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Factors in Maturation of Yellowtail Flounder (*Pleuronectes ferruginea*) on the Grand Bank

by

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Abstract

Variation in the maturation of both male and female yellowtail flounder on the Grand Bank was evident from analyses carried out on a cohort basis. Exploration of the effects of population size, growth, mortality, cohort strength and bottom temperature on maturation were carried out through statistical analyses of life history data collected during annual spring bottom trawl surveys from 1984 to 1997. There was a pronounced declining trend in the onset of maturation in males but no directed trend in females. Increased growth of a cohort over its lifetime, increased growth in the year prior to maturation, increased mortality in adults and increased bottom temperatures all appear to exert some effect on maturation of one or both sexes. Population abundance did not appear to have any direct effect even though there has been a substantial decline in abundance during the study period which led to the implementation of a directed fishery moratorium in 1994. The significance of these findings is discussed in terms of life history theory.

Keywords: yellowtail flounder, maturity, growth, cohort, mortality, reproduction.

Introduction

Stock productivity in marine fish is influenced by growth, maturation, mortality and fecundity. These life history traits are strongly correlated and governed by the energy budget of the fish. Roff (1984) concluded that these correlations are the result of adjusting the tradeoffs between growth, reproduction and survival. Natural variation in size and age at maturity within a population of a species can occur in stable populations but is generally small. However, within declining populations, large variations in maturation, as with other life history traits, can occur, for example, Atlantic cod, *Gadus morhua*, (Beacham 1983a; Jørgensen 1990), American plaice, *Hippoglossoides platessoides*, (Pitt 1975; Morgan et al. 1996; Morgan and Colbourne 1998) and North Sea plaice, *Pleuronectes platessa* and sole, *Solea solea*, (Rijnsdorp 1989; Rijnsdorp and Vethaak 1997). Also there may be large differences between different populations of the same species, for example Atlantic cod (Fleming 1960; Godø and Moksness 1987), and American plaice (Roff 1982; Walsh 1994). Although some of these variations in size and age at maturity may reflect genetical changes (which are difficult to detect) others reflect changes in phenotypic plasticity. Phenotypic plasticity is generally associated with changes in environmental conditions on the nursery grounds or later during the juvenile/adult stage (Alm 1959, Carscadden and Leggett 1975; Stearns and Crandall 1984; Rijnsdorp 1993a).

Changes in age-specific growth and mortality or survival rates have been shown to favour either an increase or a decrease in age at maturity (Roff 1982; Stearns and Crandall 1984, Stearns and Koella 1986; Hutchings 1993) and size at maturity (Reznick and Endler

1982; Reznick et al. 1990; Kasperski and Kozlowski 1993). For example, North Sea plaice with the highest juvenile growth rates mature at an earlier age and at a larger size (Rijnsdorp 1989). Hutchings (1993) showed that in unexploited populations of brook trout (*Salvelinus fontinalis*) with higher adult-to-juvenile survival, there was a delay in age at maturity compared to populations with lower adult-to-juvenile survival ratios.

Changes in age and size at maturity have been recognized as one of the main biological indicators of stress in marine populations that have undergone serious declines (see Trippel 1995 for a review). Rijnsdorp and Vethaak (1997) showed that juvenile growth rates and fishing effort made significant contributions to the variation in maturation parameters of North Sea plaice and sole during their1960-95study period. Natural or fishery induced declines in population size are thought to lead to an increase in growth rates, hence a reduction in age at maturity, as a result of reduced intra-specific competition for food (see for example Pitt 1975; Power and Gregoire 1978; Policansky 1993; Rijnsdorp 1993b; Rijnsdorp and Vethaak 1997). This assumes that the compensatory response is density dependent.

Yellowtail flounder (*Pleuronectes ferruginea)* is at its northern limit of commercial concentrations on the Grand Bank, off the east coast of Newfoundland (Walsh 1992). It is a relatively short-lived species with a historical maximum age of 13 years and size of 56 cm; however, in recent years there has been a truncation in age structure of females. Female yellowtail flounder over the age of 9 yr. are rarely found in survey samples. The average maximum length for males is 48 cm (age 9 yr.) and for females it is 54 cm. Data on age and length at 50% maturity in yellowtail flounder on the Grand Bank was first reported by Pitt (1970) from data collected during biological surveys of the Grand Bank from 1959 to 1968. Males reached A_{50} at 5.04 years with a L_{50} of 31.3 cm and females reached A_{50} at 6.12 years with a L_{50} of 3~~7~~4.4 cm. Using survey data for the 1975-95 period, Morgan and Walsh (1997) reported that annual estimates of age (A_{50}) and size (L_{50}) at maturity of yellowtail flounder have shown a steady decline in both sexes from 1988-95. Coincident with this decline was a systematic decline in biomass from 217,000 t in 1984 to 56,000 t in 1994, and heavy fishing mortality on juveniles during the late 1980's and early 1990's (Walsh et al. 1995; Walsh et al. 1998). As the stock size declined in the late 1980's, there was a contraction in the northern range of the species (Brodie et al. 1998). In addition, there was a generally cooling off of bottom temperatures (0.5 to 1.0^{0} C below normal) and heat content (26% below normal) on the bank (Colbourne et al. 1997). During the 1994-98 period the fishery was under moratorium and the stock has since shown good signs of recovery

In this paper, we will examine size and age of maturation on a cohort basis, rather than an annual basis, and then explore the relationship between variation in maturation and the effects of temporal changes in population size, growth, mortality, cohort strength and temperature. Given the enormity of the task it is not our intention to consider all facets of the various parameters in one paper.

Materials and Methods

Data

Data on life history parameters were collected during annual bottom trawl surveys of the Grand Bank, Northwest Atlantic Fisheries Organization (NAFO) Division 3L, 3N and 3O, from the spring period of 1984-1997. These surveys employed a stratified random sampling design and were carried out mainly by the research vessel, *CCG Wilfred Templeman* and, on occasion, by it's sister ship, *CCG Alfred Needler*. Because two different trawls have been used in these surveys, catches were standardized to the new trawl using length-based conversion factors derived from comparative fishing experiments in 1996 (Walsh and Orr 1998). These standardized values were used in the estimation of abundance, maturity, mean length at age, cohort strength and mortality.

For the analyses of life history traits and environmental variables only data from the southern Grand Bank, NAFO Divisions 3N and 3O, were used. This is the area where the majority of the stock is concentrated and in some years there were no catches in the northern section of the Grand Bank. NAFO Division 3L (Brodie et al. 1998).

Maturity ogives

Fish were classed as juvenile (immature) or adult (mature) using visual examination of gonads as described by Templeman et al. (1978). Proportions mature at age were calculated according to the method described in Morgan & Hoenig (1997) which corrects for bias introduced by length-stratified sampling. Estimates of the age and size at

50% maturity (A_{50} and L_{50}) for each cohort were derived using a logistic model with a logit link function and binomial error. The data were fitted to the model using the Probit procedure of SAS (SAS, 1989). A_{50} and L_{50}'s were produced only for those cohorts for which both the slope and intercept of the maturity ogive were significant at the p=0.01 level.

Hypotheses

Variations in maturation were investigated by testing the following hypotheses:

a) cohorts experiencing lower population size matured at a younger age and smaller size;

b) cohorts experiencing higher growth matured at a younger age and smaller size;

c) cohorts experiencing higher mortality mature at a younger age and smaller size;

d) cohorts exhibiting higher year-class strength matured at a younger age and smaller size; and

e) cohorts experiencing higher temperature matured at a younger age and smaller size.

