

Variation in maturity-at-age and size in three populations of American plaice

M. J. Morgan and E. B. Colbourne



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American plaice (*Hippoglossoides platessoides*) is a flatfish species that has a wide distribution throughout the North Atlantic. Variability in age and size at maturity was examined for cohorts of American plaice from the early 1960s to early 1990s for the three main stocks off the coast of Newfoundland, Canada. Large changes in age and size at maturity have occurred among cohorts since the 1960s, with males and females of all three stocks maturing at an earlier age and smaller size in the latter part of the time period. Maturation was most closely related to total population abundance over the life of a cohort, with cohorts maturing at an earlier age and smaller size when population size was low. Cohorts which experienced higher temperatures appeared to mature earlier and smaller as did cohorts which experienced increased juvenile growth and increased adult mortality.

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M. J. Morgan and E. B. Colbourne: Science Branch, Department of Fisheries and Oceans, PO Box 5667, St John's, Newfoundland, Canada A1C 5X1. Correspondence to M. J. Morgan: tel: +1 709 772 2261; fax: +1 709 772 4188; e-mail: morganj@dfo.mpo.gc.ca

Introduction

The age and size at which individuals of most species mature are not fixed, but rather show considerable variability. This variability is the result of both genotypic differences and variation induced by the environment to which the individuals are exposed (Stearns and Koella, 1986; Baird *et al.*, 1987).

In fishes, there are many examples of variability in maturity-at-age and/or size. A variety of species has been shown to exhibit interpopulation differences in maturation. Some of these include bluegill sunfish (*Lepomis macrochirus*, Belk, 1995); brook trout (*Salvelinus fontinalis*, Hutchings, 1993); pumpkinseed sunfish (*Lepomis gibbosus*, Fox, 1994); northern pike (*Esox lucius*, Diana, 1983); Atlantic cod (*Gadus morhua*, Fleming, 1960); and American plaice (*Hippoglossoides platessoides*, Walsh, 1994). In addition, intrapopulation changes in maturation over time have been demonstrated for Atlantic cod in the northeast Arctic (Jorgensen, 1990) and on the Scotian Shelf (Beacham, 1983), North Sea plaice (*Pleuronectes platessa*, Rijnsdorp, 1989), witch flounder (*Glyptocephalus*

cynoglossus, Bowering, 1989), and American plaice (Pitt, 1975; Bowering and Brodie, 1991).

In numerous studies, changes in maturity schedules have been associated with changes in abundance. At low population size, growth rate has been found to increase in response to increased resources available to individuals, and is thought to result in maturation at a younger age (Pitt, 1975; Bowering, 1989; Jorgensen, 1990; Rijnsdorp, 1993). Increased temperature has also been shown to lead to earlier maturity through increased growth (Alm, 1957; Sandstrom *et al.*, 1995). Changes in mortality have also been identified as a cause of variation in maturity in fishes. In particular, increased mortality can select for maturation at a younger age (Diana, 1983; Roff, 1992; Hutchings, 1993; Fox, 1994) and smaller size (Kasperski and Kozlowski, 1993) since those that delay maturation have a decreased probability of surviving to reproduce. The level of adult mortality relative to juvenile mortality is also thought to affect age and size of maturity (Gadgil and Bossert, 1970; Hutchings, 1993).

American plaice is a commercially exploited flatfish species that has a wide distribution throughout the

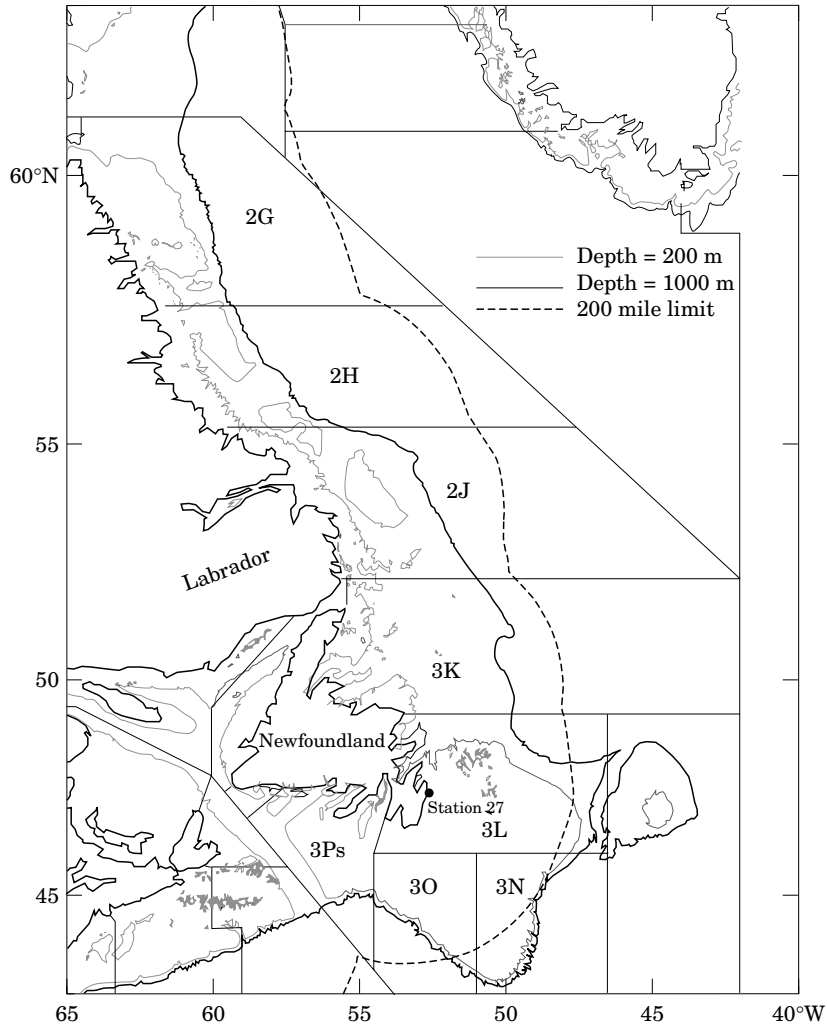


Figure 1. Map showing study area. The three populations of American plaice studied here are the Labrador and northeast Newfoundland stock (2+3K), Grand Bank stock (3LNO), and the St Pierre Bank stock (3Ps). The location of station 27 is also shown.

northwest Atlantic. Off the coast of Newfoundland there are three major stocks: the Labrador and northeast Newfoundland stock, Grand Bank stock, and the St Pierre Bank stock, referred to here as 2+3K, 3LNO, and 3Ps stocks, respectively, after the Northwest Atlantic Fisheries Organization (NAFO) Divisions in which they occur (Fig. 1). All three of these stocks have shown large declines in abundance in recent years. At the same time, age and size at maturity estimated on an annual basis have been declining (Bowering *et al.*, 1996; Morgan *et al.*, 1996; Bowering *et al.*, 1997). These recent changes in the population dynamics of American plaice have occurred during a period of anomalous environmental conditions. Colbourne *et al.* (1997) observed that shelf bottom temperatures were 0.5–1.0°C below normal from 1986 to 1994, the longest continuous period of

negative temperature anomalies since measurements began in 1946, and that the total heat content of shelf waters was significantly below normal during this time period.

To date, trends in maturity based on the analyses of cohorts has not been examined for these stocks. Since it is the cohort that matures, the purpose of this paper is first to examine maturity-at-age and size on a cohort (rather than on annual) basis and then to explore any association between variation in maturity and changes in abundance, growth, mortality, and ambient temperature. The following hypotheses were tested: (1) cohorts experiencing lower population size mature at a younger age and smaller size; (2) cohorts experiencing higher growth mature at a younger age and smaller size; (3) cohorts experiencing higher mortality mature at a

younger age and smaller size; (4) cohorts experiencing higher temperature mature at a younger age and smaller size. Commonalities and differences between stocks may elucidate the causes of variability in maturation in this and other species.

