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Maturation of Newfoundland American Plaice (*Hippoglossoides platessoides*): Long-Term Trends in Maturation Reaction Norms despite Low Fishing Mortality?

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Abstract: To interpret long-term trends in age and size at maturation, new statistical methods have recently been devised for estimating probabilistic maturation reaction norms based on data collected for the management of fisheries. Here we apply these methods to three Newfoundland stocks of American plaice (NAFO Divisions 2J3K, 3LNO, 3Ps) and report a clear long-term shift in the maturation reaction norms of these stocks towards maturation at younger age and smaller size. Theory predicts that such trends could result from fishing acting as a selective force, inducing evolutionary changes in the life histories of exploited populations. Matching long-term trends in maturation reactions norms have already been documented for several stocks that have experienced high fishing pressures (Gulf of Maine and Georges Bank cod, Northeast Arctic cod, North Sea plaice). Our results add a new dimension to these earlier findings: since fishing pressures for two stocks of Newfoundland plaice (2J3K and 3Ps) have been relatively low, our results imply that fishing is likely to result in the evolution of life histories even when fishing mortality is low, or that natural mortality has played a important role in determining selective pressures in these populations. Both options suggest that conditions for rapid life-history evolution in exploited stocks are less restrictive than previously appreciated.

Keywords: reaction norm, maturity ogive, logistic regression, probability of maturing, maturation dynamics, American plaice

Introduction

In several commercially exploited fish stocks, age and size at maturation have systematically decreased during recent decades. Alternative explanations have been put forward. First, these trends could amount to a purely phenotypic response to environmental variability, with such phenotypic plasticity having its own adaptive value (Stearns, 1989). In particular, fishery-induced reductions in stocks biomass may indirectly trigger phenotypically plastic responses. Second, maturation dynamics could have evolved, with fishing mortality being increasingly recognized as a potent evolutionary force (Law and Grey, 1989; Heino, 1998). Distinguishing between these options by disentangling phenotypic plasticity and evolution is *a priori* difficult in the absence of experimental controls. In all cases where decreases in age and size at maturation have been documented, a long-term decrease in stock biomass parallels the long-term maturation trend. A decrease in stock biomass is likely to weaken density-dependent negative effects, for example through an increase in per capita food availability. This could then result in a phenotypic increase in growth rate, which could in turn lead to a decreased age at maturation.

The estimation of probabilistic maturation reaction norms (Heino *et al.*, 2002b) is a relatively (?) new statistical tool particularly suitable for disentangling phenotypic plasticity and evolutionary change, and is readily applicable to the long-term time series often available for commercially fished stocks. This approach derives from the realization that the probability of being mature as a function of age and/or size (the so-called maturity ogive), and the probability of maturing as a function of age and size (the maturation reaction norm) do not have the same biological meaning. A disadvantage of maturity ogives in this type of analysis is that they are influenced not only by the maturation process itself but also by variations in growth and survival rates. A novel method for estimating maturation reaction norms in the common case where data are available on the size and age structure of immature and mature individuals has recently been designed and tested (Barot *et al.*, 2004a; Barot *et al.*, 2004b). Here we apply this method to three populations of Newfoundland American plaice. These populations have all experienced large declines in abundance, but have been subject to different levels of fishing mortality (Bowering *et al.*, 1996; Morgan *et al.*, 2002a; Morgan *et al.*, 2002b). The estimation of maturation reaction norms for these stocks offers a unique scientific opportunity: to examine possible evolutionary change in the maturation processes of populations of the same species that have experienced different levels of exploitation.

Material and Methods

Natural history and fishing history

American plaice (*Hippoglossoides platessoides*) is a long-lived flatfish species with individual fish reaching ages in excess of 20 years. It is found throughout the northwest Atlantic (Bowering *et al.*, 1996). There are three populations of American plaice living (a) off the east and south coasts of Newfoundland, Labrador, and Northeast Newfoundland (Northwest Atlantic Fisheries Organization, NAFO, Divisions 2J3K), (b) on the Grand Bank (NAFO Divisions 3LNO), and (c) on St Pierre Bank (NAFO Division 3Ps). Although there are seasonal movements of plaice in the study area (Morgan and Brodie, 1991), tagging indicates that the fish do not undertake long-distance movements (Morgan, 1996). In particular, the three populations investigated here are thought to be distinct, with little or no movement between them (Bowering *et al.*, 1996; Bowering *et al.*, 1998).