These hypotheses were set up to explore the effects of each parameter on the proportion mature at age and length.

a) Population size effects

For each year, stratified estimates of population abundance at age were used to calculate the mean total population size for each cohort during its lifetime (or the period during which it occurred in the survey if its entire life was not sampled). If the mean population abundance during the lifetime of the cohort was below or above the average for all cohorts then it was classified as occurring either during a low or high population abundance period. A similar approach was used on ages 1 to A_{50} for each cohort and sex to examine effect of population abundance during the juvenile period.

b) Growth effects

Mean length at age was calculated by sex for each cohort[1]. For each sex the effect of age on mean length was modeled. The average of the residuals from this model 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. A similar procedure was carried out over ages 1 to A_{50} for each cohort and sex to examine the effect of juvenile growth. The effect of growth on maturation was also examined by testing the effect of juvenile growth in the last year before maturation, i.e. the mean length at age 4 for males and age 5 for females.

c) Mortality effects

Adult mortality[2] was calculated for each cohort as the number of fish age 8 in year i divided by the number of fish of that cohort at age 9 in year $i+1$. Juvenile mortality[3] was calculated as the number of fish of a cohort at age 3 in year i divided by the number of fish of that cohort at age 4 in year $i+1$. Cohorts were classified as experiencing low or high mortality when compared to the average. The difference between the value for adult mortality and juvenile mortality served as a measure of the ratio of adult to juvenile mortality.

d) Cohort strength effects

The relative strength of each cohort was calculated using the general approach of Sinclair and Chouinard (1991). The model took the form:

$$\log(N_{ikt})=\tau + \alpha_i+\beta_j+\delta_k+\varepsilon$$

where: N_{ikt} = number at age i belonging to cohort k in year t

τ = intercept

α_i = age effect for i=3....5

δ_k = cohort effect

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[1] These means were calculated correcting for bias introduced by the length-stratified sampling used (i.e. an adjusted age-length key was used).

[2] Age 8 is the age at which yellowtail flounder are fully recruited to the survey trawl.

ε = residuals from the fitted model

Cohorts were classed as having a relative strength less than the overall average or greater than the overall average.

e) Environmental effects

During the annual surveys, bottom temperature data were calculated at each fishing station using either mechanical bathyothermographs, expendable bathyothermographs or trawl mounted Seabird-19 conductivity-temperature-depth (CTD) probes. The temperature at each fishing station was weighted by both fish abundance and total stratum area to calculate the average temperature occupied by the fish population as suggested by Perry and Smith (1994). The average temperature experienced over the lifetime of each cohort was then calculated for each sex. If the mean temperature during the lifetime of the cohort was below or above the average for all cohorts then it was classified as occurring either during a low or high temperature period. The same procedure was carried out for each cohort/sex combination for the juvenile period from birth to their respective A_{50}.

Hypotheses testing

The effect of cohort, average population size over a lifetime, average population size over the juvenile period, growth, juvenile growth, growth in the year prior to maturation, adult mortality, juvenile mortality, adult:juvenile mortality, temperature over a lifetime, temperature

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[3] Age 3 is the first age represented in every year of the survey.

over the juvenile period, and relative cohort strength on the proportion mature at age and size for each sex was explored using generalized linear models with a logit link function and binomial error (McCullagh & Nelder, 1983; SAS 1993). Each model had the general form of:

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

where: *pmat*= proportion mature at age or length

$u = \tau + \alpha \nu_i + \beta_j$

τ = intercept

ν_i = age or length

α = age or length effect

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

The statistical significance of each parameter examined was determined after first removing the effect of age or size. Each sex was tested separately.. Because 48 tests were being conducted, increasing the likelihood of a significant result by chance alone, the significance level was adjusted so that only tests where $p<0.001$ were considered significant. Also, the proportion of the Deviance, i.e., the pseudo-coefficient of determination r^2 (Swartzman et al., 1992; Swain, 1993), accounted for by each parameter was calculated. 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. For males these were ages 4-7 and lengths 18.5-34.5 cm and for females, ages 5-8 and lengths 24.5-42.5 cm were used.

Results

There was a significant effect of cohort on maturity at age for both males (p=0.001, pseudo r^2=0.52) and females (p=0.0008, pseudo r^2=0.35). Males have shown a general decline in A_{50} over the time period, with a high of 5.8 years for the 1979 cohort and a low of 4.6 years for the 1988 cohort, a decline of 21% (Fig. 1). Since the 1988 cohort, A_{50} has increased to 4.9 years. Female showed less change, with a high of 6.8 years for the 1979 cohort and a low of 6.1 years for the 1987 cohort, a decline of only 10%. As well, female maturity appeared to be more variable than male maturity with the trend over time less clear.

There was also a significant effect of cohort on maturity at length for both males (p=0.0001, pseudo r^2=0.45) and females (p=0.0001, r^2=0.24). Male L_{50} generally declined over the time period, from a high of 30.7 cm for the 1979 cohort to a low of 25.0 cm for the 1988 cohort, a decline of 18.5% (Fig. 2). Since the 1988 cohort, L_{50} for males has increased slightly to 26.2 cm. Female L_{50} showed less of a consistent trend than the males and a smaller change over the time period. The largest L_{50} was for the 1978 cohort at 34.9 cm and the smallest for the 1987 cohort at 32.5 cm, a difference of 6.7%. The L_{50} for the 1991 cohort was 33.0 cm.

There was no significant effect of population size on maturation when population size examined over the lifetime of a cohort. Similarly, there was no effect during the juvenile period of a cohort (Table 1).

Growth over the lifetime of a cohort had a significant effect on maturity at length in males and approached significance in females (Table 1). Growth over the lifetime had a significant effect on maturity at age for males only. In general, cohorts with higher than average growth, matured at a younger age and a smaller size (Fig. 3&4). Growth over the juvenile period did not have a significant effect on maturity at age or size for either males or females. Growth in the last year before maturity, i.e. age 4 for males and age 5 for females, had a significant effect on maturity at age (but not size) in both sexes (Table 1). This meant that cohorts with higher than average growth in the year prior to maturation matured at a younger age (Fig. 5&6).

Mortality had a significant effect on maturity at length for adult males only (Table 1). Male cohorts with a higher than average mortality tended to mature at a smaller length (Fig. 7). There was no significant effect on the ratio of adult to juvenile mortality on maturation.

Relative cohort strength did not have a significant effect on maturity at age or size for either males or females (Table 1).

Male cohorts which experienced higher than average temperatures over their lifetime had a significantly higher proportion mature at age and length than those that experienced lower than average temperatures (Table 1, Fig. 8&9). There was no significant effect of temperature over the lifetime of the cohort on maturity in females or over the juvenile period in either sex.

In summary, it would appear that growth over the lifetime of the cohort, growth of the cohort in the year prior to maturation (age only), mortality (length only) and temperature had the greatest effect on maturity in males. For females, only the effect of growth over the lifetime of the cohort (length only) and growth of the cohort in the year prior to maturation (age only) showed any significant effect on maturation. None of the factors examined over the juvenile period had any significant effect. Those parameters that had a significant result also accounted for the largest proportion of the Deviance (r^2).

Discussion

Variation in both size and age at maturity in the Grand Bank yellowtail flounder population was evident in both males in females during our 14-year time series. Age and size at maturity are strongly correlated in both sexes. However, only males showed a distinct declining trend; females varied around the long term average for both parameters. Although there was a 21 % decline in A_{50} ($\bar{x}$ = 5.04 yr.) in males and a 10% decline in A_{50} ($\bar{x}$ = 6.12 yr.) in females, the overall mean values are similar to those reported by Pitt (1970) for the 1959-68 period, 5.04 yr. and 6.44 yrs. respectively. There was an 18.5% decline in L_{50} in males ($\bar{x}$ = 27.1cm) and a 6.7% decline in L_{50} in females ($\bar{x}$ = 33.9 cm) over the study period. The overall mean value for males was 13% below that value ($\bar{x}$ = 31.3 cm) reported for Pitt (1970), but there was no difference in overall mean L_{50} in females between the two study periods (~~34.4~~ 33.9 cm for 1984-95 and ~~33.9~~ 34.4 cm for 1959-68).