Materials and methods

Data

Biological data for American plaice were collected during annual surveys by research vessels towing a bottom otter trawl with a small mesh liner in the codend. All surveys were conducted using a stratified random design (Doubleday, 1981). Data collected during the autumn surveys in 2J3K from 1978 to 1994, spring surveys in 3LNO from 1975 to 1995 and winter/spring surveys in 3Ps from 1972 to 1995 were used. For the 2+3K stock, insufficient information was available on the 2GH portion to include this area in the analyses. As two different vessels and two different trawls were used during the time period, catch numbers at length were standardized with conversion factors developed by Gavaris and Brodie (1984) from comparative fishing studies conducted between the two vessel/gear types. These standardized values were used in measures of abundance, maturity, mean length-at-age, and mortality.

Maturity ogives

Fish were classed as juvenile or adult based on the method of visual examination of gonads devised by Templeman *et al.* (1978) for haddock (*Melanogrammus aeglefinus*) and since applied to most groundfish species in the area. The first stage in this classification is immature (juvenile) and all other stages show some evidence of maturing to spawn or of having spawned in the past and are classed as mature (adult). To examine trends in maturity, the number of adults and juveniles at each length class and age group was calculated for males and females for each stock. Proportions mature-at-age were calculated according to the method described in Morgan and Hoening (1997) to correct for bias introduced by length-stratified sampling. A logistic model with a logit link function and binomial error was fit to the data to estimate the age and size at 50% maturity (A_{50} and L_{50}) for each cohort. Estimation of parameters was performed using the Probit procedure of SAS (SAS, 1989). These estimates of A_{50} and L_{50} were produced only for cohorts for which both the slope and intercept of the maturity ogive were significant at the $p=0.01$ level.

Population abundance

For each stock, in each year, population abundance estimates were derived from stratified estimates of

survey catch based upon standard swept area of the trawl. For each cohort the mean total population size during its lifetime (or the period during which it occurred in the survey if its entire life was not sampled) was calculated. Total population size refers to the abundance of fish from all cohorts present at the time of the survey. A cohort was then classed as occurring during periods of low population abundance if the mean population during its lifetime was below the average for all cohorts, and classed as occurring during a period of high abundance if it was above average. The same procedure was carried out over ages 1 to A_{50} for each cohort, sex, and stock to examine the effect of population abundance over the juvenile period.

Growth

Mean length-at-age was calculated for males and females separately for each stock and cohort. These means were calculated in a similar fashion to the maturities at age, correcting for bias introduced by the length-stratified sampling used. Residuals for mean lengths-at-age for each cohort from the overall mean for that stock and sex were calculated and the average of the residuals was then calculated for each cohort. For each sex, cohorts with a mean residual greater than zero were considered to have higher than average growth, while those with a mean residual less than zero were considered to have lower than average growth. The same procedure was carried out over ages 1 to A_{50} for each cohort, sex, and stock to examine the effect of juvenile growth.

Mortality

Total adult mortality was calculated for each cohort and sex of each stock by fitting the following general linear model to population numbers at age for each stock:

$$\log(N_{ijk}) = \tau + \gamma_{jk} + \alpha\gamma_{jk} \text{ age}_i + \varepsilon, \quad (1)$$

where: N_{ijk} = population abundance at age i for cohort j and sex k , τ = intercept, γ_{jk} = cohort effect for sex k , $\alpha\gamma_{jk}$ = cohort and age combined effect for sex k – separate slope for each cohort/sex, and ε = residuals from the fitted model.

American plaice do not fully recruit to the survey gear until age 8 and the maximum age that the two sexes reach differs. Therefore, only ages 8–12 for males and ages 8–17 for females were used in the mortality model. Only cohorts that had at least two ages in the appropriate age range during the survey time series were included in the calculations of relative mortality. The separate slopes parameter $\alpha\gamma_{jk}$ was used as the estimate of mortality experienced by each cohort relative to each of the other cohorts. Each cohort was then classified as experiencing high adult mortality if its estimate of

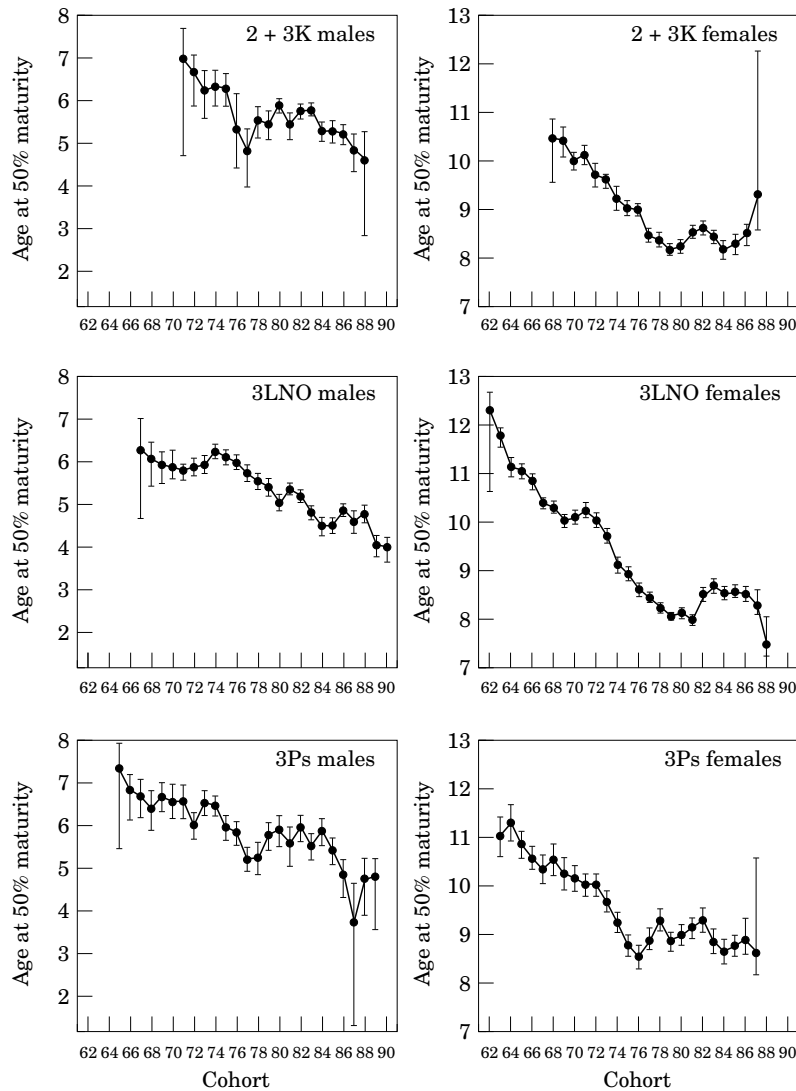


Figure 2. Age at 50% maturity for males and females of each cohort of American plaice in the three stocks. Ninety-five percent fiducial limits are also shown.

relative mortality was higher than the average for all cohorts and low mortality if its estimate of relative mortality was lower than the average. To provide an estimate of relative juvenile mortality the ratio of the number of age 3 in year i to age 4 in year $i+1$ for males and age 7 in year i to age 8 in year $i+1$ for females was calculated and cohorts classed as experiencing higher or lower juvenile mortality relative to the average. One further measure of mortality was calculated as follows. The separate slopes parameter (adult mortality) for each sex/cohort/stock was divided by the juvenile mortality estimate to produce a ratio of adult to juvenile mortality (written as adult:juvenile mortality). Cohorts were then classed as experiencing high adult:juvenile mortality or low adult:juvenile mortality.