Fisheries on all three populations began in the 1960’s, but the relative level of exploitation has varied considerably among the populations. For the 2J3K stock, there has been little directed fishing, and it seems that fishing mortality was too low to have caused the decline in the population (Morgan *et al.*, 2002b). For the 3LNO stock, a substantial fishery has operated throughout recent history. For the 3Ps stock, a directed fishery existed, but at a much lower level than for 3LNO: fishing on the 3Ps stock was probably not at high enough a level to cause the initial decline in the stock, but increased fishing pressure in the early 1990s may have contributed to the further stock decline (Bowering *et al.*, 1996). All three populations have been under moratoria on directed fishing since the mid-1990’s. Although bycatch mortality has continued, catch levels on all three stocks were very small from the beginning of the moratoria until the late 1990’s (Morgan *et al.*, 2002a; Morgan *et al.*, 2002c; Dwyer *et al.*, 2003).

Data collection

Data on the three stocks, 2J3K, 3LNO and 3Ps, were collected during annual surveys by research vessels towing a bottom otter trawl. Data are available, respectively for each stock, for most years during the following periods: 1973-1999, 1969-2000, and 1972-1999. Sampling of fish during these surveys was based on a length-stratified design. For each sampled fish, the maturity status was determined by macroscopic examination of the gonad, age was assessed using otoliths, and length was measured directly.

Estimation of maturation reaction norms

Let m be the probability of maturing, o the probability of being mature (i.e., the maturity ogive), and $\Delta size$ the age-specific annual growth increment. These quantities are related as follows (Barot *et al.*, 2004a):

$$m(age, size) = \frac{o(age, size) - o(age-1, size-\Delta size)}{1 - o(age-1, size-\Delta size)} \quad .(1)$$

We estimated the probabilities of being mature, *o*, as a function of both age and size using logistic regression models. After preliminary analyses, the following model was used for males, using age and size as variates (i.e., as continuous explanatory variables), cohort as a factor (i.e., as a discrete explanatory variable), and including only the interaction between age and cohort:

$$\operatorname{logit} o = c_0 + c_{1,cohort} + c_{2,cohort} age + c_3 size \ .$$

For females, no significant direct effect of cohort was found; we therefore used a simplified model:

$$\operatorname{logit} o = c_0 + c_{1,cohort} age + c_2 size \ .$$

For each cohort, age-specific growth increments were estimated as the difference between the mean sizes at age in two successive years. Robustness tests showed that by using equation (1), which is exact only under some simplifying assumptions (Barot *et al.*, 2004a), and by neglecting other interaction terms in the logistic regression models (Barot *et al.*, 2004b) no strong bias is introduced in reaction norm estimates. In particular, the detection of long-term trends in the maturation reaction norms is unimpeded.

Maturation reactions norms can effectively be illustrated by contour lines connecting combinations of ages and sizes with equal probabilities of maturing. The most interesting contour line connects the so-called reaction norm midpoints, that is, those age-specific sizes at which the probability of maturing equals 50%. The inter-quartile range, given by the length interval over which the probability of maturing increases from 25% to 75%, illustrates the strength of the size effect on maturation at a certain age. Midpoints and inter-quartile ranges were estimated using a logistic regression expressing, for each cohort and each age, the probability of maturing as a function of size (Barot *et al.*, 2004a; Barot *et al.*, 2004b). Notice that the estimated midpoints and inter-quartiles at a certain age can lie well outside the range of sizes observed at that age. This does not imply badly estimated reaction norms, but occurs naturally at early and late ages at maturation, when no fish is large or small enough, respectively, to experience the middle range of the reaction norm.

Confidence intervals and randomisation tests

To compute confidence intervals, we bootstrapped the original data set (Barot *et al.*, 2004a) by resampling individuals with replacement, separately for each cohort. Statistical tests were built using a randomisation approach (Barot *et al.*, 2004a). The sex effect was tested using the following logistic regression model, where size was considered as a variate (continuous variable) and cohort and sex as factors (discrete variables):

$$\operatorname{logit} m = c_0 + c_{1,cohort} + c_{2,sex} + c_3 size \ .$$

The difference between the maturation reaction norms of the different stocks was tested using the following model on data sets for which the stock identity of each observation was randomised:

$$\operatorname{logit} m = c_0 + c_{1,cohort} + c_{2,stock} + c_3 size \ .$$

The existence of a long-term linear trend in maturation was tested using a model incorporating a cohort effect by treating cohort as a variate (continuous variable) on data sets for which cohort had been randomised:

$$\operatorname{logit} m = c_0 + c_1 size + c_2 cohort \ .$$

A randomisation test was also used to test for the shape of the reaction norm. We tested whether age has a significant effect on the probability of maturing using the following model on data sets for which age had been randomised:

$$\operatorname{logit} m = c_0 + c_{1,age} + c_{3,cohort} + c_{4,cohort} size \ .$$

Results

Temporal variations in growth of American plaice were very high (Figure 1), but there was no long-term trend: the regression of growth increments on cohort was always non-significant ($p > 0.05$ for all combinations of stock, sex, and age). There was no significant difference in growth increments between the sexes (based on linear models treating sex and age as factors, and including their interaction: $p > 0.05$). Growth rates among the three stocks were not different for females (based on linear models treating stock and age as factors, and including their interaction: $p > 0.05$). However, for males, growth rates were significantly different among the three stocks ($p < 0.05$), with growth being slightly higher in 3Ps than in the two other stocks.