Most studies support the idea that variations in size and age at maturity occur in both sexes and similar trends are expected, i.e. if there is a decreasing trend in either size and/or age it occurs in both sexes (see for example Morgan et al. 1996). Such is not the case in this study.

Population size had no regulatory effect on maturation of male and female yellowtail flounder, even though there was a significant decline in stock size during the study period due to overfishing and poor recruitment (Walsh et al. 1998). Declines in age and size at first maturity is often associated with natural or fishery induced reduction in population size (see for example: Craig 1982; Stearns and Crandall 1984; Rijnsdorp 1989; Kasperski and Kozlowski 1993:Policansky 1993; Rowell 1993). Using a similar statistical methodology to that used in this study, Morgan and Colbourne (1998) found large declines in age and size at maturity evident in three populations of American plaice off the east coast of Newfoundland. Population abundance was cited as the critical factor in their conclusions. Changes in population size and the onset of maturation are generally correlated with changes in growth, mortality and to some extent environmental conditions under the assumption that there is a density dependent compensatory effect.

Growth over the lifetime of yellowtail flounder cohorts had a significant effect on size at maturation in both sexes and age at maturity in males only. Higher growth led to early maturity (males only) and a reduction in size. Growth during the juvenile period has been shown to have an effect on maturation in unexploited populations of fish (Hutchings 1993). However, in Grand Bank yellowtail flounder, only high growth in the year prior to maturation, not over the juvenile period, resulted in a reduction in age at maturity. Rijnsdorp (1993a) concluded that maturation in North Sea plaice depended upon length reached within a certain year and also on growth in the three preceding years. For many species, size may be the most critical factor in maturation (Alm 1959; Roff 1981, 1982,1991; Rijnsdorp 1993a) and variation in age at maturity reflects the variation in growth in the year prior to maturation. This is likely the case for yellowtail flounder.

The cost of reproduction is influenced by schedules of growth, survival and fecundity that shape the age and size at maturity (Williams 1966; Charlesworth 1980; Bell and Koufopanou 1986; Gadgil and Bossert 1970, Roff 1984, 1991; Hutchings 1993). Age-specific survival should respond to changes in growth rate. High adult mortality relative to juveniles should favor delayed maturity (Hutchings 1993). Mortality over the lifetime of the adult yellowtail flounder cohort had the only measurable effect on size at maturity in males. Mortality (Z) in exploited populations consist of natural (M) and fishery (F) induced components. In this study, the method used to estimate juvenile and adult mortality (Z) may not have given accurate results because of the selectivity of the survey gear, i.e. cohorts are not fully recruited to the gear until age 8.

Growth rates of fish are generally correlated with cohort strength and it is often assumed that this is a density dependent effect. For example, an inverse relationship between year class size and growth rates has been demonstrated for the Georges Bank yellowtail flounder population (Ross and Nelson 1992). Fish with faster juvenile growth rates are expected to mature earlier than slow growing fish (Alm 1959; Nikoloskii 1969;

Roff 1982; Hutchings 1993). Our analysis did not demonstrate any significant effect of cohort strength on maturation even though there were large variations in the abundance of individual cohorts.

Environmental conditions, such as temperature, have been shown to affect growth rates and hence the onset of maturation (Alm 1959; Carscadden and Leggett 1975; Godø and Moksness 1987; Sandstrom et al 1995). Male yellowtail flounder cohorts experiencing higher than average temperatures during their lifetime matured at a younger age and smaller size. Such was not the case for female yellowtail flounder. The temperature regime also had no effect over the juvenile period. A species inhabiting warmer waters generally show higher growth rates, early maturation and maturation at a smaller size than those found in colder waters (Gunter 1950; Beacham 1983b; Walsh 1994). As described above, increased growth had some effect on maturity at size and age in both male and female yellowtail flounder, while temperature had a significant effect on size and age at maturity in males only. Why the sexes differ in their response to temperature is unclear.

There are differences in maturation between populations of yellowtail flounder in the Northwest Atlantic. For example, populations of yellowtail flounder populations farther south on the Scotian Shelf, Georges Bank, Cape Cod bank, and the southern New England bank mature at a smaller size and age than the Grand Bank population (Pitt 1970). There is also evidence to suggest that, in these populations, both males and females have shown declines in size and age at maturity. Royce et al. (1959) estimated mean age and size at first maturity in males and females at 1.0 yr. (26 cm) and 2.0 yr. (32 cm), respectively, in samples taken from the southern New England population in 1943. O'Brien et al. (1993) estimated the mean age and size at first maturity in males and females at 1.8 yr. (19.6 cm) and 1.6 yr. (25.5 cm) respectively during the 1985-90 period for the same population.

The pattern of allocating surplus energy into growth and reproduction differs between males and females. It is common in many species of fish for males to mature earlier and at a smaller size, to have a shorter lifespan and a smaller asymptotic length than females. This sexual dimorphism is evident in the life history traits of yellowtail flounder. Rijnsdorp and Ibeling (1980) estimated that male North Sea plaice allocate proportionately more energy into reproduction than females. In the juvenile stage surplus energy levels should be equal in both sexes and channeled towards somatic growth, however, at a certain size, male surplus energy is channeled towards reproduction while the female continues to grow. Size dependent survival is thought to underline size dependent maturity (Roff 1991; Hutchings 1993). If there has been more of an increased risk of mortality in males than in females then yellowtail flounder may respond by reducing its size at maturity and channeling more energy into reproduction. Differential mortality between sexes has been shown in North Sea plaice by Beverton (1982) who estimated M in males to be 13% and 8% in females. If such a difference in mortality exist in male and female yellowtail flounder, this may explain why we detected mortality effects only in males.

In this study of yellowtail flounder on the Grand Bank, increased growth led to maturation at an earlier age in males and smaller size in both males and females. Males have shown a greater response over the time period particularly to increased mortality and temperature. The reason for these sex difference is not obvious. O'Brien et al. (1993) found spatial differences in mean size and age at maturity for males but not for females in populations of yellowtail flounder on Georges Bank, Cape Cod bank and the southern New England bank. This may be a common feature in yellowtail flounder populations.

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Table 1. Results of generalized linear models testing the significance of each variable on proportion mature at age and length. As 48 separate tests were conducted only tests with $p<0.001$ are considered significant. The pseudo-coefficient of determination (r^2) is also given for each test.