Environment

During the annual surveys from 1972 to 1989 a temperature profile of the water column was obtained using a mechanical bathythermograph (MBT), or an expendable bathythermograph (XBT), from which a bottom temperature for each fishing set was extracted, usually at the end of the tow. Since 1989, a trawl mounted Seabird-19 conductivity-temperature-depth (CTD) probe was used to provide a horizontal average bottom temperature for the fishing tow. For the years during which there were surveys these temperatures were used to calculate the average temperature occupied by fish in each stock based on the methods of Perry and Smith (1994) in which the temperature for each fishing set was weighted

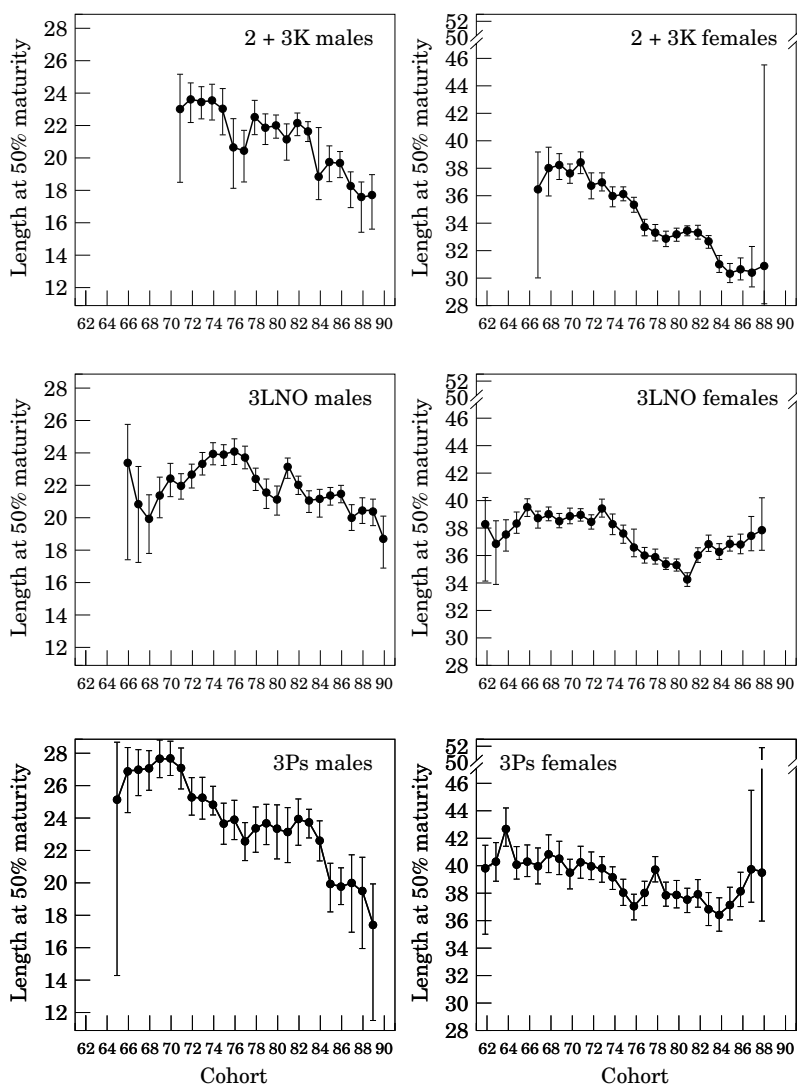


Figure 3. Length at 50% maturity for males and females of each cohort of American plaice in the three stocks. Ninety-five percent fiducial limits are also shown.

by both fish abundance and total stratum area. For the years prior to the surveys, we used the historical Marine Environmental Data Service (MEDS) temperature database from which we extracted near-bottom values for each of the three stock areas. In keeping with the approach of using temperatures experienced by the population, we approximated the weighting scheme used for the surveys by pooling the temperatures for each year into 20 m depth bins. We then obtained an average temperature for each depth bin and weighted it by the proportion of the population found in each depth bin averaged over the years 1975–1985 (1978–1985 for 2+3K). The combination of the two sets of data (survey and MEDS) gave a time series of average temperature

occupied by each population in each year. The average temperature experienced over the lifetime of each sex of each cohort was then calculated for each stock. Cohorts which had an average temperature less than the overall average for the appropriate stock and sex were considered to have experienced low temperatures during their lifetime while those with an average temperature higher than the overall average were considered to have experienced higher temperatures. The same procedure was carried out for each cohort/sex combination for the period from their birth to their respective A_{50} . The effect of temperatures over a cohort's lifetime and during the juvenile stage on proportion mature-at-age and size was then examined.

Table 1. Results of generalized linear models testing the significance of each variable on proportion mature at age and length. As 108 separate tests were conducted, only tests with $p < 0.0005$ are considered significant, these are shown in bold. The pseudocoefficient of determination (r^2) is also given for each test.

Stock				2+3K		3LNO		3PS	
				Male	Female	Male	Female	Male	Female
Var Abundance	Age	Total	p	0.0001	0.0001	0.0001	0.0001	0.0001	0.0002
			r^2	0.23	0.36	0.46	0.44	0.22	0.09
		Juvenile	p	0.0194	0.9077	0.0001	0.0041	0.042	0.6669
			r^2	0.07	0.0002	0.32	0.09	0.05	0.003
	Length	Total	p	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
			r^2	0.19	0.47	0.15	0.32	0.23	0.07
	Juvenile	p	0.0001	0.0001	0.0001	0.0001	0.0027	0.0259	
		r^2	0.26	0.35	0.13	0.09	0.04	0.03	
Growth	Age	Total	p	0.7230	0.7939	0.0001	0.0001	0.0803	0.0001
			r^2	0.001	0.0005	0.16	0.36	0.02	0.10
		Juvenile	p	0.6432	0.0001	0.0001	0.0001	0.7756	0.0001
			r^2	0.002	0.31	0.20	0.29	0.0006	0.12
	Length	Total	p	0.0009	0.0001	0.3103	0.0001	0.0038	0.0007
			r^2	0.05	0.06	0.003	0.09	0.02	0.03
	Juvenile	p	0.1274	0.0001	0.0001	0.0001	0.0043	0.0001	
		r^2	0.01	0.19	0.10	0.25	0.03	0.05	
Mortality	Age	Total	p	0.0344	0.1349	0.0001	0.0001	0.0005	0.0001
			r^2	0.04	0.02	0.10	0.51	0.09	0.28
		Juvenile	p	0.2521	0.0144	0.4577	0.0001	0.0505	0.2871
			r^2	0.02	0.05	0.004	0.31	0.03	0.01
	adlt:juv	p	0.5790	0.1040	0.9809	0.0001	0.0111	0.0505	
		r^2	0.0006	0.024	0	0.20	0.06	0.03	
Length	Total	p	0.0043	0.1315	0.8837	0.0001	0.0005	0.0001	
		r^2	0.05	0.09	0	0.38	0.04	0.12	
	Juvenile	p	0.0041	0.0192	0.7205	0.0001	0.0001	0.4210	
		r^2	0.08	0.03	0.0006	0.22	0.06	0.002	
adlt:juv	p	0.9476	0.5219	0.6594	0.0001	0.0001	0.7590		
	r^2	0	0.002	0.001	0.22	0.10	0.0005		
Temperature	Age	Total	p	0.0001	0.0001	0.0001	0.5175	0.0001	0.0001
			r^2	0.10	0.13	0.29	0.003	0.27	0.13
		Juvenile	p	0.0011	0.0516	0.0001	0.0001	0.0191	0.0001
			r^2	0.09	0.03	0.11	0.33	0.04	0.17
	Length	Total	p	0.0001	0.0001	0.0001	0.5295	0.0008	0.0002
			r^2	0.28	0.22	0.13	0.0	0.04	0.06
	Juvenile	p	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	
		r^2	0.20	0.21	0.05	0.37	0.06	0.05	

Hypotheses testing

The effect of each of the above factors (average population abundance over a lifetime, average population abundance over the juvenile period, growth, juvenile growth, adult mortality, juvenile mortality, adult:juvenile mortality, temperature over a lifetime, and temperature over the juvenile period) on the proportion mature-at-age and size was explored using generalized linear models with a logit link function and binomial error (McCullagh and Nelder, 1983; SAS Inst. Inc., 1993). Each model had the general form of:

$$pmat = \log\left(\frac{u}{1-u}\right), \tag{2}$$

where: pmat=proportion mature-at-age or length, $u = \tau + \alpha v_i + \beta_j$, τ =intercept, v_i =age or length, α =age or

length effect, and β_j =effect of factor being examined e.g. high or low population abundance.