As shown by the maturation reaction norm estimated for males of cohort 1982 in Division 3LNO (Figure 2), and by the corresponding maturation reaction norms averaged over five successive cohorts (Figure 3), reaction norms tended to have a negative slope: for any given size, old immature individuals were more likely to mature than younger ones. The effect of age on maturation, tested by randomisation tests, was significant ($p < 0.01$) for each combination of stock and sex. Confidence intervals for the reaction norm midpoints were narrow (less than 5 cm) at all ages at which individuals were likely to mature (i.e. in the vicinity of the intersection between the mean size at age curve and the reaction norm: for males at ages 5 and 6 and for females at ages 7 and 8). These confidence intervals are wider at younger and older ages (e.g., about 10 cm at age 9) because data were scarcer at these ages (see also Figure 2). The inter-quartile range, measuring the effect of size on maturation, was always about 15 cm wide.

Males consistently matured at smaller size than females: the probability of maturing was always higher for males than for females at a given size (Figures 3 and 4). This was confirmed by randomisation tests showing significant differences for all combinations of sex and age (Table 1).

Differences between stocks were less clear, but at a given size the probability of maturing tended to be higher in the 2J3K stock than in the two other stocks (Figures 3 and 4). Seven randomisation tests out of twelve supported the existence of a significant difference between stocks, the probability of maturing being the highest in the 2J3K stock (Table 1). A temporal trend was evident in all stocks and for both sexes: probabilities of maturing at a given size increased from the first observed cohorts to the most recent ones (Figures 3 and 4). Randomisation tests showed that this trend was significant (20 significant tests out of 24, Table 1).

Discussion

Sex-specific maturation

The differences observed in this study between the maturation reaction norms of males and females are consistent with earlier findings based on maturity ogives (Morgan and Colbourne, 1999). The reaction norm analysis presented here shows that the observed differences are due to the maturation process itself and not only to differences between male and female survival or growth rates. Males thus seem genetically geared to reproduce at younger ages and smaller sizes than females. This difference is as expected, since males generally experience a lower reproduction cost than females (Stearns, 1992) so that they can start to invest energy into reproduction at younger ages and smaller sizes. However, it is not clear why some stocks clearly exhibit this difference while others do not. For example, sex differences in maturation have been demonstrated to be minor in Gulf of Maine and Georges Bank Atlantic cod stocks (Barot *et al.*, 2004b). This may result from the difference between male and female reproduction costs being smaller for the cod stocks than for the plaice stocks. Future research will have to determine whether such an explanation is indeed sufficient.

Age-specific maturation

Maturation reaction norms of the Newfoundland American plaice have negative slope. This means that, at any given size, older individuals are more likely to mature than younger ones. This implies that increased growth rates would result in decreased age at maturation and potentially also in increased size at maturation. The same pattern has already been found for other species, including North Sea plaice and Atlantic cod (Grift *et al.*, 2003; Barot *et al.*, 2004b). The opposite pattern – a maturation reaction norm with positive slope – has been found for Northeast Arctic cod (Heino *et al.*, 2002a). Models show that the shape of evolutionarily stable maturation reaction norms is expected to be very sensitive to changes in the trade-offs between growth, fecundity, and survival (Stearns and Koella, 1986; Ernande *et al.*, 2004). Yet, to our knowledge there is no theory available yet to predict which fish stocks should have negatively sloped or positively sloped maturation reaction norms.

Cohort-specific maturation: Long-term maturation trends

The temporal trend in maturation reaction norms supports the hypothesis that the observed long-term decrease in the age and size at maturation of Newfoundland American plaice is not simply due to phenotypic plasticity but instead results from evolutionary change (Stearns and Koella, 1986).

