

**Not to be cited without prior reference to the author**

**Fisheries-induced trends in reaction norms for maturation  
in North Sea plaice**

R.E. Grift<sup>1,2</sup>, A.D. Rijnsdorp<sup>1</sup>, S. Barot<sup>2</sup>, M. Heino<sup>3,2</sup>, and U. Dieckmann<sup>2</sup>

- 1) *RIVO Netherlands Institute for Fisheries Research, P.O. Box 68, 1970 AB, IJmuiden, The Netherlands*
  - 2) *Adaptive Dynamics Network, International Institute for Applied Systems Analysis, Schlossplatz 1, A-2361 Laxenburg, Austria.*
  - 3) *Institute of Marine Research, P.O. Box 1870, Nordnes, N-5817, Bergen, Norway*
- Correspondence to Rob Grift at RIVO (email: [Rob@rivo.dlo.nl](mailto:Rob@rivo.dlo.nl); phone: +31-255-564702; fax: +31-255-564644).*

## ABSTRACT

We analyse the potential of intensive exploitation to have caused evolutionary changes in the age and length at maturation in North Sea plaice *Pleuronectes platessa*. Such evolutionary change in the onset of maturation is expected given that fishing mortality is more than four times higher than natural mortality. In order to disentangle phenotypic plasticity from evolutionary change, we employ the probabilistic reaction-norm approach. This technique allows us to estimate the probabilities of maturing at each relevant age and size, and to disentangle the plasticity in age and size at maturation that results from changes in growth rates from evolutionary changes in maturation propensities themselves. This recently developed method is here applied to females of 41 cohorts (1955-1995) of North Sea plaice. We focus on trends in fishing mortality, in growth rates, and in the probabilities of maturing, and test the hypothesis that the decrease in age and length at maturation is partly caused by fisheries-induced adaptive change. We find that the reaction norm for age and length at maturation has indeed significantly shifted towards younger age and smaller length. The reaction-norm analysis suggests a picture in which short-term fluctuations originating from plastic responses are superimposed on a persistent long-term trend resulting from genetic responses.

**KEY WORDS:** fisheries-induced change, phenotypic plasticity, evolution, growth rates.

---

## INTRODUCTION

Fishing is almost always selective and may therefore induce changes in exploited populations (Law, 2000). This can occur in various ways and may lead to both phenotypically plastic and genetic changes in the exploited population. Fishing may decrease intraspecific competition by decreasing population sizes (Law, 2000), it may directly or indirectly change food availability (Rijnsdorp and Van Leeuwen, 1996), or it may cause evolutionary change by selecting for genotypes less affected by fishing (Borisov, 1978; Law, 2000). Superimposed on the effects of fishing, other changes in the physical and biotic environment occur, such as temperature fluctuations and changes in food conditions, which may also influence the processes of growth and maturation (Law, 2000). In many exploited stocks changes in age and size at maturation have been attributed to high fishing pressures, e.g., in Pacific salmon *Oncorhynchus spp.* (Ricker, 1981), North East Arctic cod *Gadus morhua* (Law and Grey, 1989), North Sea cod *Gadus morhua* (Rowell, 1993), North Sea plaice *Pleuronectes platessa* (Rijnsdorp, 1993a), American plaice *Hippoglossoides platessoides* (Morgan and Colbourne, 1999), and grayling *Thymallus thymallus* (Haugen and Vøllestad, 2001). It is, however, still unclear to which extent these changes are due to phenotypic plasticity on the one hand or to evolutionary change on the other. Disentangling phenotypically plastic and evolutionary changes in age and size at maturation is a challenging task of great importance for management purposes. Phenotypic changes are readily reversible by, for example, relaxing the exploitation rate, while genetic changes are not (Law, 2000; Reznick, 1993). For the purpose of our discussion here, we define phenotypic plasticity as a general term that covers all types of environmentally induced phenotypic variation (Stearns and Koella, 1986).

The age or size at which most species mature is not fixed, but is described by a norm of reaction that is given by a well-defined curve in age and size space (Stearns and Koella, 1986). In their definition of reaction norms, Stearns and Koella (1986) assume that an organism matures once its growth trajectory hits this reaction norm curve. The reaction norm thus characterizes, under the assumption that variation in size-at-age reflects environmental variability, the phenotypic plasticity in maturation the organism exhibits in response to growth conditions.

The combinations of ages and sizes at which maturation occurs strongly influence an individual's expected reproductive success. The resulting evolution of the reaction norm for age and size at maturation is determined by environmental conditions such as size-dependent mortality rates (Heino and Kaitala, 1999) and resource availability (Siems and Sikes, 1998). Since fecundity and the viability of eggs and larvae are often positively related to maternal size (Murawski *et al.*, 2001), there is a trade-off between current and future reproduction (Heino and Kaitala, 1999) as well as a trade-off between reproduction and growth within a season (Reznick, 1983): allocation to reproduction within a given season will thus decrease growth rate and future fecundity. In general, ecological settings with low survival and growth rate among potentially reproducing individuals, favour high reproductive effort at early ages (Hutchings, 1993; Reznick *et al.*, 1990; Reznick *et al.*, 1997). Therefore, removal of large individuals from a population by selective fishing is expected to select for genotypes with a lower age and size at maturation. Compared with the implications of size-selective mortality rates, the implications of resource availability for life-history characteristics are as yet less well understood.

In the North Sea plaice stock, the continued high levels of fishing mortality and the selective removal of larger and adult fish (Rijnsdorp and Millner, 1996) are

---

thus expected to be partially responsible for the significant decrease throughout the 20<sup>th</sup> century observed in the age and length at maturation. The age at which 50 % of the females were mature ( $A_{50}$ ) has decreased by two years between the early (1904-1911) and late (1960-1990) 20<sup>th</sup> century, whereas for age group 4 the length at which 50 % of the females were mature ( $L_{50}$ ) has decreased by 5.8 cm (16 %) in the same period. Statistical analysis suggested that phenotypic plasticity could explain about 2.7 cm of this decrease (Rijnsdorp, 1993a). On that basis, Rijnsdorp (1993a) proposed that the unaccounted remaining 3.1 cm reflect fisheries-induced evolution. This proposition was supported by the finding that selection differentials calculated for this stock showed that, given the current fishing mortality (**Figure 1**), a reduced length at maturation would lead to increased fitness (Rijnsdorp, 1993c). If this interpretation of an evolutionary change in age and length at maturation is correct, one must expect that a further decrease in the age and length at maturation will have occurred within the period 1960-1990 and potentially thereafter.

In this paper we follow up on the earlier work by disentangling phenotypic and evolutionary changes in age and length at maturation in North Sea plaice. This strategy allows for a refined test of the hypothesis that the observed decrease in age and length at maturation is partly caused by fisheries-induced adaptive change. To disentangle plasticity in the maturation process from evolution, Heino et al. (2002b) introduced the probabilistic reaction-norm method to characterize the probability of maturing given a certain age and size. In contrast both to observed ages and sizes at maturation and to maturity ogives, probabilistic reaction norms are independent of changes in growth and/or survival (Heino et al. 2002b; the method is further explained in the Materials and Methods section), a feature that is of crucial importance when disentangling plastic and genetic responses. Up to date, the probabilistic reaction-

norm method has been applied to Northeast Arctic cod (Heino *et al.*, 2002b) and Georges Bank cod (Barot *et al.*, 2002). Here we apply the new method to females of 41 cohorts (1955-1995) of North Sea plaice and analyse trends in growth rates and age and length at maturation.