The significance of the factor being examined was determined after first removing the effect of age or size. Each factor was examined for each sex and stock separately. Since 108 tests were being conducted, increasing the likelihood of a significant result by chance alone, the significance level was adjusted so that only tests where $p < 0.0005$ were considered to be significant. Also, the proportion of the Deviance accounted for by the factor of interest was calculated. This value is the pseudocoefficient of determination r^2 (Swartzman *et al.*, 1992; Swain, 1993). Only ages or lengths that had some contrast in the data were included (i.e. ages and lengths where all observations were mature or all were immature were excluded) since only these data would show any affect of the factors being examined. For 2+3K males

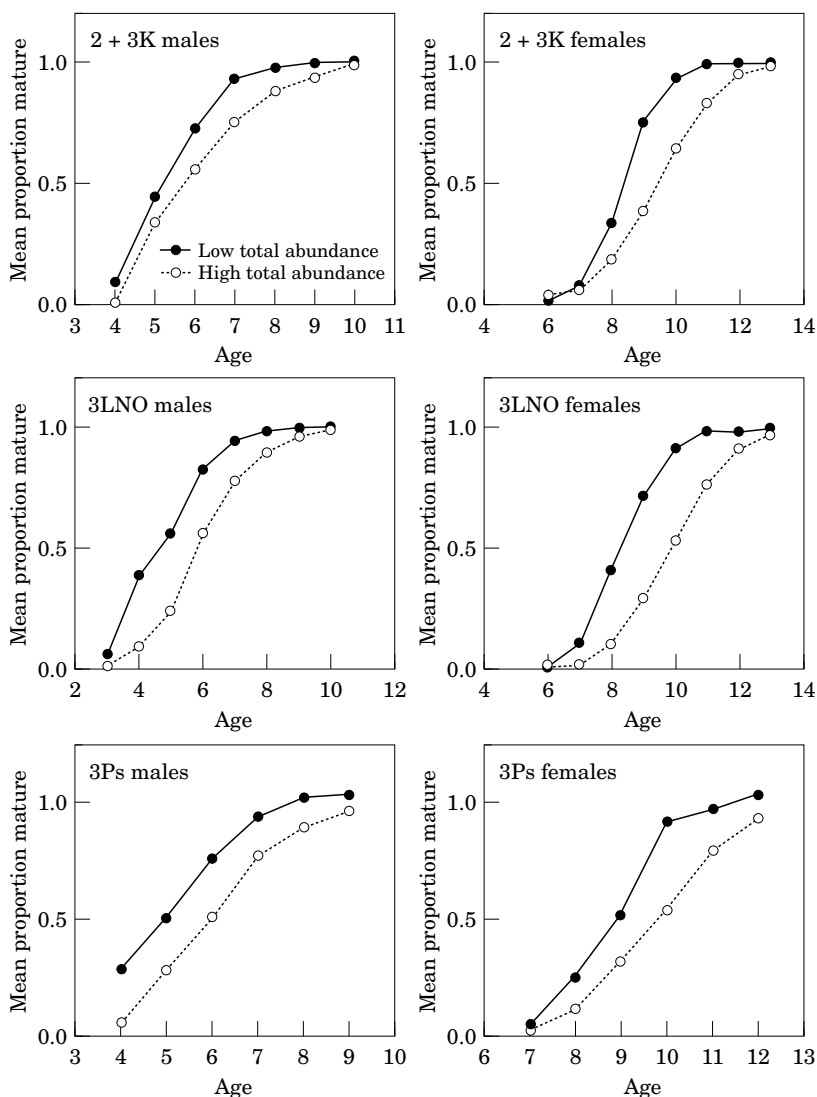


Figure 4. Mean proportion mature at each age for cohorts experiencing a higher than average population abundance during their lifetime (open circles) and those experiencing a lower than average population abundance during their lifetime (solid circles). Both sexes from each population are shown.

these were ages 4–10 and lengths at 16.5–34.5 cm, 2+3K female ages 6–13 and lengths 24.5–48.5 cm, 3LNO male ages 3–10 and lengths 14.5–36.5 cm, 3LNO females ages 6–13 and lengths 24.5–52.5 cm, 3Ps males ages 4–9 and lengths 16.5–38.5 cm, and 3Ps females ages 7–12 and lengths 28.5–50.5 cm. Results of all tests were presented in tabular form. Figures are presented for each factor being tested but only for the time period (e.g. juvenile) that showed the most effect.

Results

There has been a general decline in age at 50% maturity for both males and females in all stocks, although female

A_{50} has shown some stability for cohorts produced since the mid-late 1970s (Fig. 2). Overall, for the three stocks, there has been a 35% decline in male A_{50} and a 24% decline in female A_{50} from the peak values to the present level. Length at 50% maturity has also declined for both sexes over most of the time period in 2+3K (Fig. 3). In 3LNO, L_{50} began declining in both sexes for the early to mid 1970s cohorts but increased for females since the 1981 cohort. Males in 3Ps have shown a general decline in L_{50} since the cohorts of the early 1970s, while female L_{50} declined from the 1964 cohort and has been increasing since the cohort of 1984. Overall, for the three stocks, there has been a 28% decrease in male L_{50} and a 10% decrease in female L_{50} , over the time period.