Two issues have to be discussed to appreciate the relevance of these findings. First, selection is not expected to affect only the maturation process. In particular, size at age is partially determined by environmental variations and partially determined genetically. Also growth variability among and within stocks will usually be partially genetic and may thus enable selection on growth rates (Conover and Schultz, 1995; Conover and Munch, 2002). Evolutionary changes in maturation reaction norms and growth rates are thus expected to occur concurrently. While the selection differentials on the two traits can be estimated separately, the resulting selection responses might be coupled, to some extent, because of genetic correlations between the traits. The tighter the coupling, i.e., the more growth rates are genetically linked to maturation reaction norms through some common genes acting on both, the more selection pressures on either trait will affect evolution of the other. The long-term trends in maturation reaction norms documented in this study could thus partially reflect selection on growth rates. Determining the extent to which this is the case remains an open empirical problem, but to our knowledge nothing suggests that this extent would be anything but small.

Second, environmental variations might influence maturation probabilities directly. For instance, the probability of maturing could theoretically increase in a good year (involving high temperatures or ample food supplies), without resulting in an increase in the growth rates of fish that would be noticeable at the time of the year when fish are sampled. This could cause some variability in reaction norm midpoints, which would then not reflect any genetic change. If there were a long-term trend in any relevant environmental variable (spanning the period from 1970 to 2000), this trend might thus explain the long-term decrease in age and size at maturation as a result of phenotypic plasticity alone. An obvious possibility in this context is that the long-term decreases in stock biomass (Morgan *et al.*, 2002a; Morgan *et al.*, 2002c; Dwyer *et al.*, 2003) have released stocks from some density-dependent negative effects. This could, in principle, directly cause the observed maturation trend. However, we consider this scenario very unlikely. It presumes that there are density-dependent effects that leave no trace on growth rates: since stock biomass did not influence growth rates at the scale of 30 years, it is unlikely to influence the probability of maturing at the same time scale. This conclusion is further supported by the fact that growth rates have been shown to be very sensitive to most environmental variables (Wootton, 1998; Imsland and Jónsdóttir, 2002). Other environmental variables that might have caused the observed maturation trends through plasticity would have to exhibit a long-term trend paralleling the decrease in age and size at maturation. Yet, no data supports this possibility. In particular, even though there have been large changes in water temperature, no long-term trend in water temperature exists over the 30-year period spanned by the available maturity time series (Colbourne *et al.*, 1997).

Explaining the long-term maturation trends

Long-term trends in maturation reaction norms have already been documented for four stocks: Georges Bank and Gulf of Maine Atlantic cod (Barot *et al.*, 2004b), North Sea plaice (Grift *et al.*, 2003), and Northeast Arctic cod (Heino *et al.*, 2002a; Heino *et al.*, 2002b). In each of these cases there is a parallel declining trend in maturation and in stock biomass. In all cases, including that of American plaice studied here, the reaction norm approach supports the hypothesis of an evolutionary trend. What would be the selective pressure causing such a trend? It is recognized that fishing, as any source of mortality, is likely to exert selective pressure influencing the evolution of life history in commercially fished stocks (Law and Grey, 1989; Conover, 2000; Law, 2000). Thus, any change in fishing mortality should lead to an evolutionary change in age and size at maturation. Moreover, fishing is always size-selective, for example due to the mesh size of gear; it is also age-selective, at least because of the size selectivity and the relation between size and age. For example, fishing both immature and mature fish should favour a shift of maturation reaction norms towards younger ages and smaller sizes because reducing the length of the juvenile period increases the probability of individuals to reproduce before they die.

Despite these clear-cut qualitative predictions there is an urgent need to better understand the quantitative evolutionary changes in maturation reaction norms expected for a stock with a given life history and fishing history. It is therefore intriguing that the three stocks analyzed here present similar long-term trends in maturation reaction norms – there is no obvious difference in the slopes of these trends – although their fishing histories have been very different. Three hypotheses can be advanced to explain this unexpected pattern. (1) The long-term maturation trends are only phenotypic and, as mentioned earlier, could be explained by a long-term trend in some relevant but currently unidentified environmental factor. Although we consider this hypothesis unlikely, it can never be ruled out without experimental controls or direct genetic measurements. (2) A second option is that the differences among the stocks have been underestimated in our analyses and the trends in maturation are due to an evolutionary process in which fishing mortality is the main selective pressure. This cannot be excluded since it has been shown that our estimation method permits one to detect long-term trends in maturation (Barot *et al.*, 2004b), but it is not known how efficient the method is in comparing different trends. (3) Finally, there is the possibility that the observed trends in maturation reaction norms reflect an evolutionary process that is partly driven by factors other than fishing mortalities. In particular, it is evident that changes in natural mortality result in selective pressures on maturation reaction norms, just as changes in fishing mortality do (Hutchings, 1994): the selective effects of high fishing mortalities and high natural mortalities are therefore expected to act together. Hence it is interesting that an increase in natural mortality has indeed been stipulated for these stocks