VARIABLE				***male***	***female***
Abundance	AGE	Total	p	0.0634	0.0997
			r^2	0.06	0.05
		Juvenile	p	0.0265	0.0718
			r^2	0.09	0.06
	LENGTH	Total	p	0.7971	0.0333
			r^2	0.001	0.03
		Juvenile	p	0.0055	0.0233
			r^2	0.06	0.04
Growth	AGE	Total	p	0.0002	0.0076
			r^2	0.20	0.12
		Juvenile	p	0.1879	0.3108
			r^2	0.03	0.02
		Age 4 or 5	p	*0.0005*	*0.0001*
			r^2	0.17	0.23
	LENGTH	Total	p	0.0001	0.0012
			r^2	0.14	0.07
		Juvenile	p	0.0846	0.6147
			r^2	0.02	0.002
		Age 4 or 5	p	0.0026	0.3012
			r^2	0.07	0.01
Mortality	AGE	Adult	p	0.016	0.4223
			r^2	0.13	0.01
		Juvenile	p	0.0739	0.1434
			r^2	0.07	0.05
		adlt:juv	p	0.0505	0.2081
			r^2	0.12	0.05
	LENGTH	Adult	p	0.0006	0.2218
			r^2	0.11	0.01
		Juvenile	p	0.1867	0.1156
			r^2	0.02	0.02
		adlt:juv	p	0.0064	0.8663
			r^2	0.10	0
Cohort Strength	AGE		p	0.8889	0.7363
			r^2	0	0.002
	LENGTH		p	0.8584	0.9659
			r^2	0	0
Temperature	AGE	Total	p	0.0001	0.0968
			r^2	0.26	0.05
		Juvenile	p	0.0318	0.6026
			r^2	0.09	0.006
	LENGTH	Total	p	0.0001	0.1060
			r^2	0.18	0.02
		Juvenile	p	0.6658	0.4105
			r^2	0.002	0.006

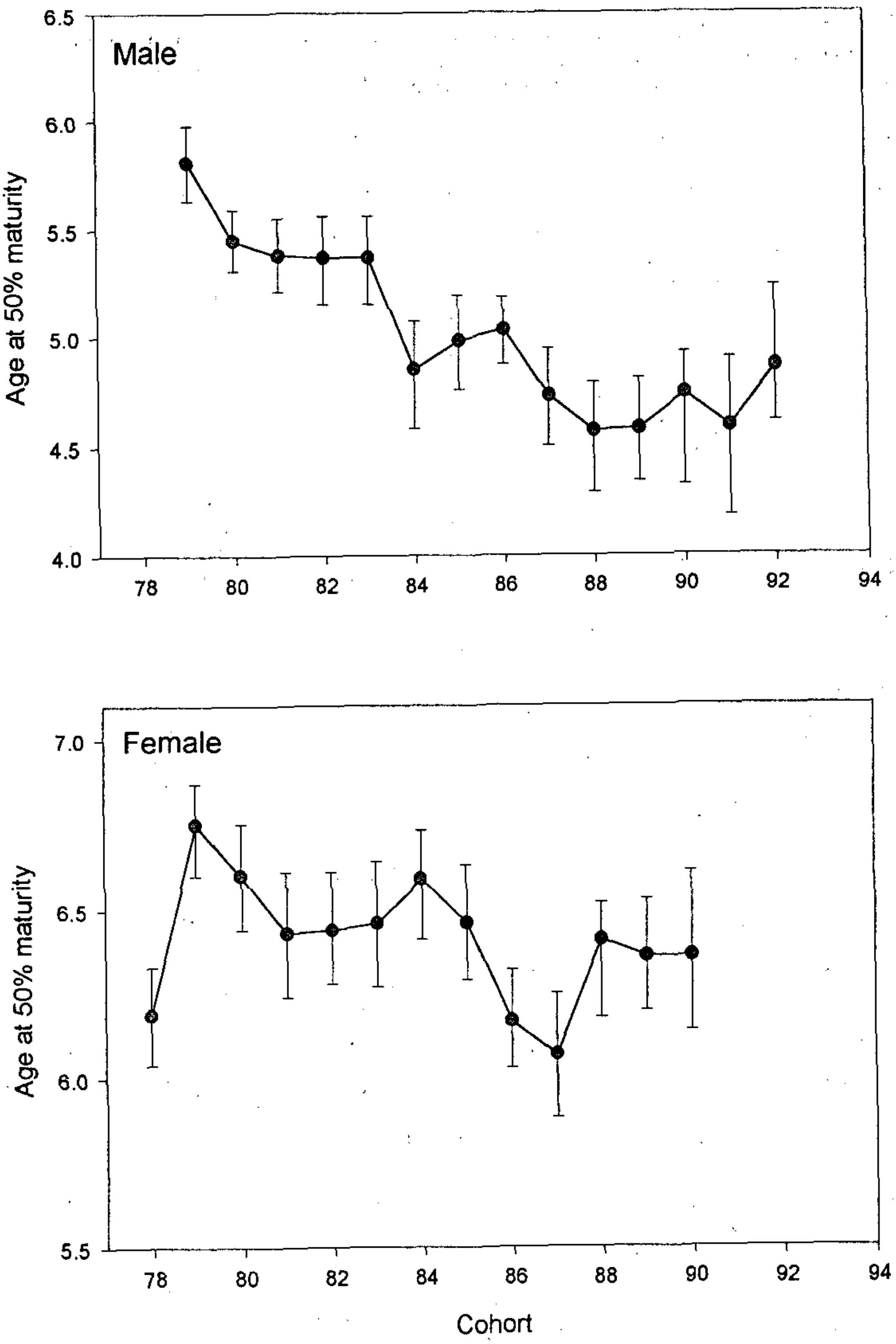


Figure 1. Age at 50% maturity for male and female yellowtail flounder cohorts. (95% fiducial limits are shown).