## MATERIALS AND METHODS

### North Sea plaice

Plaice has been a main target species of the mixed demersal fisheries in the North Sea since the start of the industrial revolution in the second half of the 19<sup>th</sup> century (Rijnsdorp and Millner, 1996). In 2000, landings of plaice by Dutch vessels amounted to roughly 50,000 tons, representing an economic value of about €100,000,000. As a result of intensive exploitation, mortality rates imposed by fishing have been high (**Figure 1**), exceeding the natural mortality rate by a factor of two to four. Moreover, size-selective fishing mortality changed from a dome-shaped curve in the 1930s to a flatter curve from the 1950s onwards (**Figure 1**; Rijnsdorp & Millner 1996), probably due to a decrease in the proportion of untrawlable areas following the introduction of heavier gear. Superimposed on changes in fishing mortality, water temperature and food availability increased, leading to accelerated growth of plaice smaller than 30 cm (Rijnsdorp and Van Leeuwen, 1992).

### Data collection

Data on female plaice were collected in the Dutch market-sampling programme that has been carried out since 1957. Since the Dutch fleet catches on average 43 % of the total landings of plaice from the North Sea (from 1993-2000; ICES 2002), and covers the major distribution area of plaice in the southern and central North Sea (Rijnsdorp

---

*et al.*, 1998), these data are considered representative of the entire population and are reliable for analysing maturation of female plaice (Rijnsdorp, 1989). Collection of market samples is stratified according to geographical areas and to the four market-size categories used in the Netherlands (27-34 cm, 34-38 cm, 38-41 cm, and >41 cm). Of each area and each category, 20 plaice individuals were sampled at random on a monthly basis. In addition to the date of landing and the position of the catch, length (mm), weight (g), sex, maturity stage (1-7), and age (years, January 1 as birthday) were determined. Complementing the market samples, otoliths were collected through research surveys.

The age of fish was determined from the pattern of growth zones in the otoliths under the standard assumption that each zone corresponds to one year. A subset of otoliths was used to calculate yearly length increments of individual females. Yearly increments were estimated from the back-calculated length-at-age. The length-at-age was estimated by relating the proportion of the distance between growth zones relative to the total size of the otolith, to the length of the fish when it was caught. Evidence for the validity of the methods for ageing and for estimating length increments is given by Rijnsdorp *et al.* (Rijnsdorp *et al.*, 1990), including a discussion on their precision and accuracy.

### **Data selection**

Maturity ogives describe the fraction of mature fish of a particular age and/or size class in a given population. To assess these ogives for North Sea plaice, a selection from the market-sampling data was made. Only data of cohorts from 1955 and onwards were used, since this cohort was the first that occurred in the sampling programme from age 2 onwards. Landings were sampled throughout the year but in

this study only data collected in the first quarter of each year were selected, since only in this period maturity stages of female plaice can be identified well. Sample locations were restricted to the southeastern North Sea (51°-56°N and east of 2°E, and 51°-53.5°N and 1°-2°E). Data of females of ages 2-6 of 0-60 cm total length were selected, since younger female plaice are not being caught commercially and since at age 7 all females were mature. After these selections, data on the length, age, and maturity status of 18,996 females were available (**Table 1**). For the analysis of yearly length increments, all data available from the back-calculations were used. In total, back-calculated lengths of 2429 females were used (**Table 1**). The otoliths considered all originated from the southeastern North Sea.

### **Analysis of age and length at maturity**

The fraction of mature fish of a particular age or length (maturity ogives) were modelled using logistic regression, with the proportion mature as the dependent variable and cohort and age (Equation 1) or cohort and length (Equation 2) as independent variables. The linear predictor was linked to the fraction of mature fish ( $o$ ) using a logit link function,  $\text{logit}(o) = \ln [o/(1-o)]$ :

$$\text{logit}(o) \sim \text{Cohort} + \text{Age} + \text{Cohort} \times \text{Age} \quad , \quad (1)$$

$$\text{logit}(o) \sim \text{Cohort} + \text{Length} + \text{Cohort} \times \text{Length} \quad , \quad (2)$$

where age and length are variates and cohort is a factor. The descriptive quantities  $A_{50}$  and  $L_{50}$  refer to the age and length, respectively, at which the estimated fraction of mature fish reaches 50 %. To investigate trends in  $A_{50}$  and  $L_{50}$ , similar models were used in which cohort was treated as a variate.



---

### The reaction-norm method

A reaction norm is the full set of phenotypes that a given genotype will express in interaction with the full set of environments in which it can survive (Stearns, 1992). Specifically, the reaction norm for age and size at maturation describes how variability in growth conditions, reflected by variations in size-at-age, influences maturation. The probabilistic reaction norm for maturation is defined as the probability that fish mature at a certain age and size during a given time interval (Heino *et al.*, 2002b). This method has two major benefits. First, it treats the maturation process as a probabilistic process, whereas previous theoretical studies simplified the maturation process as being deterministic. If maturation were deterministic, maturation would occur with certainty once juvenile growth trajectories intersect the reaction norm for age and size at maturation. However, since maturation is a relatively complex physiological process, it is also influenced by factors such as resource availability and body reserves, which, in turn, are affected by the local environmental and individual experiences. Because of this individual-level variation maturation must usually be considered probabilistically: at one and the same age and size, some fish may mature while others do not. A second important advantage of the method is that it cleanly separates changes in growth and survival from a description of the maturation process; previous empirical studies could not conclusively disentangle these aspects (Rijnsdorp, 1993a; Rochet *et al.*, 2000; Rowell, 1993).

Maturity ogives do not distinguish between first-time spawners and repeat spawners and are influenced by maturation probabilities but also by mortality rates and growth rates (Heino *et al.*, 2002a). This is because the proportion of mature fish is affected by fish that have newly matured (maturation), losses of fish that had previously matured (mortality) and by transitions of fish from one size class to

another (growth). By contrast, the maturation reaction norm focuses on the maturation process itself and thus is not affected by mortality and growth. A fish can only mature once, so that life after maturation does not influence the maturation reaction norm. Moreover, since the maturation reaction norm describes maturation probabilities conditional on individuals attaining a certain age and size while not yet being mature, any changes in the probability of attaining a certain age and size leave the reaction norm unaffected (Heino *et al.*, 2002a).

To estimate the probability to mature, age and size distributions of immature and maturing fish are required (Heino *et al.*, 2002b). For some species (such as cod) first-time and repeat spawners can be distinguished based on differential growth zones in the otoliths. For plaice, however, such a distinction is infeasible and the probability to mature at a certain age and size needs to be estimated with a method based on ogives and growth rates. This method has been developed by Barot *et al.* (2002) and will be applied here. It is based on the fact that the probability  $p(a, s)$  of maturing at a certain age  $a$  and size  $s$  can be expressed through two values,  $o(a, s)$  and  $o(a-1, s-\delta s)$ , taken from the maturity ogive  $o$ :

$$p(a, s) = [o(a, s) - o(a-1, s-\delta s)] / [1 - o(a-1, s-\delta s)] \quad , \quad (3)$$

where  $a-1$  is the age previous to the one for which we estimate the maturation probability and  $s-\delta s$  is the length at that previous age,  $\delta s$  being the length gained between age  $a-1$  and age  $a$ . The rationale for Equation (3) is that the probability to mature is given by the number of fish that have matured divided by the number of fish that could have matured (Barot *et al.*, 2002). Notice that  $p$  is here defined as a backward-looking or retrospective probability: it measures the likelihood of individuals at a given age to have matured with the *previous* year of their lives. (Using an alternative assignment convention, one could define  $p$  at a given age as the

---

forward-looking probability of maturing within the *next* year after reaching the considered age.)