(Bowering *et al.*, 1996; Morgan and Brodie, 2001; Morgan *et al.*, 2002b), independently of the present study, although the cause is not known

Results of models based on adaptive dynamics theory (Dieckmann, 1997) support the conclusion that changes in fishing mortality can result in surprisingly rapid evolution of age and size at maturation, even when fishing mortality is low (Ernande *et al.*, 2004). Even a small underestimation of fishing mortality may be important for a species that, given its very late age at maturation only a few decades ago (Pitt, 1966), may have experienced relatively low natural mortality. Also the fact that decreases in age and size at maturation seem to be common in many commercial fisheries lends weight to the notion that fishing mortality is the main selective pressure. It must, however, be emphasised that both natural and fishing mortality rates are difficult to assess quantitatively, so that differentiating between hypotheses (2) and (3) is difficult. Evolutionary modelling of the life history of American plaice under various scenarios would help to distinguish between the alternative hypotheses.

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Tables and Figures

Table 1. Results of randomisation tests. Differences in maturation between the three stocks, between males and females, and between cohorts were tested using a randomisation approach (see text for details). To test for the effect of a variable, values of this variable are reattributed randomly to individuals that retain their values for all other variables. Randomisation tests are applied separately for each age. Each cell of the table indicates whether the test is significant, and what the detected effect is. M>F indicates that males have a higher probability of maturing at age and size than females; 2>1>3 indicates that the probability of maturing at age and size is largest in stock 3LNO and smallest in stock 3Ps; a + sign indicates that later cohorts have an increased probability of maturing at age and size. Significance levels: ns = not significant, * = $p < 0.05$, and ** = $p < 0.01$.

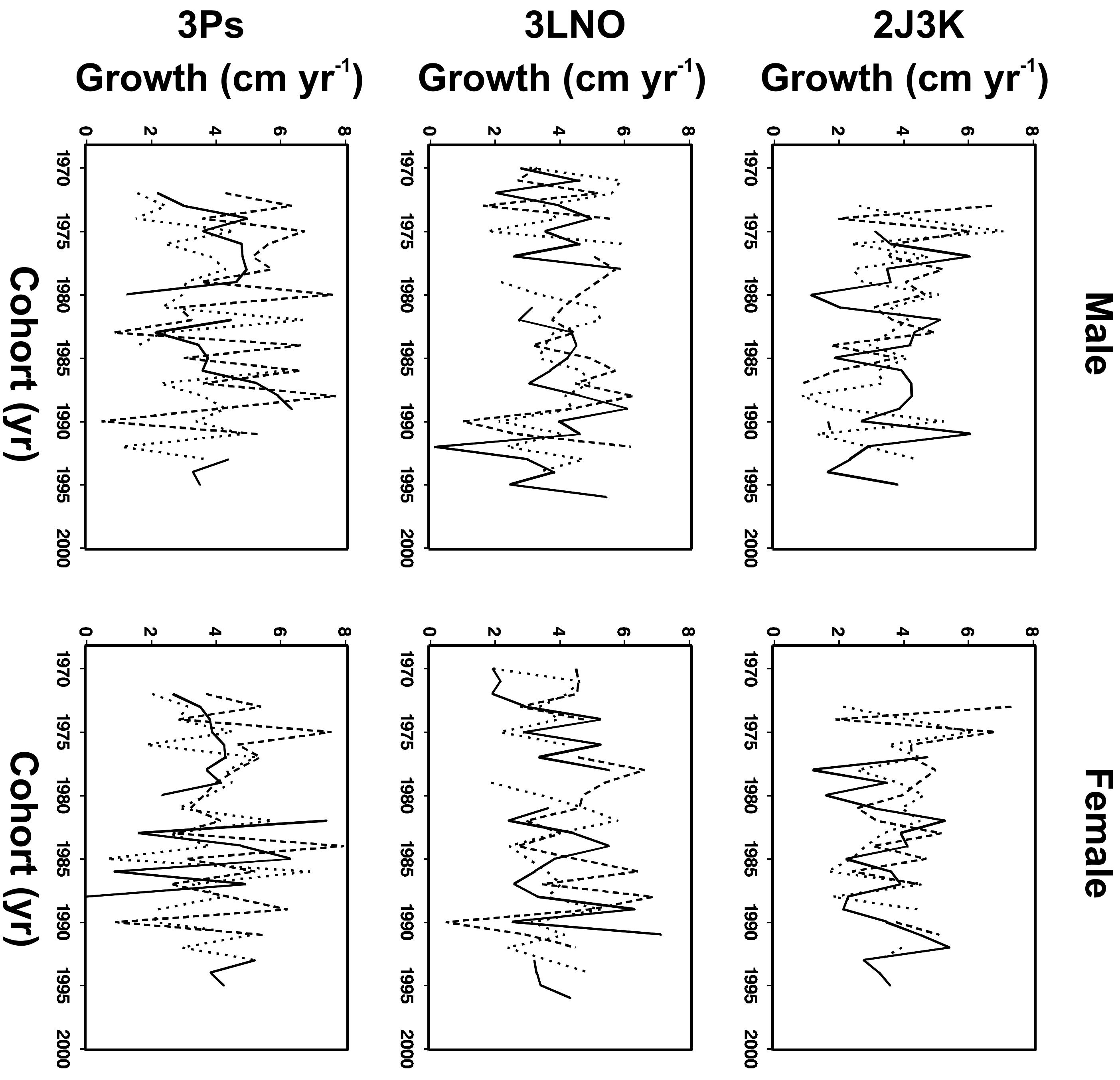
Effect	Stock and sex	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9
Sex	2J3K (1)	M>F**	M>F**	M>F**	M>F**	M>F**	M>F**
	3LNO (2)	M>F**	M>F**	M>F**	M>F**	M>F**	M>F**
	3Ps (3)	M>F**	M>F**	M>F**	M>F**	M>F**	M>F**
Stock	Males (M)	2>1>3*	2>3>1**	2>1>3*	2>1>3*	ns	ns
	Females (F)	ns	ns	2>1>3*	2>3>1*	2>3>1*	ns
Cohort (temporal trend)	2J3K Males	ns	+*	ns	+*	+**	+**
	2J3K Females	+**	+**	+**	+**	+**	+**
	3LNO Males	+**	+**	+**	+**	+**	+**
	3LNO Females	+**	+**	+**	+**	+**	+**
	3Ps Males	+**	+*	+**	+**	ns	ns
	3Ps Females	+**	+**	+**	+**	+**	+**