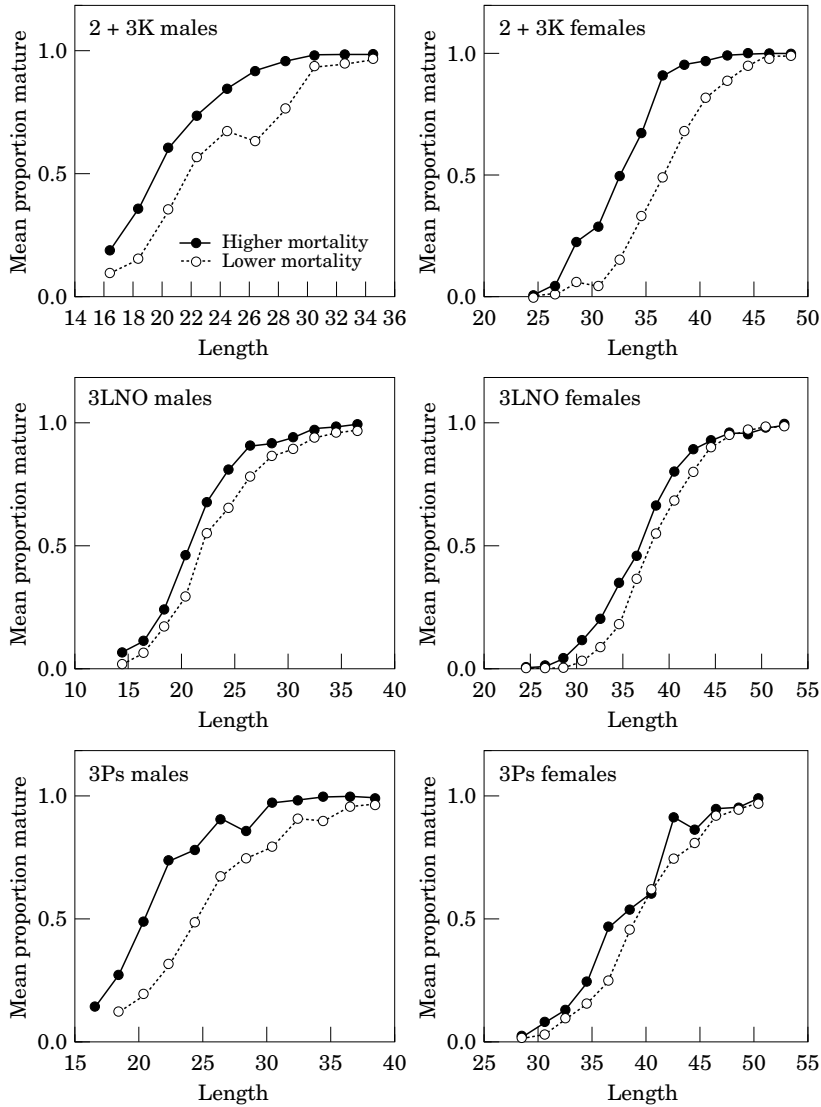


Figure 5. Mean proportion mature at each length for cohorts experiencing a higher than average population abundance during their lifetime (open circles) and those experiencing a lower than average population abundance during their lifetime (solid circles). Both sexes from each population are shown.

Table 1 presents the results of the generalized linear models testing for significance of the various factors we examined. The p-values have been adjusted for the large number of tests that were conducted. However, many of these factors will display some degree of autocorrelation. This has not been taken into account. It is not known how much correcting for this would have affected the significance of the results.

There was a significant effect of population size over the life of a cohort on the proportion mature-at-age and length for both sexes in all stocks (Table 1). Cohorts which experienced a lower than average population size during their lifetime had a higher proportion mature at a

younger age and a smaller size than those experiencing a higher than average abundance (Figs 4 and 5). Population abundance over the juvenile period was not as strongly related to proportion mature at age or length, with only 5 of the 12 tests being significant (Table 1).

There was no consistent effect of growth over the lifetime of a cohort on proportion mature at age or size across stocks. Growth over a cohort's lifetime had a significant effect on the proportion mature at age in 3 of 6 tests and length in 2 of 6 tests (Table 1). In 3LNO and 3Ps cohorts with higher growth tended to have a higher proportion mature-at-age but in 2+3K the trend was for fish with lower growth to mature at a younger age and

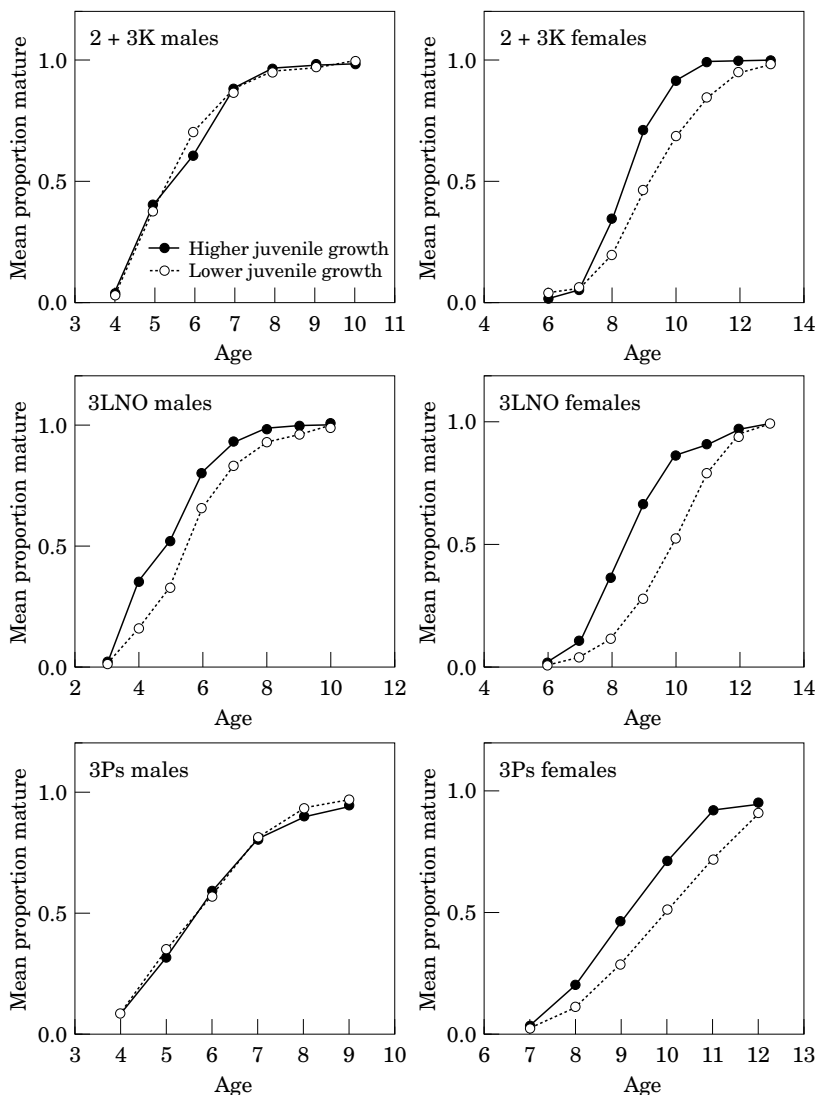


Figure 6. Mean proportion mature at each age for cohorts that had higher than average growth during the juvenile period (solid circles) and those that had lower than average growth during the juvenile period (open circles). Both sexes from each population are shown.

smaller size. For juvenile growth 8 of 12 tests were significant (Table 1) with all of the significant tests indicating higher proportion mature-at-age and size for cohorts with higher growth (Figs 6 and 7).

Cohorts with higher than average adult mortality tended to have a higher proportion mature-at-age and size (Figs 8 and 9). Although overall 5 of 12 tests were significant, there was no significant effect for 2+3K for either sex for proportion mature-at-age or length. Juvenile mortality and adult:juvenile mortality appeared to have little effect on maturity, with only 3 of 12 test results being significant for each of these variables (Table 1).