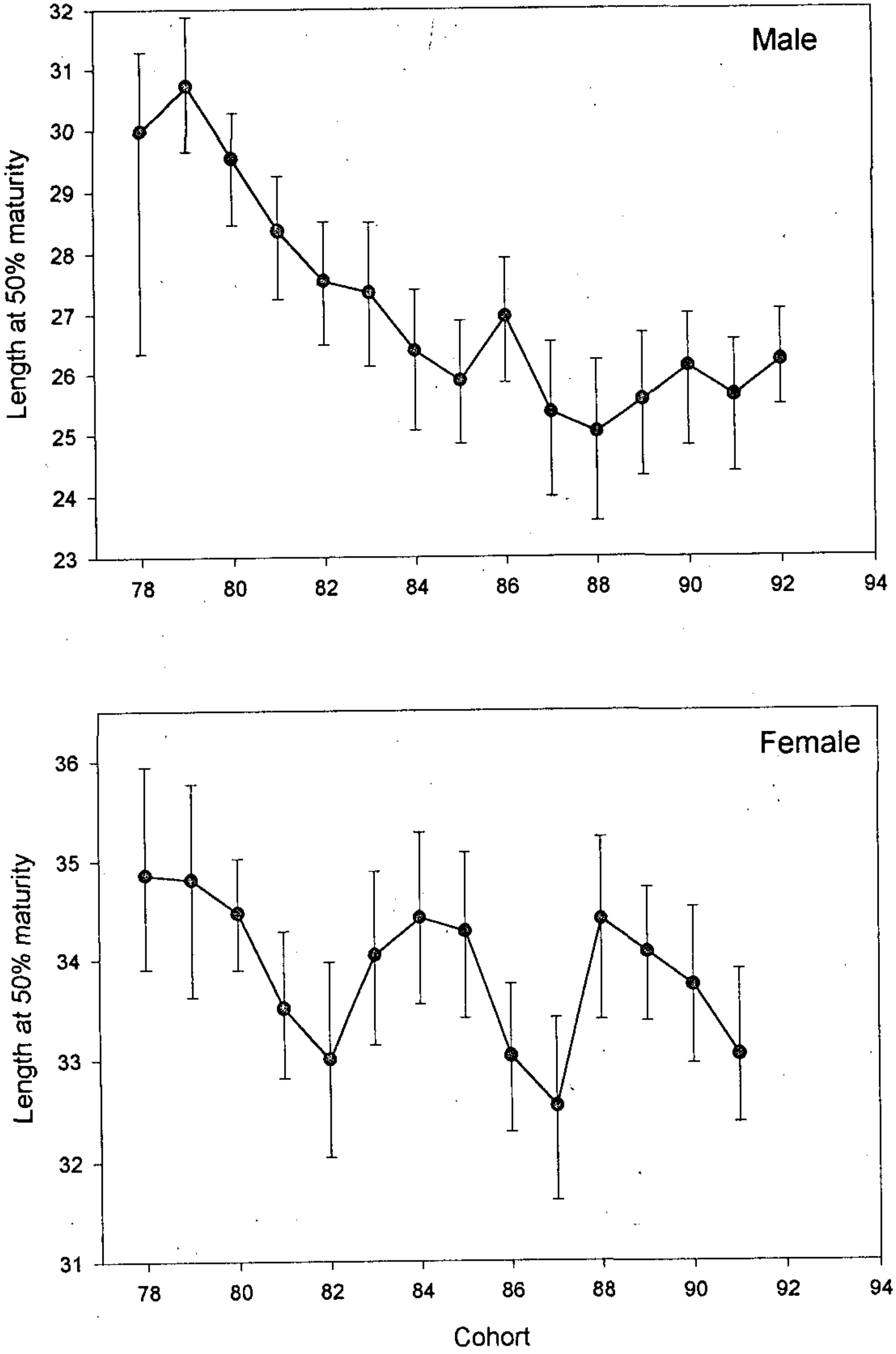


Figure 2. Length at 50% maturity for male and female yellowtail flounder cohorts. (95% fiducial limits are shown).

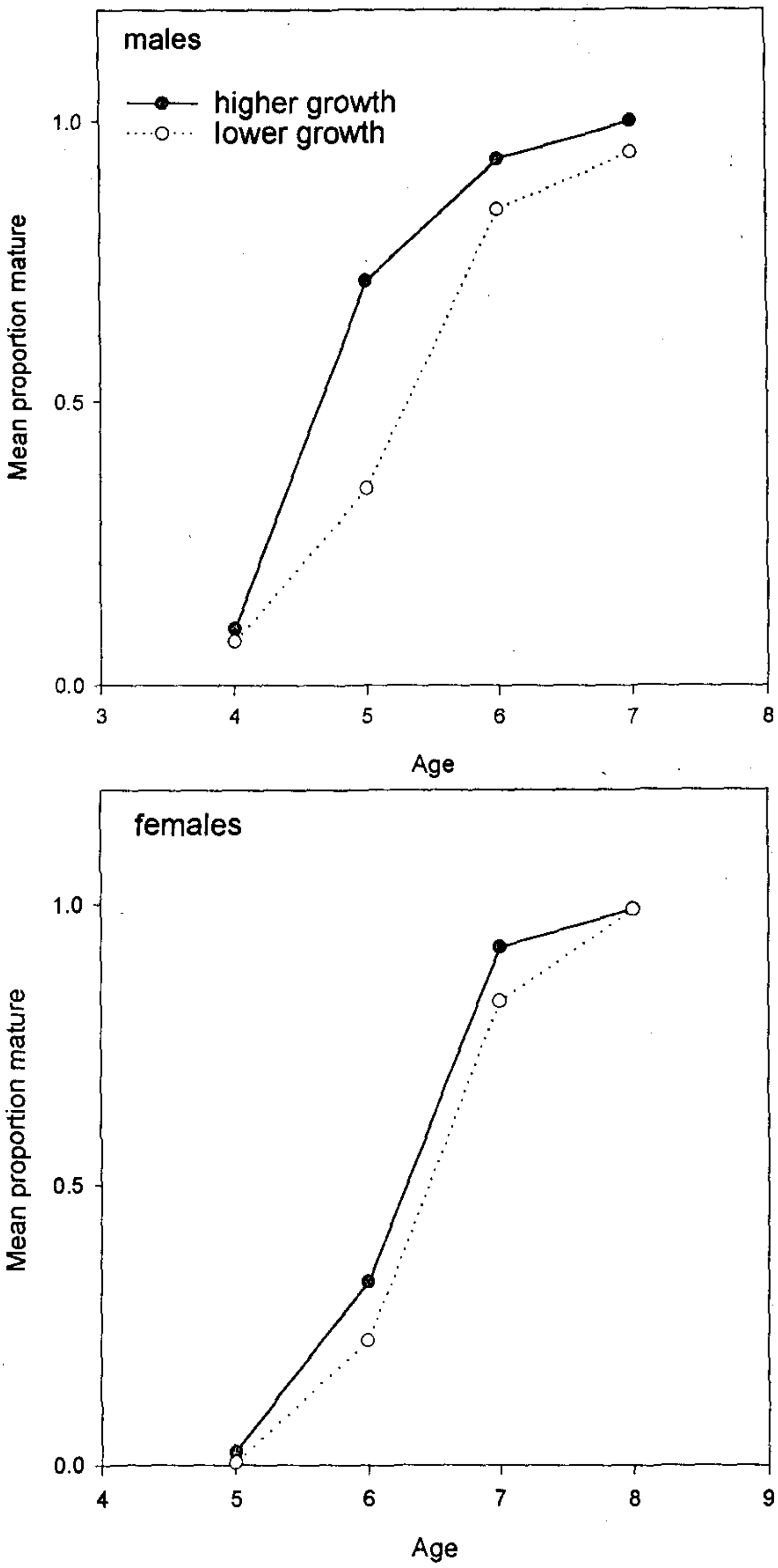


Figure 3. Mean proportion mature at each age for cohorts that had a higher than average growth during their lifetime (solid circles) and those experiencing a lower than average growth during their lifetime (open circles).