The simplicity of Equation (3) relies on two important assumptions: (1) mature and immature individuals of a certain age and size have similar growth rates and (2) they have similar mortality rates. Of course, these assumptions are not expected to be fulfilled accurately in most natural populations. However, Barot *et al.* (2002) tested the sensitivity of the estimation method to these assumptions and thereby confirmed that the method is robust to their relaxation. More complicated versions of Equation (3) that do not depend on the two simplifying assumptions can be derived (Barot *et al.*, 2002), but the resultant marginal gain in accuracy does not seem to warrant the substantial increase in complexity. The estimation method based on Equation (3) thus only requires ogives and growth rates for each cohort as a basis for estimating the probabilistic maturation reaction norm.

### **Estimation of probabilistic maturation reaction norms**

Estimation of the maturation probability for each cohort and age group comprised of three steps: (1) estimation of ogives, (2) estimation of growth rates, and (3) estimation of the probability to mature. This procedure is illustrated in **Figure 2**. Two further steps then consisted of: (4) estimation of confidence limits around the contours of reaction norms using a bootstrap method, and (5) testing the significance of trends in the probability of maturing. Below, we describe all five steps in more detail.

(1) *Estimation of ogives.* Since the maturity status is a binary response variable (individuals are either mature or immature) the ogive was estimated using logistic regression. We investigated whether the model was linear in the logit scale for the continuous variables using the method of fractional polynomials (Royston and

Altman, 1994). Inclusion of non-linear terms increased the fraction of explained deviance by only 0.007; therefore, we only used linear terms in the models. The proportion of mature fish was described as a function of cohort, age, and length. The linear predictor was linked to the fraction of mature fish ( $o$ ) through a logit link function. This predictor was modelled as follows:

$$\text{logit}(o) \sim \text{Cohort} + \text{Age} + \text{Length} + \text{Cohort} \times \text{Age} + \text{Cohort} \times \text{Length} + \text{Age} \times \text{Length} \quad , \quad (4)$$

where cohort is a factor and age and length are continuous variables. The interaction between age and length allows for the length at which plaice mature to vary with age.

(2) *Estimation of length increments.* For each cohort and age, the mean length was determined from the back-calculated lengths based on the otolith measurements. The yearly length increments ( $\delta s$ ) were then estimated as the differences in mean length between two consecutive ages of a cohort. We assumed that length increments were similar for all individuals within an age group of a cohort.

(3) *Estimation of the probability of maturing.* With the parameters obtained from Equation (4) and with the length increments obtained from the otolith-based back-calculations, the probability of maturing for each cohort, age group, and length could be estimated by Equation (3). Reaction norm midpoints ( $L_{P50}$ , the length at which the probability of maturing is 50 %) were calculated by determining the lengths that lead to probabilities of maturing of 50 %.

(4) *Estimation of confidence limits.* Since estimates of the probabilities for maturing are based on several successive steps, the direct calculation of confidence limits for reaction norms is not possible (Barot *et al.*, 2002); a bootstrap method was used instead (Manly, 1997). For this method, a new dataset was created by randomly sampling original data (observations of individual fish) with replacement. The data sampling was stratified by age and cohort. With the re-sampled data the reaction norm

midpoints were calculated by the procedure described above, steps 1-3. The dataset was re-sampled 1000 times and the confidence limits of the reaction norm midpoints were estimated as the 2.5 and 97.5 percentiles of the distribution of the 1000 midpoints of each age and cohort (Manly, 1997).

(5) *Analysis of trends in the probability of maturing.* For each age group, the effect of cohort on the midpoints of the reaction norm ( $L_{P50}$ ) was analysed using a linear model with cohort as a variate:

$$L_{P50} \sim \text{Cohort} \quad . \quad (5)$$

In this model, the estimated reaction norm midpoints were weighted with the inverse of the variance of each midpoint. The variance estimates were obtained from the bootstrapping method.

### **Effect of temperature on maturation reaction norms**

The effect of water temperature in the years preceding maturation on the probabilistic maturation reaction norms was analysed using a logistic model. In this model, the probability  $p$  of maturing, estimated in steps 1-3, was modelled by length, cohort, and water temperature. Yearly average temperatures for the second and third quarter were calculated from daily readings at a fixed time of day at Den Helder after correction for the tidal phase. Two temperatures were included in this model, describing the average water temperatures two and three years prior to the year for which the probability of maturation was calculated. Since the temperatures showed a significant trend over the study period (an average increase of  $0.02^{\circ}\text{C}$  per year) this trend was removed from the temperature data. For each age group, the effect of length, cohort, and the two resulting temperature residuals, denoted  $R_{T-2}$  and  $R_{T-3}$ , was then analysed:

$$\text{logit}(p) \sim \text{Length} + \text{Cohort} + R_{T-2} + R_{T-3} \quad . \quad (6)$$

The temperature residual  $R_{T-1}$  was not included in the model since previous analysis (Rijnsdorp, 1993b) had shown that the temperature in the very year in which maturation takes place is not expected to influence the probability at which that maturation process occurs.

## RESULTS

Growth rates at ages 1, 2, and 3 significantly increased in 1955-1995 whereas growth rates in age groups 5 and 6 decreased, although only the decrease for age 5 was statistically significant (**Figure 3**). No trend in growth rates at age 4 was observed ( $p=0.25$ ). The increase in growth rates was on average 0.03-0.04 cm year<sup>-2</sup>, whereas the decrease at age 5 was 0.01 cm year<sup>-2</sup>. Although growth rates at age 2 increased over the whole period on average, these rates showed a clear temporal structure, with dips around 1965 and 1985 and peaks around 1974 and 1995 (**Figure 3**).

Both age and length at 50 % maturity showed a significant decline, although this trend was stronger for  $A_{50}$  than for  $L_{50}$  (**Figure 4**). On average,  $A_{50}$  decreased from 4.1 years in 1955 to 2.9 years in 1995, whereas  $L_{50}$  decreased from 32.0 cm to 30.9 cm. Both showed a similar temporal structure with peaks around 1966 and 1985 and a dip around 1974.

We found that the maturation reaction norms of plaice have negative slopes such that the length at which plaice attains a certain probability to mature decreases with age: at the same length, old females have a higher probability to mature than young ones (**Figure 5**). The probabilistic reaction norms are rather narrow: the average distance between  $L_{P25}$  and  $L_{P75}$  varies between 5.4 and 9.1 cm across age groups. The width of the reaction norms decreases slightly with age. Over the whole period and for all ages, the length at which fish had a certain probability to mature

decreased, whereas the average length-at-age increased (**Figure 5**). Probabilities to mature at a given length thus strongly increased for all ages. For example, from 1955-1964 the length  $L_{P50}$  at which the probability to mature at age 4 reaches 50 % (34.4 cm) lies well above the mean length at that age (29.7 cm). By contrast, thirty years later, from 1985-1994,  $L_{P50}$  at age 4 (30.1 cm) had come to lie under the mean length (32.7 cm).