Cohorts which experienced higher than average temperatures over their lifetime generally had a significantly higher proportion mature at age and length than those that experienced lower than average temperatures with 9 of 12 tests being significant. The exceptions were females in 3LNO for both age and length and males in 3Ps for length which showed no significant effect (Table 1, Figs 10 and 11). The effect of temperature during the juvenile period was not consistently related to proportion mature-at-age or size. Nine of 12 tests were significant (Table 1) but for both males and females in 2+3K, cohorts experiencing lower than average temperatures matured earlier and at a smaller size, while for the other

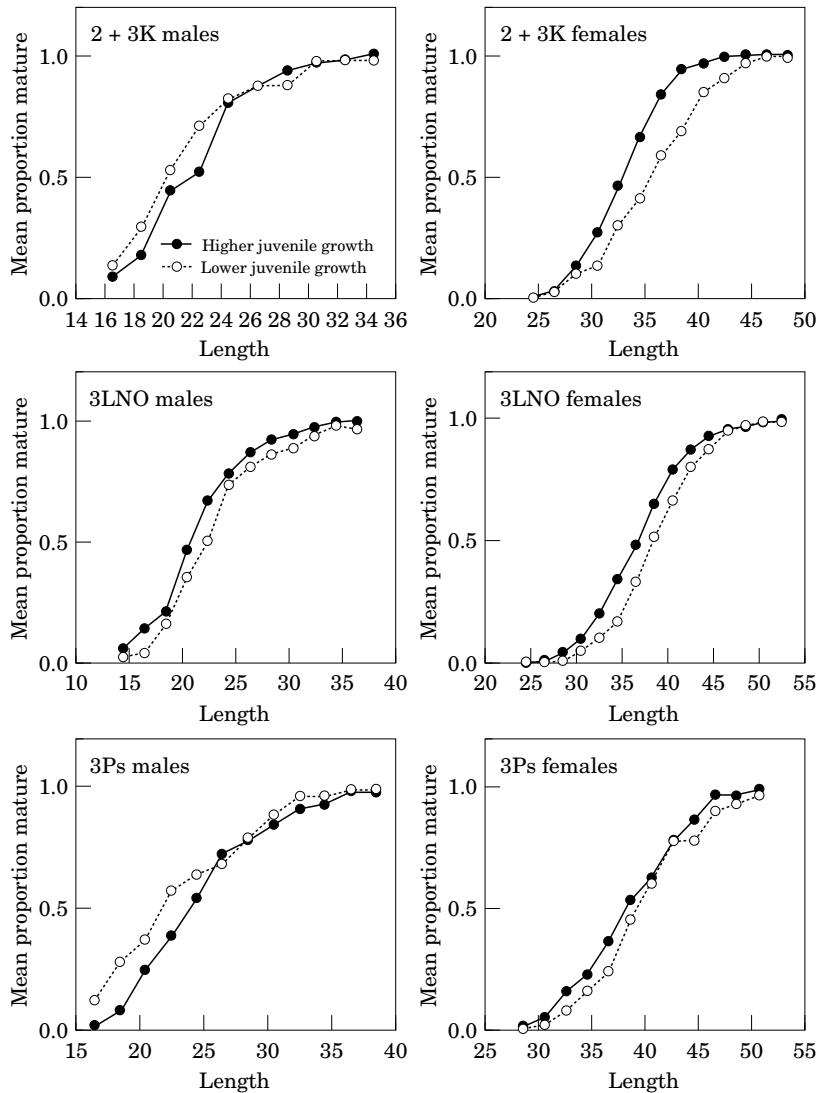


Figure 7. Mean proportion mature at each length for cohorts that had higher than average growth during the juvenile period (solid circles) and those that had lower than average growth during the juvenile period (open circles). Both sexes from each population are shown.

stocks, cohorts experiencing higher than average temperatures matured earlier and smaller.

Overall it would appear that mean population abundance over the lifetime of a cohort was most closely associated with proportion mature-at-age and size. All of the tests for this factor were significant, patterns were consistent across stocks and sexes and this factor accounted for a greater proportion of the Deviance (r^2) than the other factors (Table 1). Growth over the juvenile period, temperature over the lifetime of a cohort, and adult mortality also showed some association with proportion mature-at-age and size. Growth over the lifetime of a cohort, juvenile mortality, the ratio of adult to juvenile mortality, and temperature over the

juvenile period, showed little consistent association with maturity.

Discussion

American plaice off the coast of Newfoundland have shown large changes in age and length at maturity since the cohorts of the 1960s. Both males and females of the three stocks are maturing at an earlier age and a smaller size in recent years. There has been some indication of a tend to stabilization or to a return to previous levels, especially in size at maturity, but all values are below those of the earliest cohorts examined. For males, the

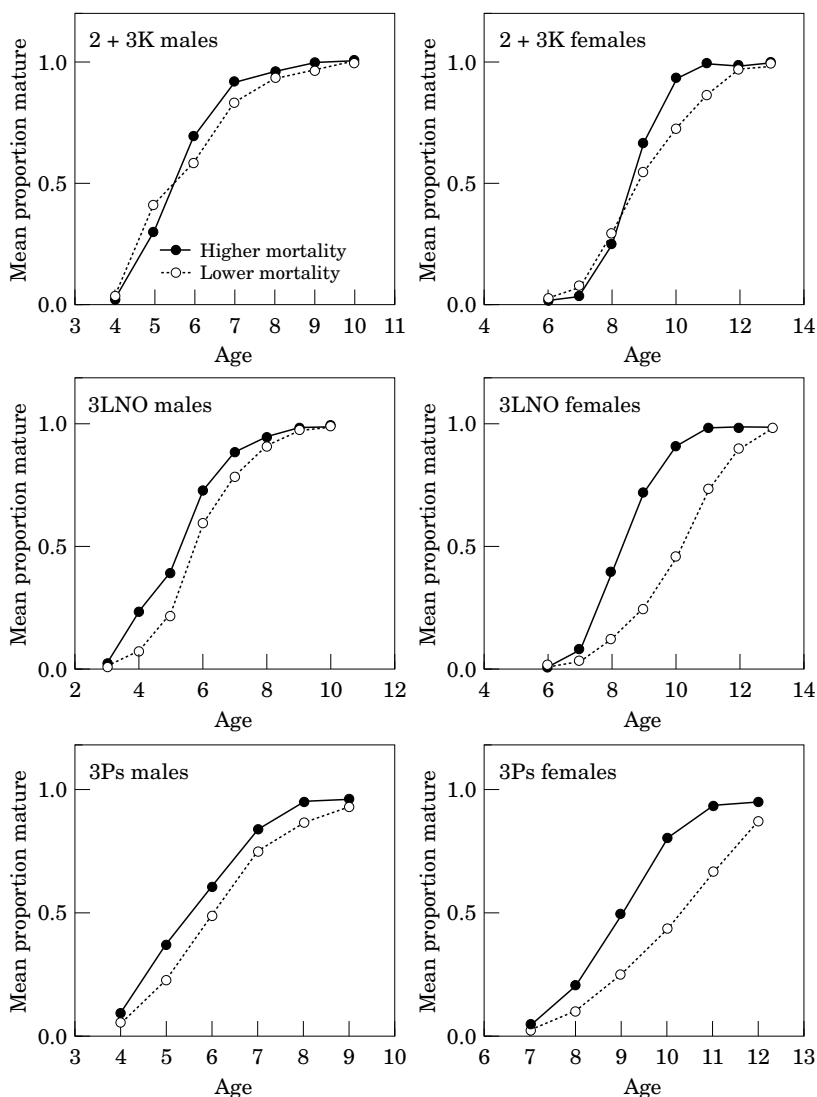


Figure 8. Mean proportion mature at each age for cohorts that had higher than average relative mortality (solid circles) and those that had lower than average relative mortality (open circles). Both sexes from each population are shown.

average L_{50} throughout the area is now 18 cm which is a 28% decrease from peak levels of the late 1960s and early 1970s, and the A_{50} is 4.5 years, a 35% decrease from peak values. For females, the mean L_{50} is 36 cm and the average A_{50} is 8.5 years, decreases of 10 and 24%, respectively. Roff (1982) hypothesized that late maturing flatfish, in particular American plaice, would exhibit changes in age but not size at maturity. The decrease in both age and size at maturity for all three stocks in this study indicates that this hypothesis does not hold, at least for this species.