Figure 1. Annual growth increments estimated for each age and cohort (▬▬ = age 4, ▬ · ▬ = age 6, **....** = age 8). Missing points correspond to very low growth rates that were estimated to be negative. For greater clarity, curves for ages 5, 7, and 9 are not displayed; they present similar oscillations as ages 4, 6, and 8.

Figure 2. Reaction norm for age and size at maturation estimated for the males of the cohort 1982. The thick continuous line shows the reaction norm midpoints (with bootstrap confidence intervals for the midpoints) at which the probability of maturing reaches 50%, while the thin continuous line shows the inter-quartile range over which the probability of maturing rises from 25% to 75%. The dotted line shows the mean size at age.

Figure 3. Reaction norms for age and size at maturation averaged over five-year periods (▬▬ = cohorts 1970-74, ▬ · ▬ = cohorts 1975-79, **....** = cohorts 1980-84, —— = cohorts 1985-89, – · – = cohorts 1990-94, ... = cohorts 1995-1999). Reaction norms were estimated separately for males and females and for the three stocks. There are some missing midpoints, especially for the period 1970-1974, because of missing data or small sample sizes that rendered the estimation impossible.

Figure 4. Temporal trend in the age-specific midpoints of reaction norms for age and size at maturation (▬▬ = age 4, ▬ · ▬ = age 5, **....** = age 6, —— = age 7, – · – = age 8, ... = age 9). Reaction norms were estimated separately for males and females and for the three stocks. Curves are not continuous because of missing data or small sample sizes that rendered the estimation impossible.



Male
Female
2J3K
3LNO
3Ps
Growth (cm yr^{-1})
Cohort (yr)
0
2
4
6
8
1970
1975
1980
1985
1990
1995
2000