The increased probabilities to mature at a given length are clearly reflected in the significant ( $p < 0.005$ ) downward trend in  $L_{P50}$  from 1955-1995 for all ages (**Figure 6**);  $L_{P50}$  decreased about 4 cm at ages 3, 4, and 5, and about 5 cm at ages 2 and 6. Apart from the downward trend,  $L_{P50}$  showed considerable variation among cohorts. This variation was largest at age 2. No clear temporal structure was visible, except perhaps at age 3, at which a small peak in  $L_{P50}$  occurred around 1985 (**Figure 6**).

The variation of reaction norm midpoints among years could to a large extent be explained by the water temperature in previous years (**Figure 7**). For all ages, the probability of maturing at a given length increased significantly with an increase of temperature two and three years earlier. At age 2, for example,  $L_{P50}$  decreased by 2.2 cm when the water temperature in the second and third quarters two years earlier was 1 °C higher (**Figure 7**).

## DISCUSSION

The significant downward trend in probabilistic reaction norms over cohorts of 1955-1995 strongly supports the hypothesis that fisheries-induced evolution has changed the maturation process in North Sea plaice towards maturation at earlier age and length. In addition to the observed change in the reaction norm, growth has accelerated during the study period. Through the phenotypic plasticity described by

the maturation reaction norm, the increased growth rates have led to an even earlier age at maturation (**Figure 8**). This corroborates previous conclusions by Rijnsdorp (1993a) based on changes in maturity observed between the early and late 20<sup>th</sup> century.

The probabilistic reaction-norm approach suggests a picture in which short-term fluctuations originating from plastic responses are superimposed on long-term trends resulting from genetic responses. The age at 50 % maturity ( $A_{50}$ ) exhibits, beyond the significant downward trend, a temporal fine structure that rather faithfully mirrors temporal changes in the growth rates at ages 1, 2, and 3 (**Figure 9**). By contrast, the reaction norm midpoints ( $L_{P50}$ ) only show a downward trend, together with some short-term fluctuations. These fluctuations were partly explained by short-term variations in water temperature (high water temperatures are likely to favour earlier maturation either directly, via physiological effects of temperature, or indirectly, by indicating favourable environmental conditions). These findings are in line with the results of Bromley (2000) who suggests that the higher water temperature in the southern North Sea causes maturation at earlier ages and smaller lengths of plaice than in the northern North Sea. Our result that water temperature influences the probability to mature two to three years later corroborates the results of Rijnsdorp (1993a) that the maturation process of plaice takes three years: high growth rates three and two years prior to sampling were associated with higher fractions of mature plaice (Rijnsdorp, 1993b).

It remains unclear to which extent the increase of growth rates is due to phenotypic plasticity or a result of evolution, but the actual cause has no implications for our analysis and conclusions: probabilistic reaction norms are not sensitive to long-term changes in growth rates. Although growth rates can be partly genotypically



---

determined (Conover and Munch, 2002; Imsland and Jonassen, 2001), it is unlikely that the short-term (decadal) fluctuations in growth rates we observed are a result of evolution (Rijnsdorp, 1993a). Yet, in addition to such short-term variation in growth rates, the intensive size-selective fishing could well have induced a longer-term evolutionary process selecting for lower growth rates (Conover and Munch, 2002; Kirkpatrick, 1993; Ricker, 1981). Phenotypically, however, observed growth rates of plaice up to age 3 have increased, so that selection for low growth rates would have to have been over-compensated by much increased food abundance. Since the probabilistic reaction-norm method largely filters changes in growth rate from the process of maturation, such effects would not influence our results. Only when pleiotropy occurs (i.e., when genes coding for maturation partially coincide with those coding for growth) would evolving growth mask evolving maturation.

Despite the relatively short period over which we could investigate the potential evolutionary response of plaice to fishing, there is no basis for assuming that evolution of life-history characteristics could not be detected within such a period. If we consider a generation time of 5-6 years, the 41 cohorts studied comprise 6 to 8 generations. Since the heritability of various life-history traits in fish are estimated at around 0.2-0.3, such a number of generations would indeed permit a significant response of these traits to selection (Roff, 1991), especially in view of the high selection differential imposed by fishing. Experiments in guppies (*Poecilia reticulata*) showed that a change in the pattern and rate of size-selective mortality caused major evolution of life-history characteristics in as few as 18 generations (Reznick *et al.*, 1990; Reznick *et al.*, 1997). In Atlantic silverside (*Menidia menidia*), the growth rate of the study population evolved within just four generations in an experimental set-up in which fish were harvested size-selectively (Conover and Munch, 2002). The

selection differential for the length at maturation of female plaice was estimated at 2.1 cm, and the fitness profiles indicate that a further decrease in the length at maturation would still increase individual fitness (Rijnsdorp, 1993c).

Our results are probably influenced by violations of the two assumptions made to estimate the reaction norms (similar growth rates and mortality rates of mature and immature fish of the same age), but we believe that the resulting biases do not influence the interpretation of the results: as Barot *et al.* (2002) have shown, the method applied here is very robust against violations of the assumptions. In plaice, growth rates of mature and immature females differ significantly (Rijnsdorp, 1993b), but it is difficult to estimate differences in mortality rates of mature and immature females. Since mature females remain on the spawning grounds for longer periods, where fishing is intense, they probably face higher mortality. The assumption that growth rate is length-independent is difficult to falsify since actual growth within an age group of a cohort is not completely dependent on fish length, but is also determined by the growth history of the fish and the moment of maturation (Rijnsdorp, 1993b). The pooling of maturity data over geographical regions may have introduced slight errors in the estimation of ogives, since age and length at maturation of plaice show a slight longitudinal trend from south to north (Bromley, 2000; Rijnsdorp, 1989). We think, however, that these regional differences have no effect on our conclusion regarding evolutionary change in the stock, since the plaice stock within our study area can be considered as being genetically homogeneous (Hoarau *et al.*, 2002).

The fact that we have revealed strong indications for fisheries-induced evolution in North Sea plaice may have implications for the sustainable exploitation of and potential yield from this stock (Browman, 2000; Pauly *et al.*, 2002). First,

---

fisheries-induced evolution is likely to decrease potential yield (Stokes and Law, 2000), and, second, finding management strategies for reversing the decreasing trend in age and length at maturation will be exceedingly difficult. As mentioned earlier, genetic changes are not reversible over the short term (Reznick, 1993) since they occur on the time scale of generations. Moreover, at low fishing pressures, fitness profiles are almost flat, indicating a weak selection for later maturation (Law, 2000; Law and Grey, 1989; Rowell, 1993). This pronounced asymmetry of selection pressures is of particular concern: mitigating measures, such as a decrease in fishing effort or an alteration of the exploitation curve, would probably only have effects over the long term. Moreover, when fishing mortality is suddenly relaxed, the surviving genotypes in the stock may be those that exhibit reduced fitness under such a new situation (Conover, 2000). In general, earlier maturation leads to retarded growth rates and could thus imply a lower biomass per age group. Spawning stock biomass may, however, increase, since more fish are mature. However, an increased spawning stock biomass does not necessarily lead to higher recruitment, since the effective spawning potential of a stock depends on its demographic composition (Murawski *et al.*, 2001): when fecundity or viability of eggs and larvae are positively correlated with maternal size, earlier-spawning females contribute less to reproduction.

Since our results clearly indicate the presence of fishery-induced evolutionary change in North Sea plaice, the resulting long-term implications for the potential yield of this stock deserve careful evaluation. The management of North Sea plaice should not remain unaffected.