Changes in maturity-at-age and size were associated with changes in population abundance for both males and females in all three stocks. Cohorts which experienced a lower than average population abundance

matured at an earlier age and a smaller size. Variation in maturity schedules with changing population size is common among fish populations (Beacham, 1983; Bowering, 1989; Rijnsdorp, 1989; Jorgensen, 1990; Rowell, 1993) and has been found previously in American plaice (Pitt, 1975; Bowering and Brodie, 1991). There is some evidence that density, or population size, itself can be a signal to mature early (Kasperski and Kozlowski, 1993). However, trends in maturity with population size are generally attributed to changes in growth or mortality (Gadgil and Bossert, 1970; Pitt, 1975; Diana, 1983; Stearns and Koella, 1986; Bowering, 1989; Jorgensen, 1990; Hutchings, 1993; Fox, 1994). Both of these factors will be discussed below.

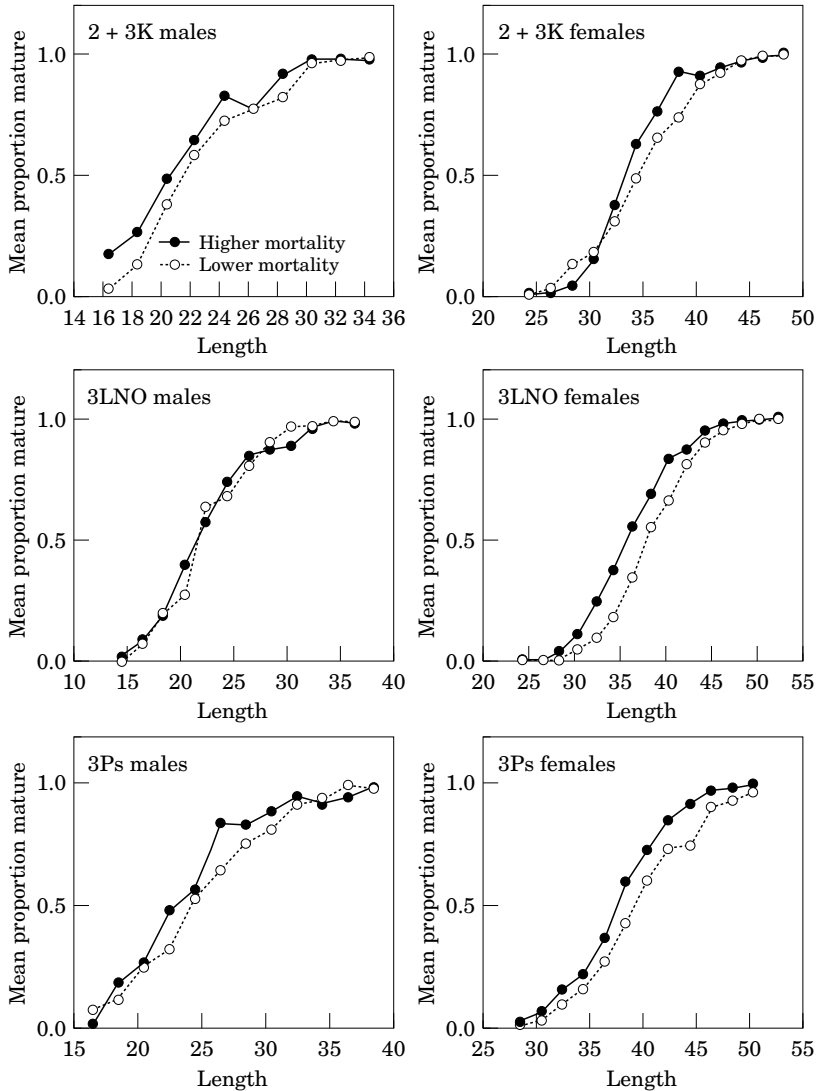


Figure 9. Mean proportion mature at each length for cohorts that had higher than average relative mortality (solid circles) and those that had lower than average relative mortality (open circles). Both sexes from each population are shown.

Cohorts which had higher growth over the juvenile period tended to mature at a younger age and a smaller size. Increased growth at low population size has often been identified as a factor leading to quicker maturation (Pitt, 1975; Bowering, 1989; Jorgensen, 1990; Rijnsdorp, 1993). As might be expected, the results of this study indicate that growth over the juvenile period is important to maturation, however the effect is not necessarily detectable when examined over the lifetime of a cohort.

Increased mortality is thought to favour declines in age and size at maturity as this increases the probability of reproducing before death (Kozłowski, 1992; Policansky, 1993; Reznick, 1993). The effect of a change in mortality can occur very rapidly, even within the first cohort produced following the increase in mortality

(Kasperski and Kozłowski, 1993). Adult mortality showed some relationship with maturation but showed no effect in 2+3K, indicating that in this study adult mortality was not consistently related to changes in maturity at age or size. The change in adult mortality relative to juvenile mortality may be an important factor in the impact of mortality on maturation (Gadgil and Bossert, 1970; Hutchings, 1993). However, in this study there was no consistent effect of the ratio of adult to juvenile mortality or of juvenile mortality. Selectivity of the survey gear meant that juvenile and adult mortality could not be calculated in the same manner and this may have impaired our ability to detect any effect.

The final factor examined in this study was temperature. Cohorts that experienced higher than average

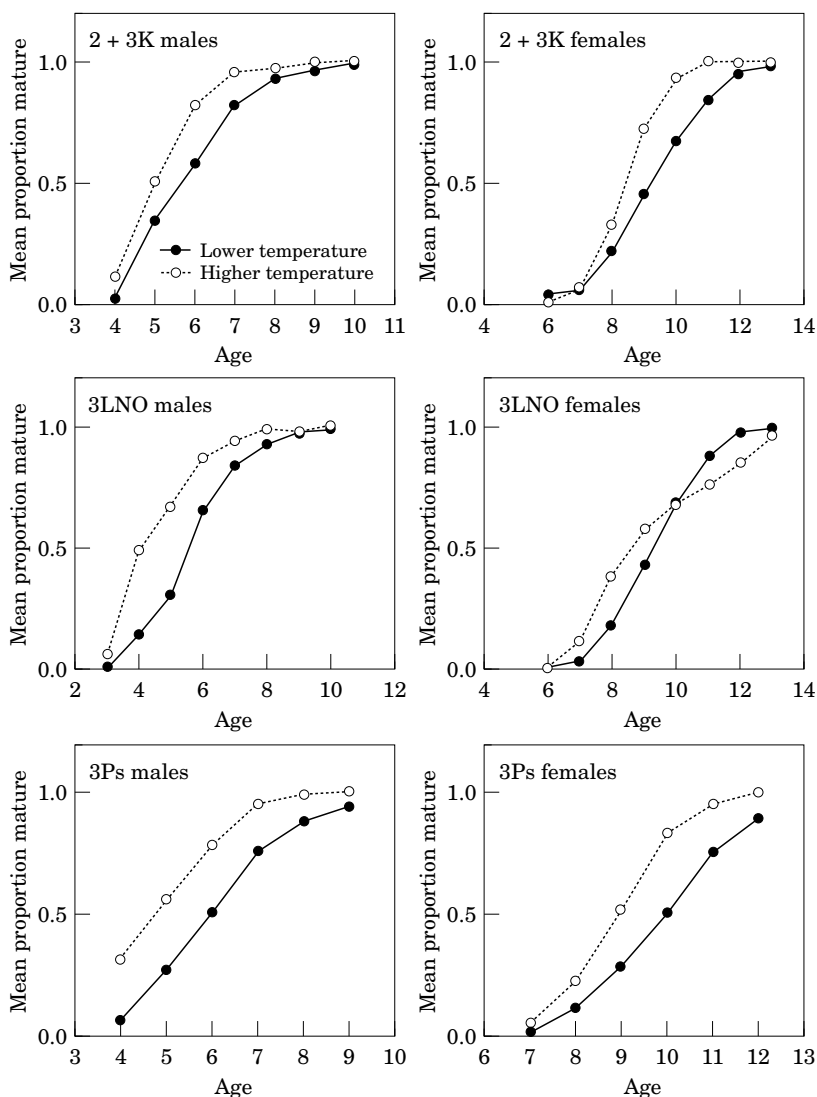


Figure 10. Mean proportion mature at each age for cohorts that experienced higher than average temperatures over their lifetime (open circles) and those that experienced lower than average temperatures over their lifetime (solid circles). Both sexes from each population are shown.

temperatures over their lifetime in each population generally matured at an earlier age and size (9 of 12 tests were significant). This is consistent with the results of a literature review of Walsh (1994) which compared various populations of American plaice. Increased temperature has been shown to lead to earlier maturity and has been linked to increased growth (Alm, 1957; Sandstrom *et al.*, 1995). The effect of temperature was greatest over the lifetime of a cohort while the effect of growth appeared to be strongest over the juvenile period. It is not known what would cause this apparent inconsistency.