Figure 1

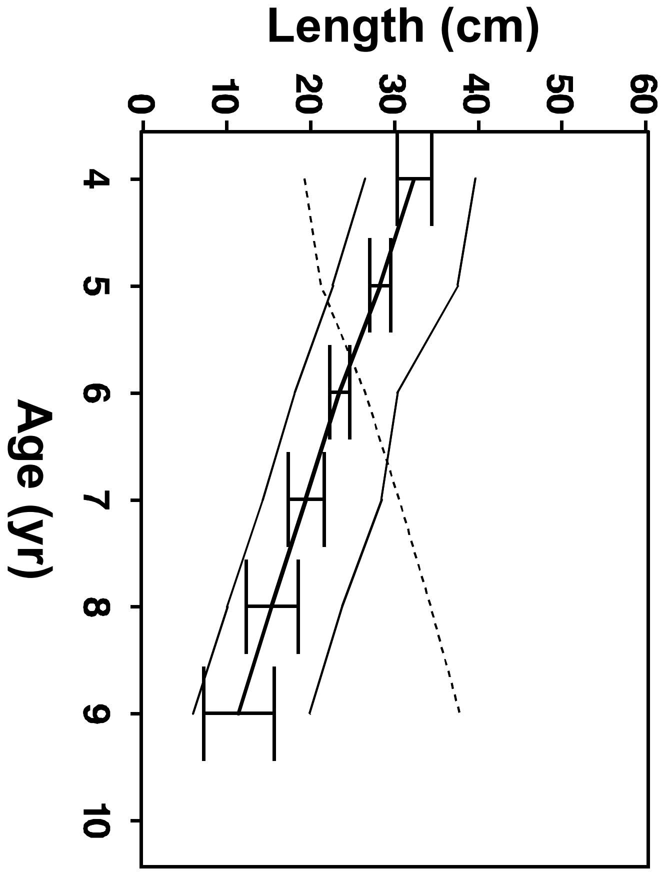


Figure 2

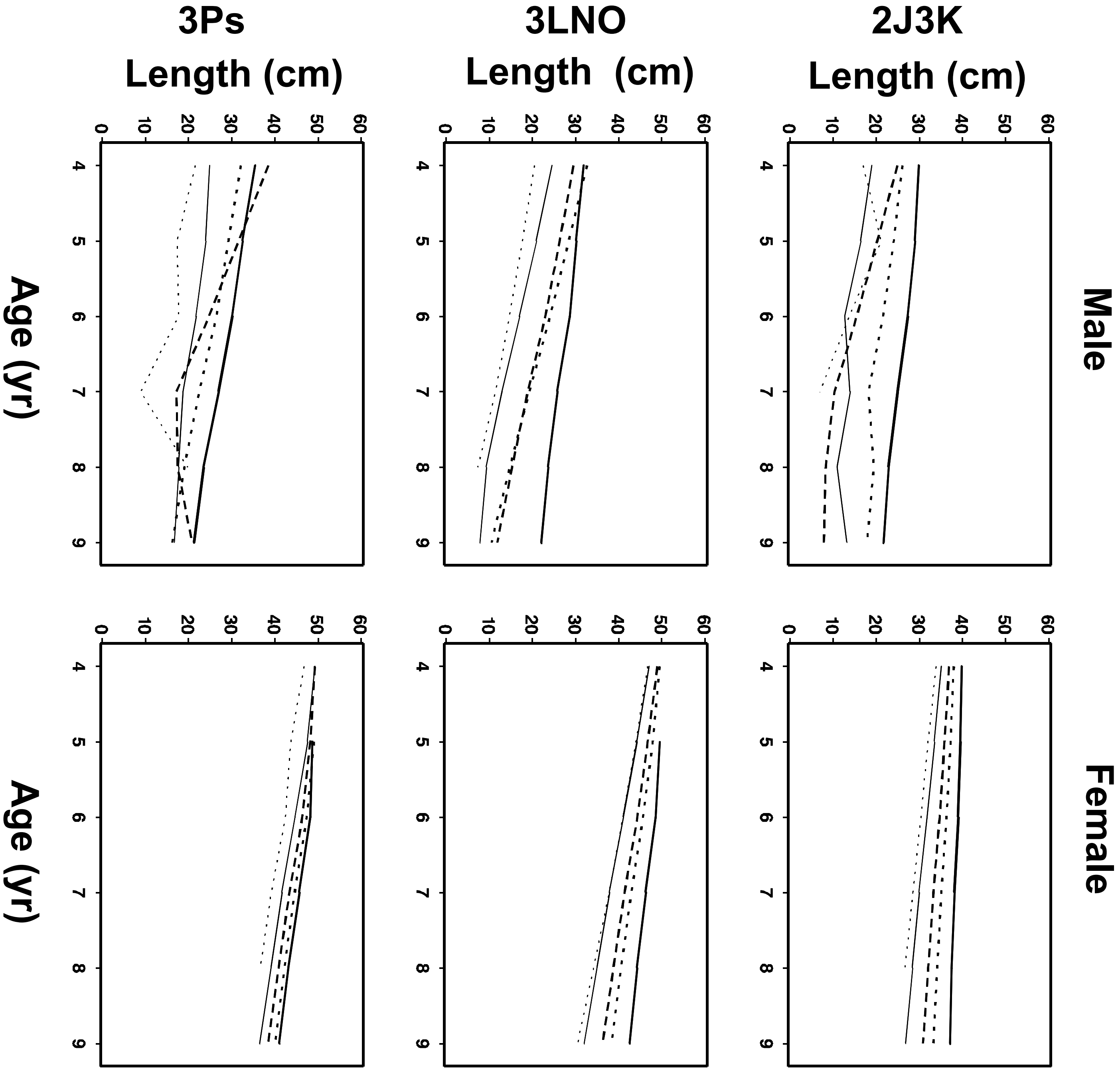

Male
Female
2J3K
3LNO
3Ps
Length (cm)
Length (cm)
Length (cm)
Age (yr)
Age (yr)
0
10
20
30
40
50
60
4
5
6
7
8
9