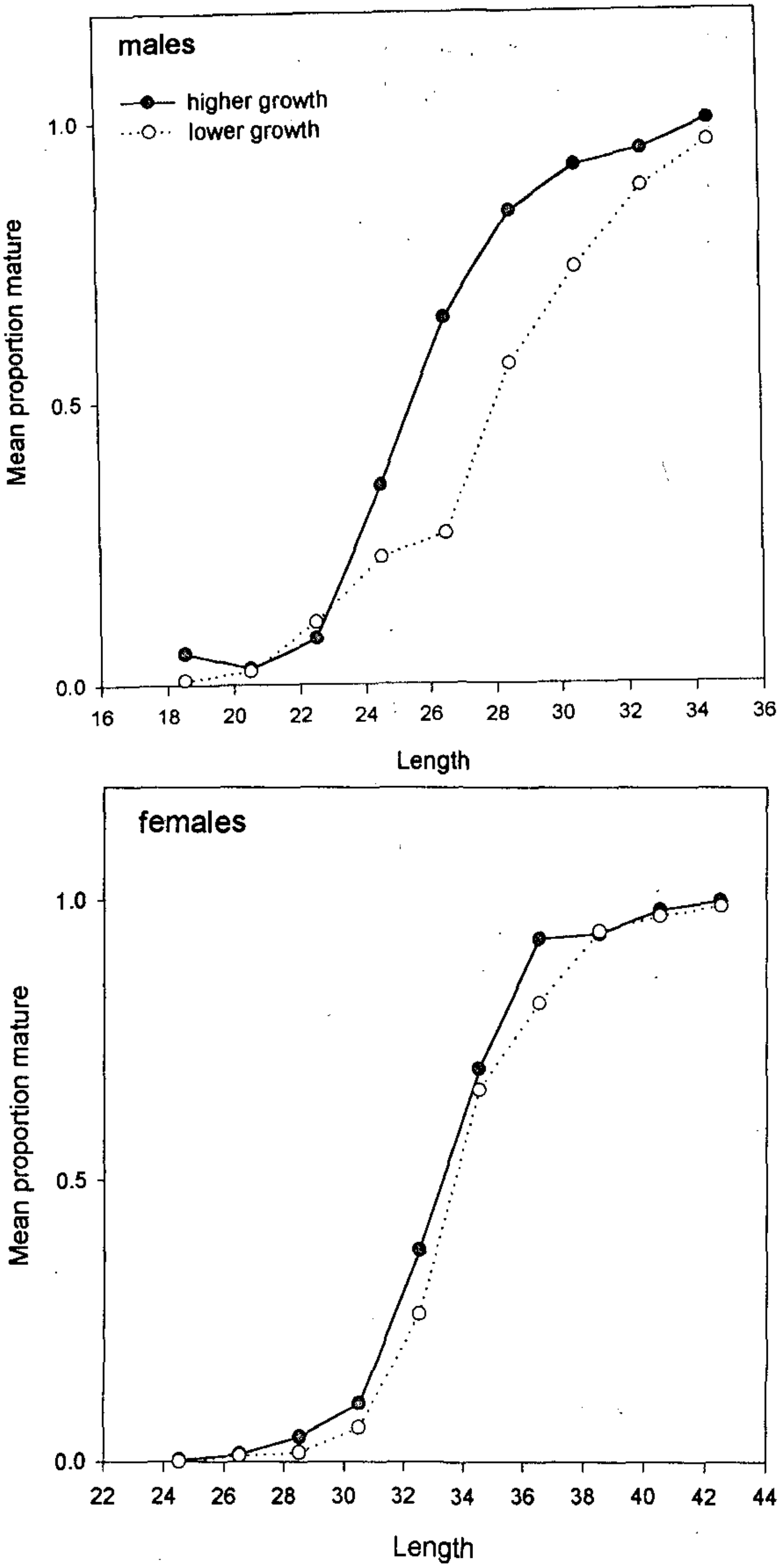


Figure 4. Mean proportion mature at each length for cohorts that had a higher than average growth during their lifetime (solid circles) and those experiencing a lower than average growth during their lifetime (open circles).

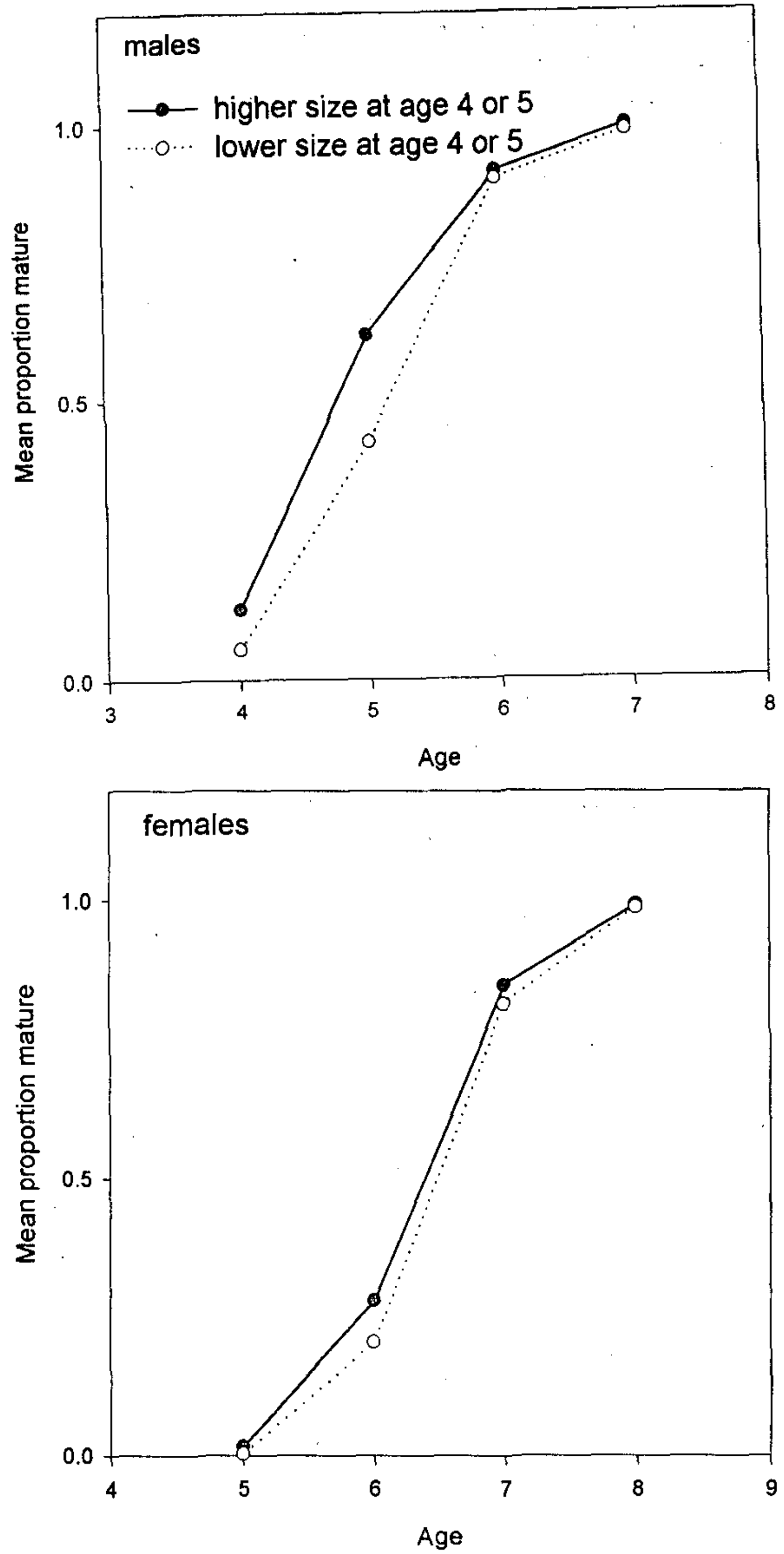
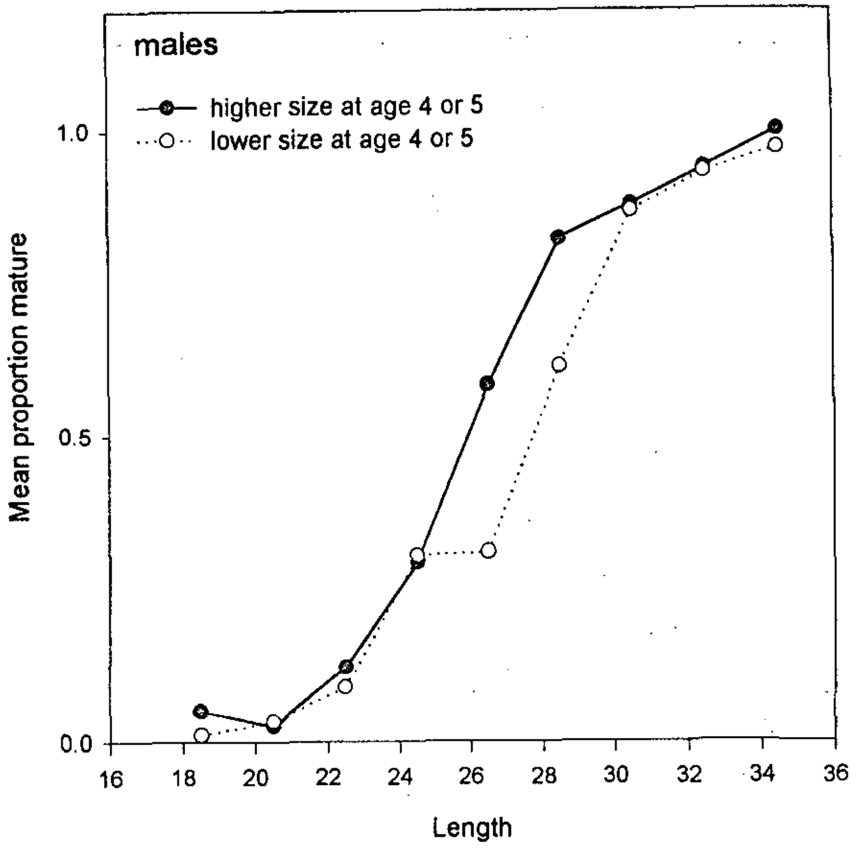


Figure 5. Mean proportion mature at each age for cohorts that had a higher than average growth in the year prior to maturation (age 4 males, age 5 females; solid circles) and those experiencing a lower than average growth in the year prior to maturation (open circles).