Regardless of the cause, the cohorts of the most recent period continue to exhibit early maturity at a small size. This has occurred at a time when temperature conditions

throughout the shelf waters off Newfoundland have been colder than normal (Colbourne *et al.*, 1997). When the temperatures occupied by American plaice from 3LNO are compared to those representative of the shelf, the vertically integrated station 27 (Fig. 1) temperatures, they show similar trends (Fig. 12, Spearman rank correlation coefficient=0.54, $p=0.0001$). However, in the 1990s, the temperature occupied by American plaice has been much warmer than average while the temperature on the shelf has been below normal. This is the result of a movement of fish from the cold, shallower water on the banks to deeper and warmer waters along the shelf edge beginning in the late 1980s and early 1990s (Bowering *et al.*, 1996; Bowering *et al.*, 1997). Whether

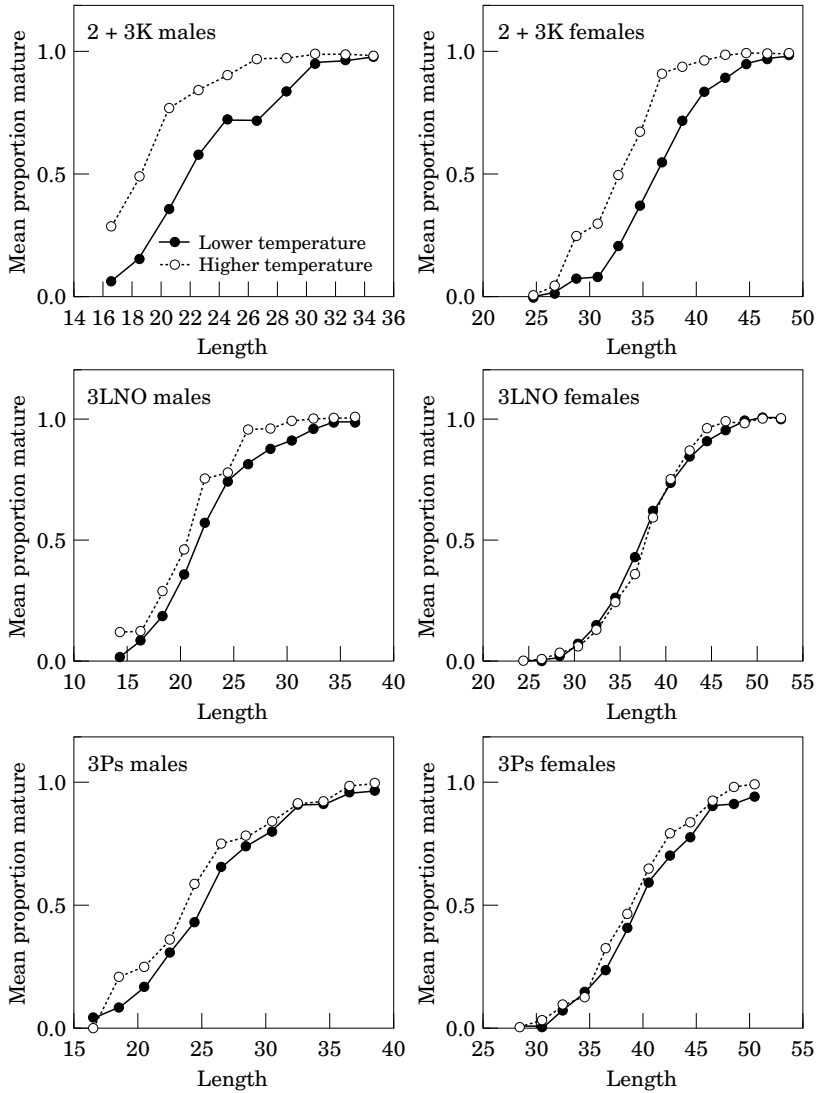


Figure 11. Mean proportion mature at each length for cohorts that experienced higher than average temperatures over their lifetime (open circles) and those that experienced lower than average temperatures over their lifetime (solid circles). Both sexes from each population are shown.

this movement into deeper water is related to the cooling on the shelf remains to be determined, but it is interesting that the apparent migration into deeper warmer water occurred around 1991, when the Newfoundland Shelf water temperatures were the lowest ever recorded. As a result of this movement, American plaice occupied warmer temperatures during a period of cold conditions and were maturing at a younger age and smaller size during this time.

Population abundance was the factor most closely related to the proportion mature at age and size, but only if considered over the lifetime of a cohort. Population abundance over the juvenile period did not appear to play a significant role. In fact, there appeared to be

little effect of any factor over the juvenile period except for growth. There are a number of possible explanations for this. All of the factors examined show considerable variability and the shorter time series used in examining their effect over the juvenile period may not be sufficient to detect trends within this variability. Also, American plaice mature over a 6–8 year period and a 20–30 cm length range. Without the ability to follow individuals a “juvenile period” had to be defined. The wide range of ages and sizes over which the fish mature could blur any effects during this juvenile period. A longer time series may help to clarify these questions.

In this study, low population abundance, increased juvenile growth, increased temperature and increased

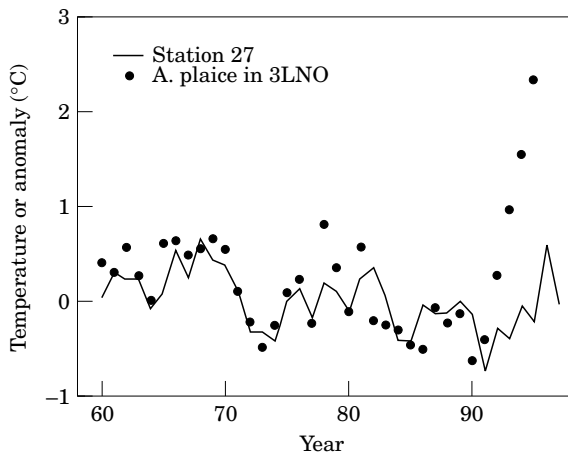


Figure 12. Vertically averaged temperature at Station 27 (—) and estimated average temperature occupied by American plaice in 3LNO (●).

adult mortality all appeared to promote maturation at a younger age and a smaller size. This confirms the findings of other studies involving this and other species. However, only low population abundance was related to earlier maturity in all stocks. This may indicate that the other factors are not always necessary requirements for earlier maturity. Of course these factors did not vary independently of one another. For example, as abundance decreased mortality was higher and fish moved to warmer waters. Observed changes in size and age at maturity will be the result of the integration of the fish's response to changes in several variables. If changes in different factors tend to exert opposite pressures on maturation then the fish will make trade-offs to find the optimal solution (Roff, 1992; Stearns, 1992). This could be the cause of some of the differences between stocks that were observed in this study.

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