## ACKNOWLEDGEMENTS

The research underlying this study was financially supported by the Netherlands Organization for Scientific Research (NWO) and by the Netherlands Institute for Fisheries Research (RIVO) by enabling a six-months postdoctoral project of RG at IIASA. Also support by the European Research Training Network *ModLife* (Modern Life-History Theory and its Application to the Management of Natural Resources), funded through the Human Potential Programme of the European Commission (Contract HPRN-CT-2000-00051), and by the Academy of Finland (Project 45928), is gratefully acknowledged.

## REFERENCES

- Barot, S., Heino, M., O'Brien, L. and Dieckmann, U. 2002. Estimating reaction norms for age and size at maturation without first-time spawner data. 29.
- Borisov, V. M. 1978. The selective effect of fishing on the population structure of species with long life cycle. *Journal of Ichthyology*, 18: 896-904.
- Bromley, P. J. 2000. Growth, sexual maturation and spawning in central North Sea plaice (*Pleuronectes platessa* L.), and the generation of maturity ogives from commercial catch data. *Journal of Sea Research*, 44: 27-43.
- Browman, H. I. 2000. Application of evolutionary theory to fisheries science and stock assessment-management. *Marine Ecology Progress Series*, 208: 299.
- Conover, D. O. 2000. Darwinian fisheries science. *Marine Ecology Progress Series*, 208: 303-307.
- Conover, D. O. and Munch, S. B. 2002. Sustaining fisheries yields over evolutionary time scales. *Science*, 297: 94-96.
- Haugen, T. O. and Vøllestad, L. A. 2001. A century of life-history evolution in grayling. *Genetica*, 112-113: 475-491.
- Heino, M., Dieckmann, U. and Godø, O. R. 2002a. Estimating reaction norms for age and size at maturation with reconstructed immature size distributions: a new technique illustrated by application to Northeast Arctic cod. *ICES Journal of Marine Science*, 59: 562-575.

---

Heino, M., Dieckmann, U. and Godø, O. R. 2002b. Measuring probabilistic reaction norms for age and size at maturation. *Evolution*, 56: 669-678.

Heino, M. and Kaitala, V. 1999. Evolution of resource allocation between growth and reproduction in animals with indeterminate growth. *Journal of Evolutionary Biology*, 12: 423-429.

Hoarau, G., Rijnsdorp, A. D., Van Der Veer, H. W., Stam, W. T. and Olsen, J. L. 2002. Population structure of plaice (*Pleuronectes platessa* L.) in northern Europe: microsatellites revealed large-scale spatial and temporal homogeneity. *Molecular Ecology*, 11: 1165-1176.

Hutchings, J. A. 1993. Adaptive life histories effected by age-specific survival and growth rate. *Ecology*, 74: 673-684.

ICES. 2002. Report of the working group on the assessment of demersal stocks in the North Sea and Skagerrak. 385.

Imsland, A. K. and Jonassen, T. M. 2001. Regulation of growth in turbot (*Scophthalmus maximus* Rafinesque) and Atlantic halibut (*Hippoglossus hippoglossus* L.): aspects of environment  $\times$  genotype interactions. *Reviews in Fish Biology and Fisheries*, 11: 71-90.

Kirkpatrick, M. 1993. The evolution of size and growth in harvested natural populations. In *The exploitation of evolving resources*, pp. 145-154. Ed. by T. K. Stokes, J. M. McGlade and R. Law. Lecture notes in biomathematics, Springer Verlag, Berlin- Heidelberg.

Law, R. 2000. Fishing, selection, and phenotypic evolution. *ICES Journal of Marine Science*, 57: 659-668.

Law, R. and Grey, D. R. 1989. Evolution of yields from populations with age-specific cropping. *Evolutionary Ecology*, 3: 343-359.

Manly, B. F. J. 1997. Randomization, bootstrap and monte carlo methods in biology. *Texts in statistical science*, Chapman & Hall. London. 399 pp.

Morgan, M. J. and Colbourne, E. B. 1999. Variation in maturity-at-age and size in three populations of American plaice. *ICES Journal of Marine Science*, 56: 673-688.

Murawski, S. A., Rago, P. J. and Trippel, E. A. 2001. Impacts of demographic variation in spawning characteristics on reference points for fishery management. *ICES Journal of Marine Science*, 58: 1002-1014.

Pauly, D., Christensen, V., Guénette, S., Pitcher, T. J., Rashid Sumaila, U., Walters, C. J., Watson, R. and Zeller, D. 2002. Towards sustainability in world fisheries. *Nature*, 418: 689-695.

Reznick, D. N. 1983. The structure of guppy life histories: the tradeoff between growth and reproduction. *Ecology*, 64: 862-873.

Reznick, D. N. 1993. Norms of reaction in fishes. In *The exploitation of evolving resources*, pp. 72-90. Ed. by T. K. Stokes, J. M. McGlade and R. Law. Lecture notes in biomathematics, Springer Verlag, Berlin- Heidelberg.

Reznick, D. N., Bryga, H. and Endler, J. A. 1990. Experimentally induced life-history evolution in a natural population. *Nature*, 346: 357-359.

Reznick, D. N., Shaw, F. H., Rodd, F. H. and Shaw, R. G. 1997. Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). *Science*, 275: 1934-1936.

Ricker, W. E. 1981. Changes in the average size and average age of Pacific Salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, 38: 1636-1656.

Rijnsdorp, A. D. 1989. Maturation of male and female North Sea plaice (*Pleuronectes platessa* L.). *Journal de la Conservation Internationale pour la Exploration de la Mer*, 46: 35-51.

Rijnsdorp, A. D. 1993a. Fisheries as a large-scale experiment on life-history evolution: disentangling phenotypic and genetic effects in changes in maturation and reproduction of North Sea plaice, *Pleuronectes platessa* L. *Oecologia*, 96: 391-401.

Rijnsdorp, A. D. 1993b. Relationship between juvenile growth and the onset of sexual maturity of female North Sea plaice, *Pleuronectes platessa*. *Canadian Journal of Fisheries and Aquatic Sciences*, 50: 1617-1631.

Rijnsdorp, A. D. 1993c. Selection differentials in male and female North Sea plaice and changes in maturation and fecundity. In *The exploitation of evolving resources*, pp. 19-36. Ed. by T. K. Stokes, J. M. McGlade and R. Law. Lecture notes in biomathematics, Springer Verlag, Berlin- Heidelberg.

Rijnsdorp, A. D., Buys, A. M., Storbeck, F. and Visser, E. G. 1998. Micro-scale distribution of beam trawl effort in the southern North Sea between 1993 and 1996 in relation to the trawling frequency of the sea bed and the impact on benthic organisms. *ICES Journal of Marine Science*, 55: 403-419.

Rijnsdorp, A. D. and Millner, R. S. 1996. Trends in population dynamics and exploitation of North Sea plaice (*Pleuronectes platessa* L.) since the late 1800s. *ICES Journal of Marine Science*, 53: 1170-1184.

Rijnsdorp, A. D. and Van Leeuwen, P. I. 1992. Density-dependent and independent changes in somatic growth of female North Sea plaice (*Pleuronectes platessa* L.) between 1930-1985 as revealed by back-calculations of otoliths. *Marine Ecology Progress Series*, 88: 19-32.