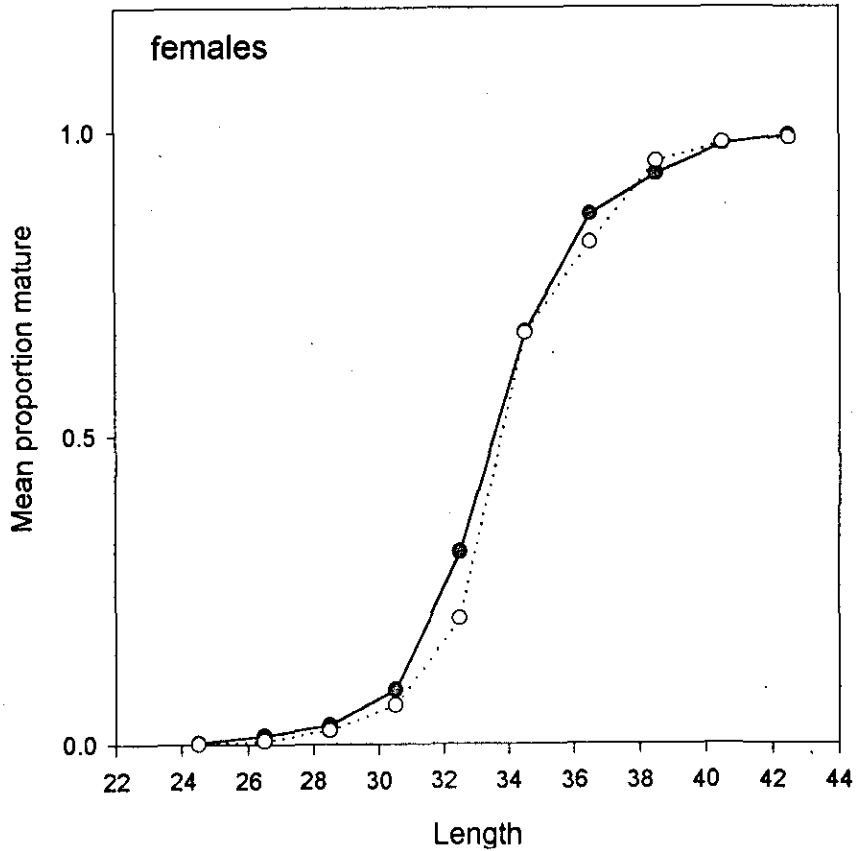


Figure 6. Mean proportion mature at each length for cohorts that had a higher than average growth in the year prior to maturation (age 4 males, age 5 females; solid circles) and those experiencing a lower than average growth in the year prior to maturation (open circles).

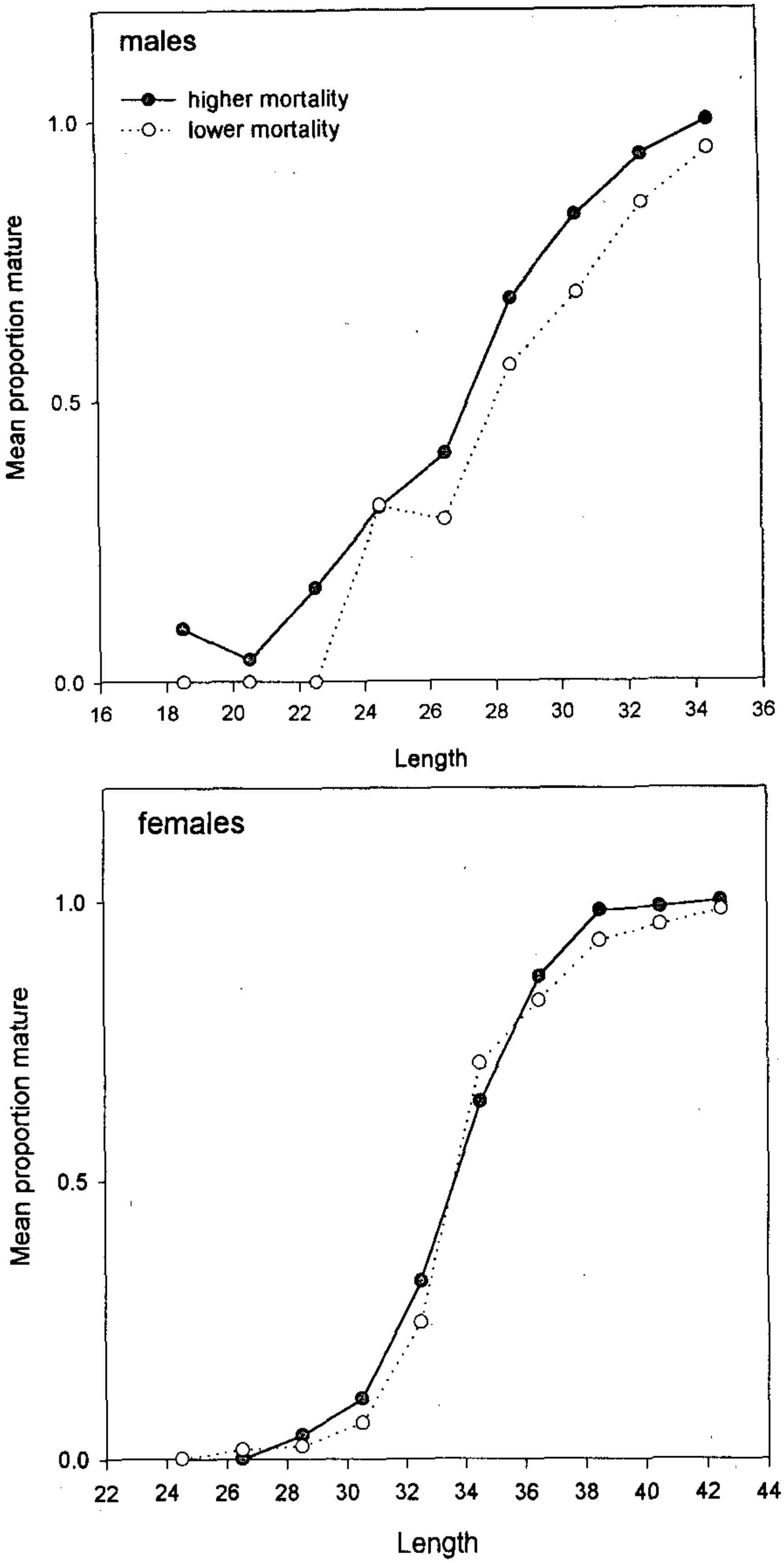


Figure 7. Mean proportion mature at each length for cohorts that had a higher than average relative mortality (solid circles) and those experiencing a lower than average relative mortality (open circles).

