 to 5.

Significant decreases in size-specific growth rate were limited to 3- to 5-year-old cod, but these decreases in size-specific growth rate carried through the cohorts leading to decreases in size through all age-classes. These results suggest first that, in the early years, growth of cod and of other species may be more sensitive to environmental influences, and therefore point to the potential utility of examining the age-classes separately to identify important environmental influences. Second, these results highlight the possibility that size-selective fishing mortality may play an important role in weight-at-age. The decline in weight-at-age of age-classes that are not fully recruited to the fishery may not be due to reduced growth rate, but may be due to the selective removal of the largest fish of a given age by the fishery (Hutchings, 1996; Shelton, 1996). Hanson and Chouinard (1992) found that the Atlantic cod fishery in the Gulf of St. Lawrence selectively removed the largest or fastest growing 3- and 4-year-olds during the earlier period they studied, 1971–76, and during the later period, 1984–89, after increases in mesh size and in boat power, the fishery consistently removed the largest 3- to 8-year-olds. If, during this later period, the southern Gulf of St. Lawrence fishery removed the fastest growing 3- to 8-year-olds, it seems likely that there would also have been size-selection against large 3- to 5-year-old northern cod. The mean length-at-age of 8-year-olds in the southern Gulf of St Lawrence during that period was 48 cm (Hanson and Chouinard, 1992), which is comparable to the mean length-at-age of the 5-year-olds (51 cm; Bishop *et al*. MS 1995) in Div. 2J and 3K over the period 1979–93 studied here.

To cause a decline in weight at ages 3 to 5 through time, fishing mortality on 3-5-year-olds would have had to be strong enough to result in the observed effect, and would have had to increase over this period. Fishing mortality on 7- to 9-year-old cod increased steadily over this period (Baird *et al*., MS 1992) but it is not clear whether fishing mortality also increased on the younger age-classes. According to the fishing mortality estimated from the Virtual Population Analysis, fishing mortality on age 3 fish did not increase between 1978 and 1991 (see Table 45 in Baird *et al*., MS 1992). However, according to survey-based estimates of mortality, juvenile (age 3) mortality did increase with adult mortality in northern cod during this same period (Myers *et al*., 1997). Even if juvenile mortality did increase, it is not known whether size-selection and fishing mortality was high enough to explain the observed decreases in weight-at-age.

If size-selective fishing was a key factor in the decline in weight at ages 3 to 5, the simulations would have underestimated the potential effect of size-selective fishing on weight-at-age for two reasons. First, smaller fish may have inherently lower size-specific growth rates, so removing the largest fish may involve removing the fastest growers. Second, size-selective fishing does not only act on the 3- to 5-year-olds; Hanson and Chouinard (1992) found that size-selection continued on the older age-classes. Therefore, observed weight-at-age of older age-classes may be lower than simulated here from weight at ages 3 to 5 partly due to lower size-specific growth rates of the remaining fish and continued size-selection on the older age-classes. To establish whether size-selective fishing mortality was strong enough to have resulted in the observed decreases in weight-at-age, one would need to simulate the effect of the size-selection given the selectivity of the types of fishing gear used, the fishing mortality, and the change in size frequency of the population.

In the longer term, size-selective fishing could cause a reduction in the inherent growth rate of the upcoming generations. To confirm that size-selective fishing has an effect on gene frequencies associated with growth rate, both the selection differential (the change in weight-at-age distribution) and the heritability of growth rate would have to be quantified. There is certainly a heritable component to fish growth rate (Busack and Gall, 1983; Gjedrem, 1983; Hoerstgen-Schwark, 1993; Tave, 1994). Heritabilies of fish growth rates have only been quantified in captive fish, however, and are therefore likely to be overestimated. Heritabilities in the wild have been found to be lower than in a controlled environment because of reduced environmental heterogeneity compared to the field (Simons and Roff, 1994). The estimation of heritability of growth rates in the wild, and therefore the evolutionary effect of size-selective fishing on growth rate, would require large-scale fishing experiments such as the one proposed by McAllister *et al*. (1992).

In summary, at least 68% percent of the decline in weight-at-age of northern cod can be attributed to a decline in weight at age 5 or earlier. This finding highlights both the importance of studying what is affecting growth processes at these young ages and the possibility that size-selective fishing may have played an important role in the decline in weight-at-age of the northern cod.

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