Rijnsdorp, A. D. and Van Leeuwen, P. I. 1996. Changes in growth of North Sea plaice since 1950 in relation to density, eutrophication, beam-trawl effort, and temperature. *ICES Journal of Marine Science*, 53: 1199-1213.

- 
- Rijnsdorp, A. D., Van Leeuwen, P. I. and Visser, T. A. M. 1990. On the validity and precision of back-calculation of growth from otoliths of the plaice (*Pleuronectes platessa* L.). *Fisheries Research*, 9: 97-117.
- Rochet, M. J., Cornillon, P. A., Sabatier, R. and Pontier, D. 2000. Comparative analysis of phylogenetic and fishing effects in life history patterns of teleost fishes. *Oikos*, 91: 255-270.
- Roff, D. A. 1991. The evolution of life-history variation in fishes, with particular reference to flatfishes. *Journal of Sea Research*, 27: 197-207.
- Rowell, C. 1993. The effects of fishing on the timing of maturity in North Sea Cod (*Gadus morhua* L.). In *The exploitation of evolving resources*, pp. 44-61. Ed. by T. K. Stokes, J. M. McGlade and R. Law. *Lecture notes in biomathematics*, Springer Verlag, Berlin-Heidelberg.
- Royston, P. and Altman, D. G. 1994. Regression using fractional polynomials of continuous covariates: parsimonious parametric modelling. *Applied Statistics*, 43: 429-467.
- Siems, D. P. and Sikes, R. S. 1998. Tradeoffs between growth and reproduction in response to temporal variation in food supply. *Environmental Biology of Fishes*, 53: 319-329.
- Stearns, S. C. 1992. *The evolution of life histories*. Oxford University Press. New York. 249 pp.
- Stearns, S. C. and Koella, J. C. 1986. The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. *Evolution*, 40: 893-913.
- Stokes, T. K. and Law, R. 2000. Fishing as an evolutionary force. *Marine Ecology Progress Series*, 208: 307-309.

---

**Tables**

**Table 1.** Numbers of female plaice of cohorts 1955-1995 of which data were used in the analysis.

	Length, age and maturity data						Back-calculated
	Total	Age 2	Age 3	Age 4	Age 5	Age 6	lengths Total
Total number	18996	457	4288	4956	4795	4500	2429
Average per cohort	463	11	105	121	117	110	59
Minimum per cohort	45	0	1	6	4	7	4
Maximum per cohort	1479	94	488	441	417	447	257

---



**Table 2.** Results of logistic regression for the maturity ogives (fraction of mature fish) as a function of length, age and cohort, based on 18,996 observations for cohorts 1955-1995, ages 2-6 (Equation 4).

Source	Deviance	$R^2$	d.f.	$\chi^2$	$P$
		(cumulative)			
Intercept	23111				
Length	14105	0.39	1	9006	<0.0001
Age	13772	0.40	1	332.6	<0.0001
Cohort	13257	0.43	40	515.6	<0.0001
Length x age	13213	0.43	1	44.2	<0.0001
Length x cohort	13028	0.44	40	185.0	<0.0001
Age x cohort	12883	0.44	40	144.3	<0.0001

---

### Figure legends

**Figure 1.** Trends in fishing mortality in North Sea plaice (averaged over ages 2-10, panel a) and in the age-specific exploitation pattern (averaged over intervals of 10 years, panel b). Data from ICES (2002). For comparison, the natural mortality rate of North Sea plaice is estimated at  $0.1 \text{ yr}^{-1}$ .

**Figure 2.** Illustration of how the probability of maturing is calculated. For a given age  $a$ , and based on the observed length-dependent fraction of mature fish (open circles) the maturity ogive (thin continuous curve) is estimated by logistic regression of the fraction of mature fish on length  $s$ . With the parameters obtained from this regression, the fraction of mature fish in the preceding year (i.e., at age  $a-1$  and size  $s-\delta s$ ) is estimated (thin dashed curve). From these two fractions, the length-dependent probability of maturing (thick curve) is obtained through Equation (3). The length  $L_{p50}$  at which this probability reaches 50 % is also shown (dotted lines). Data of cohort 1970, age 4.

**Figure 3.** Trends in growth rates (lines) of ages 1, 2, 3, and 5. For these four ages the slopes of the regression lines were significantly different from 0 (linear model with cohort as a variate and age as a factor, including interaction between cohort and age;  $p < 0.005$ ;  $R^2 = 0.48$ ; 11 d.f.; 12,725 observations). For each age and cohort, open circles and error bars represent arithmetic means and standard errors of the growth rate. All data originate from the annual length increments of individual fish inferred from otolith measurements.

**Figure 4.** Trends in the age ( $A_{50}$ ) and length ( $L_{50}$ ) at which 50 % of fish are mature in each cohort. Data from logistic models with cohort either as a factor (open and filled circles;  $R^2 = 0.34$  and  $0.42$  for age and length at maturation, respectively) or as a variate (dashed and

---

continuous lines;  $R^2=0.30$  and  $0.40$ , respectively). In both cases, the decline of  $A_{50}$  and  $L_{50}$  with time (cohort) is significant ( $p<0.0001$ ).

**Figure 5.** Maturation reaction norms and growth curves. The lengths at which the probability of maturing reaches 10, 50, and 90 % ( $L_{P10}$ ,  $L_{P50}$ , and  $L_{P90}$ ) are shown as continuous curves. Distributions of growth trajectories are depicted in terms of arithmetic mean length-at-age together with 10 and 90 % percentiles (Length,  $p_{10}$ , and  $p_{90}$ ). All values are averages over 10-year periods.

**Figure 6.** Reaction norm midpoints  $L_{P50}$  (filled circles) and 95 % confidence limits (error bars) for ages 2-6 of all cohorts. Trends in midpoints from the linear model in Equation (5) are shown by thick continuous lines. Notice that the scales of vertical axes vary with age.

**Figure 7.** Effect of variation in water temperature on reaction norm midpoints. The lines illustrate the effect of temperature (over the observed range of temperature residuals) on the change in the reaction norm midpoint  $L_{P50}$ . Data for cohort 1990.

**Figure 8.** Reaction norm midpoints and growth curves for the cohorts of 1960 and 1990. From 1960 to 1990, the reaction norm has shifted downwards, while size-at-age has increased. For the cohort of 1990, growth curves thus hit the reaction norm at a lower age and a smaller length, leading to earlier maturation at smaller length. The graph illustrates that an increase in growth rate affects the age and length at maturation, but not the maturation reaction norm.

**Figure 9.** Trends in the North Sea plaice stock from 1955 to 1995. (a) Maturation reaction norm midpoints  $L_{P50}$  for three age groups. (b) Length  $L_{50}$  and age  $A_{50}$  at 50 % maturity. (c) Growth rates for five age groups.