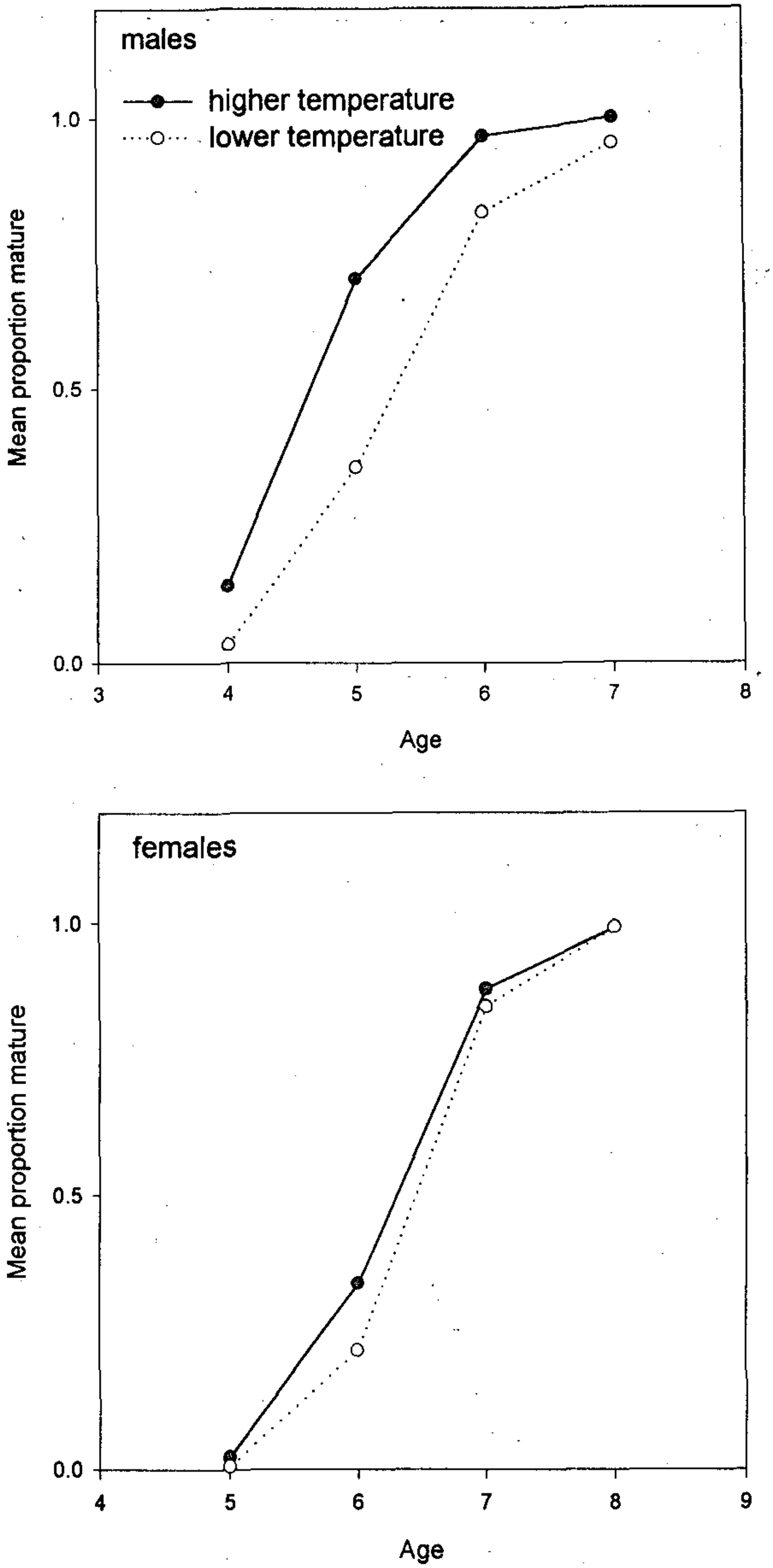


Figure 8. Mean proportion mature at each length for cohorts that experienced higher than average temperatures (solid circles) and those experiencing lower than average temperatures (open circles).

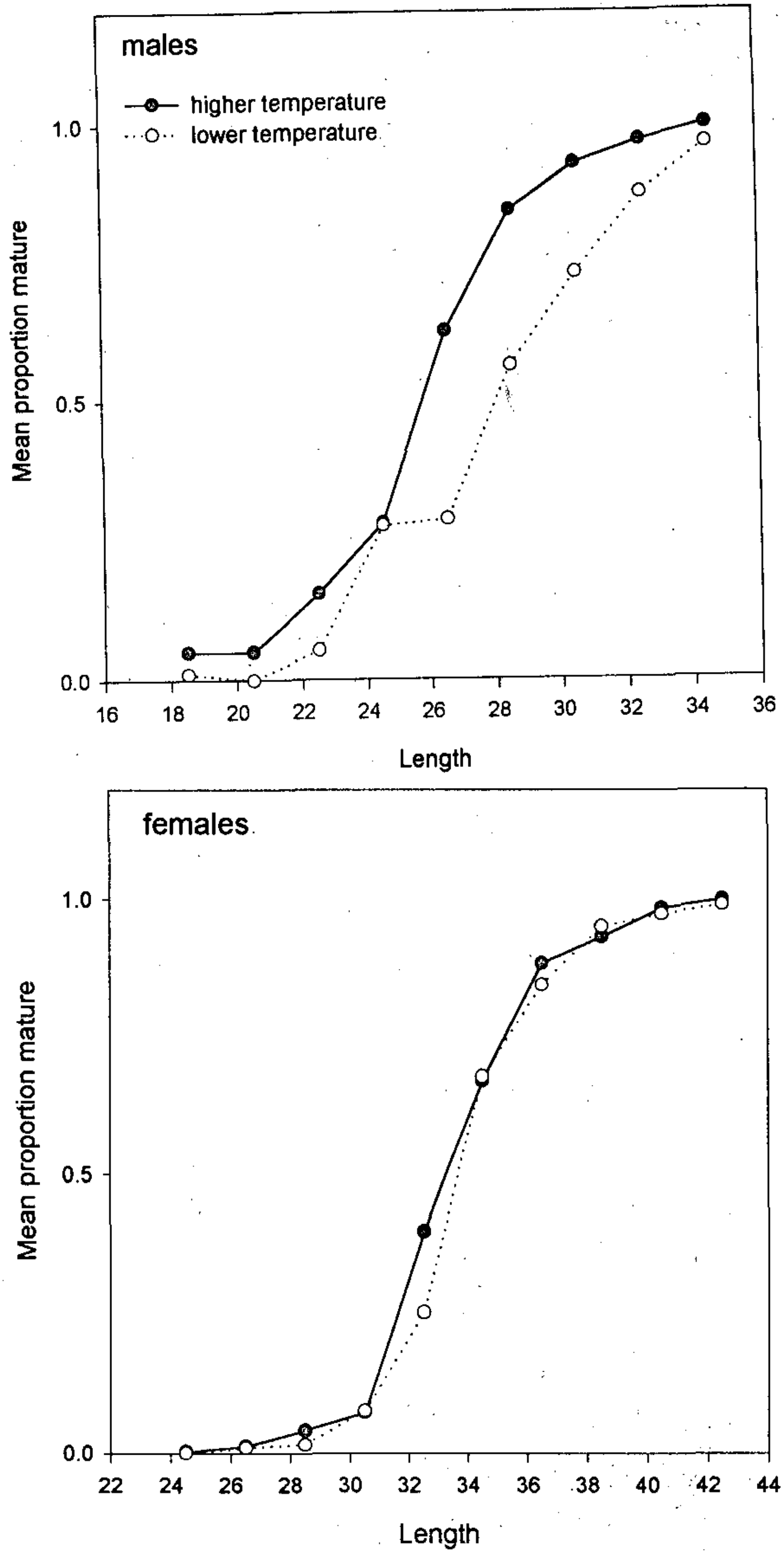


Figure 9. Mean proportion mature at each age for cohorts that experienced higher than average temperatures (solid circles) and those experiencing lower than average temperatures (open circles).