Figure 3

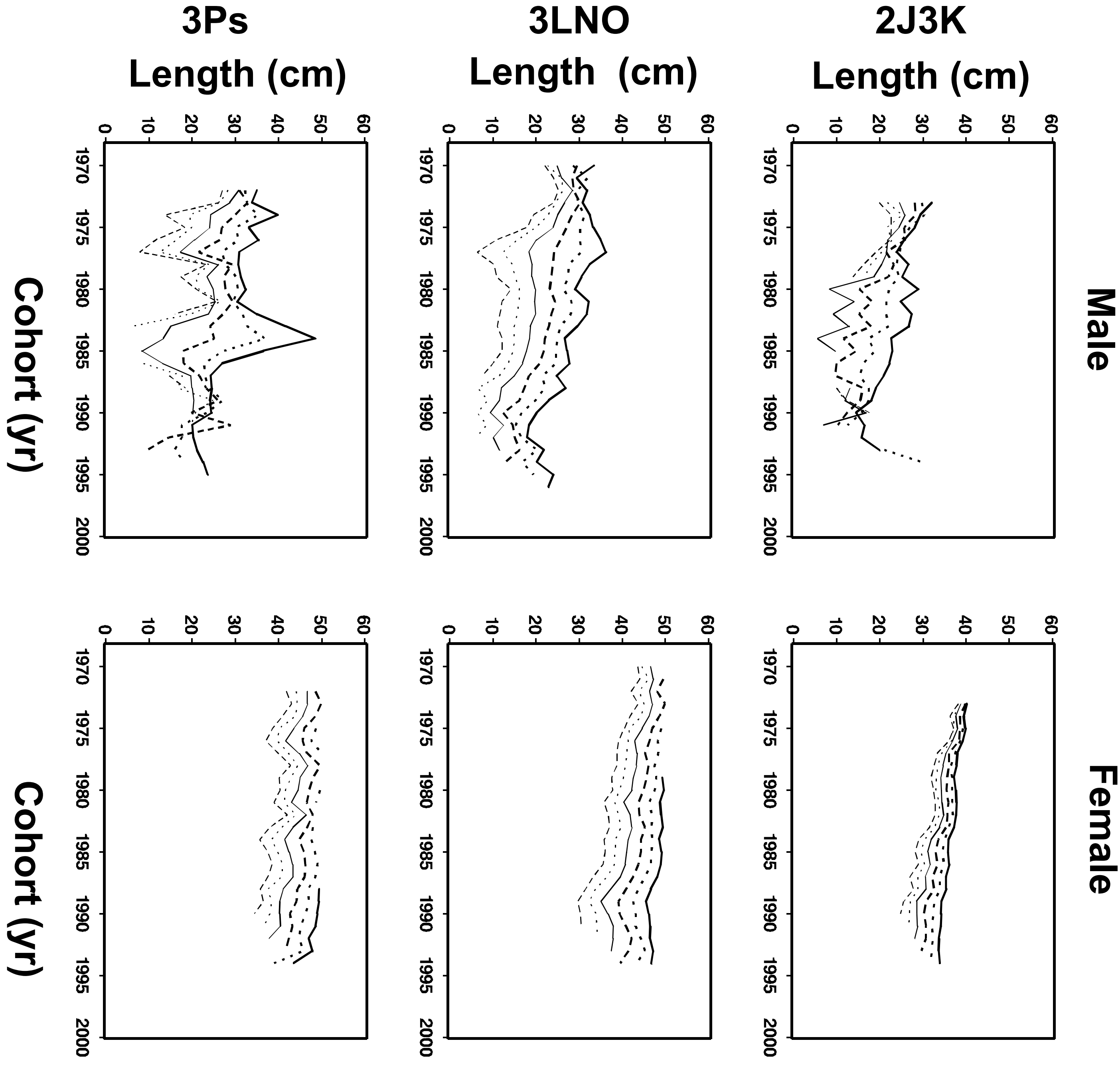

Male
Female
2J3K
3LNO
3Ps
Length (cm)
Cohort (yr)
0
10
20
30
40
50
60
1970
1975
1980
1985
1990
1995
2000

Figure 4