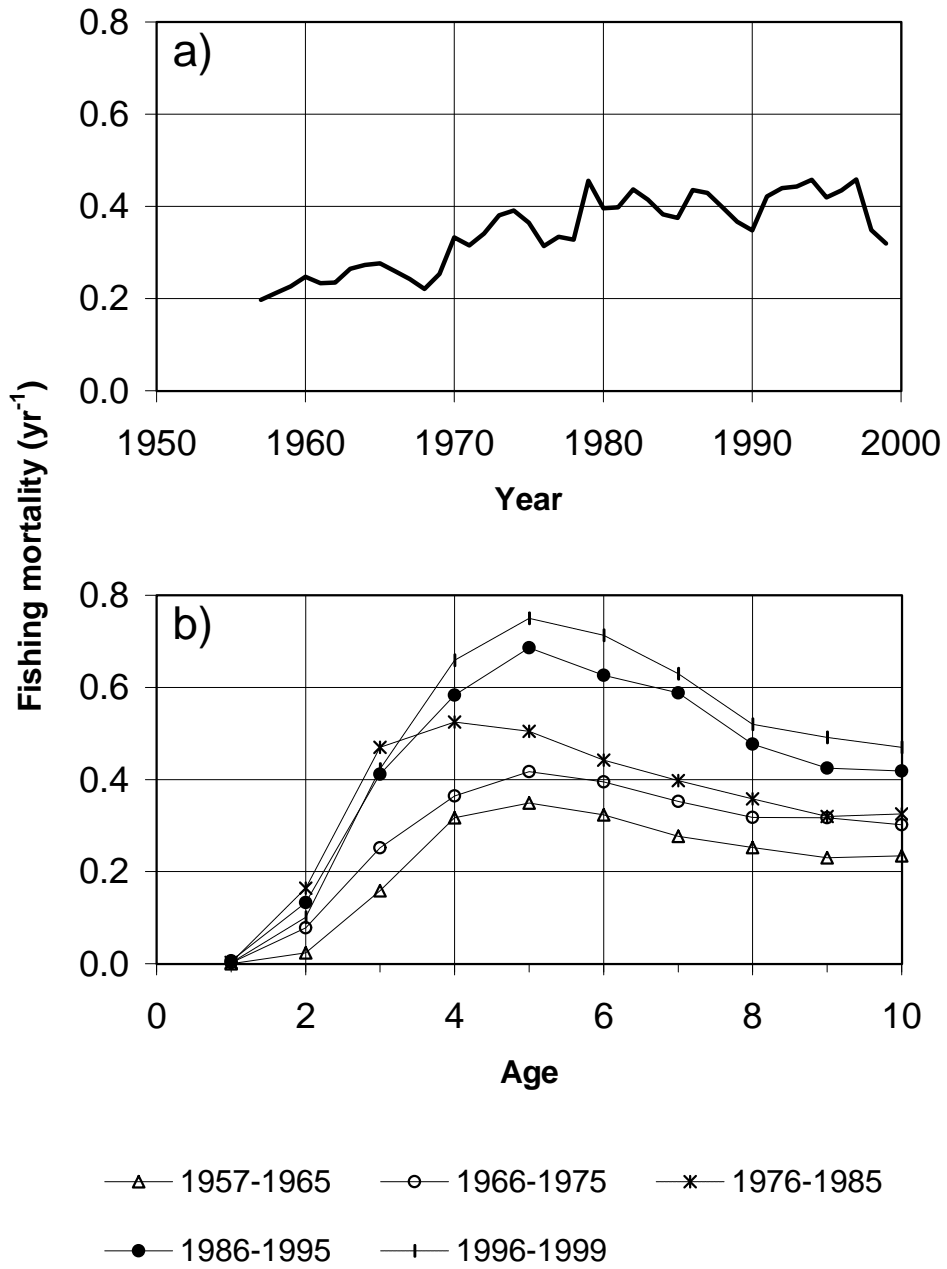


Figure 1.

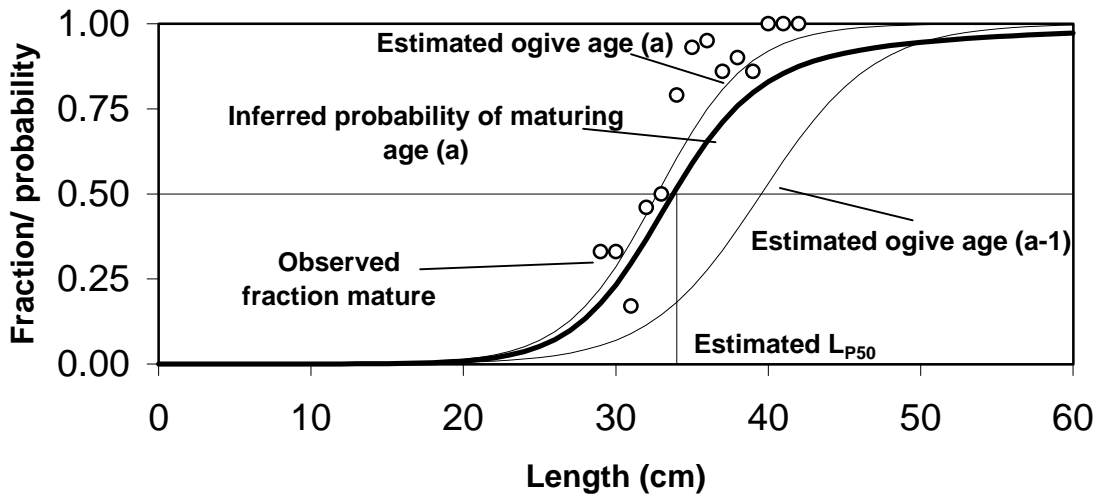


Figure 2.

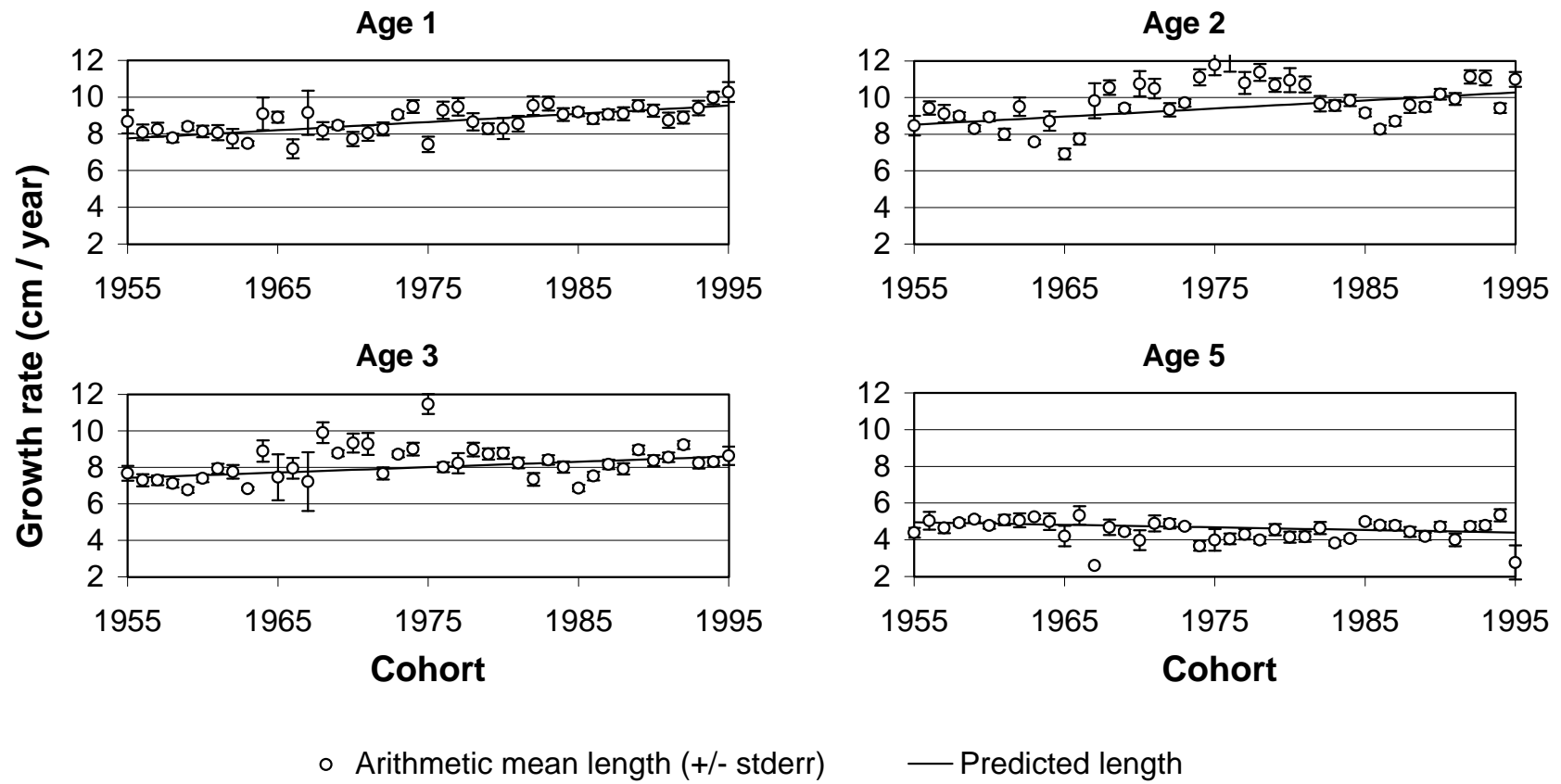


Figure 3.

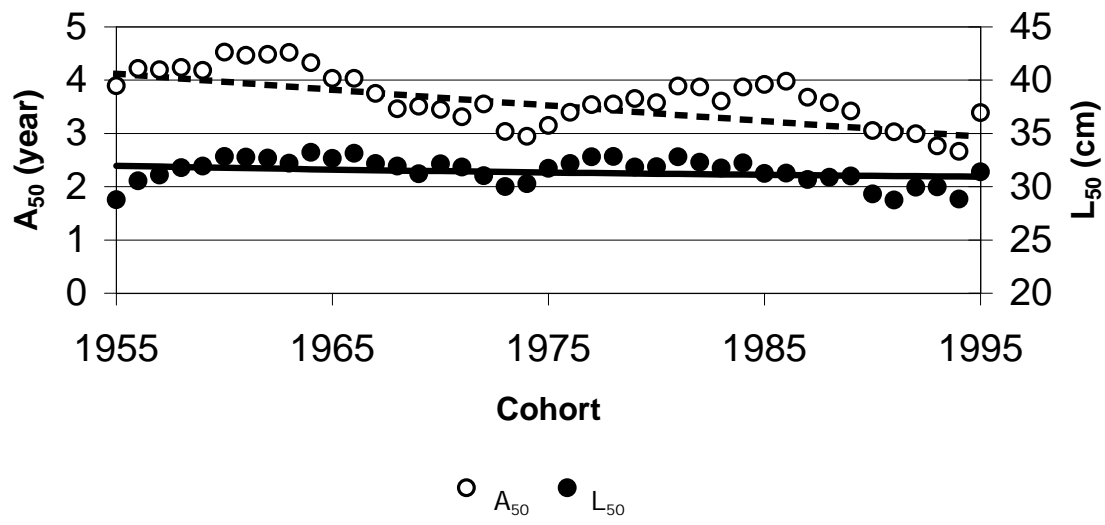


Figure 4.



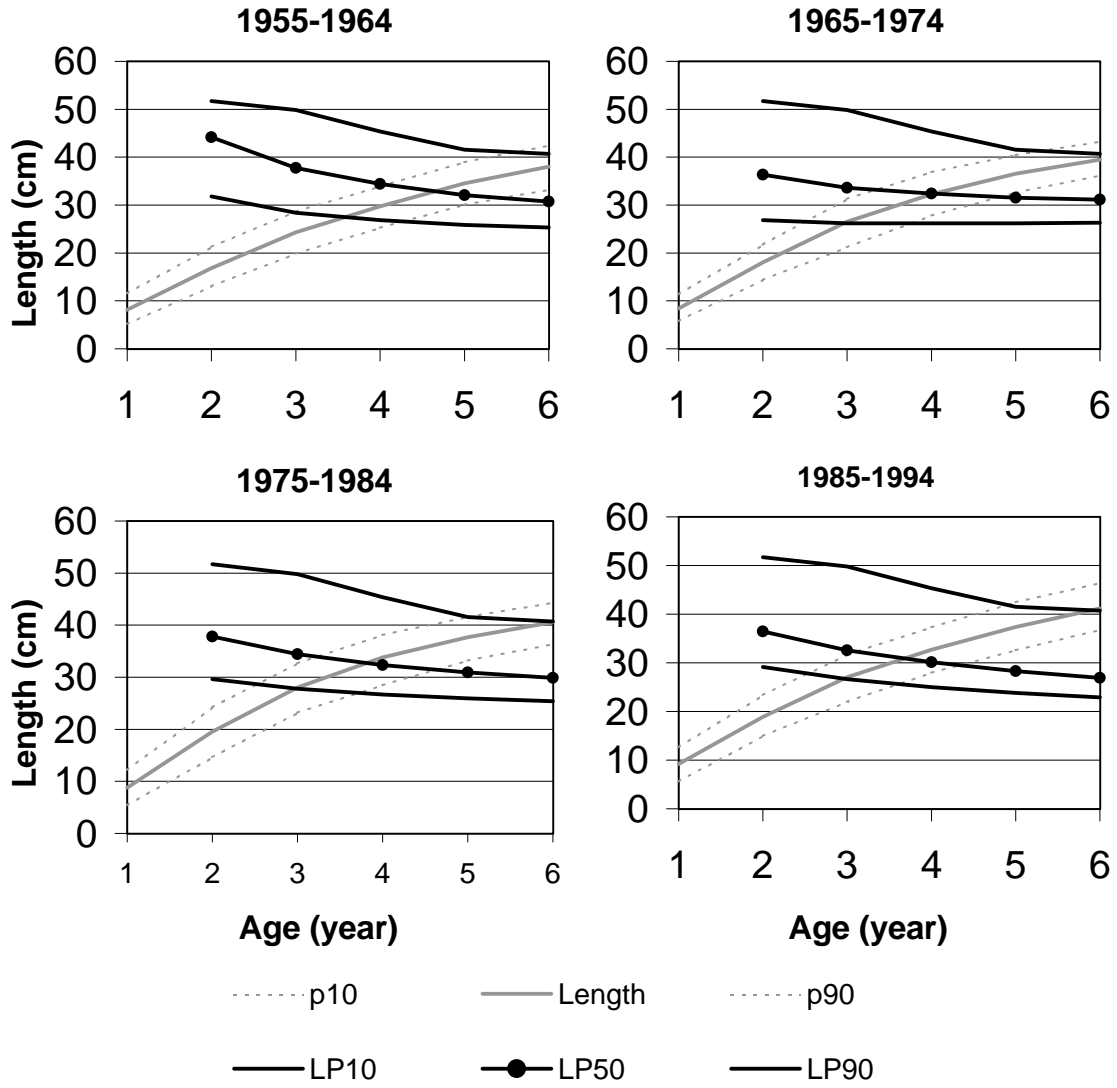


Figure 5.

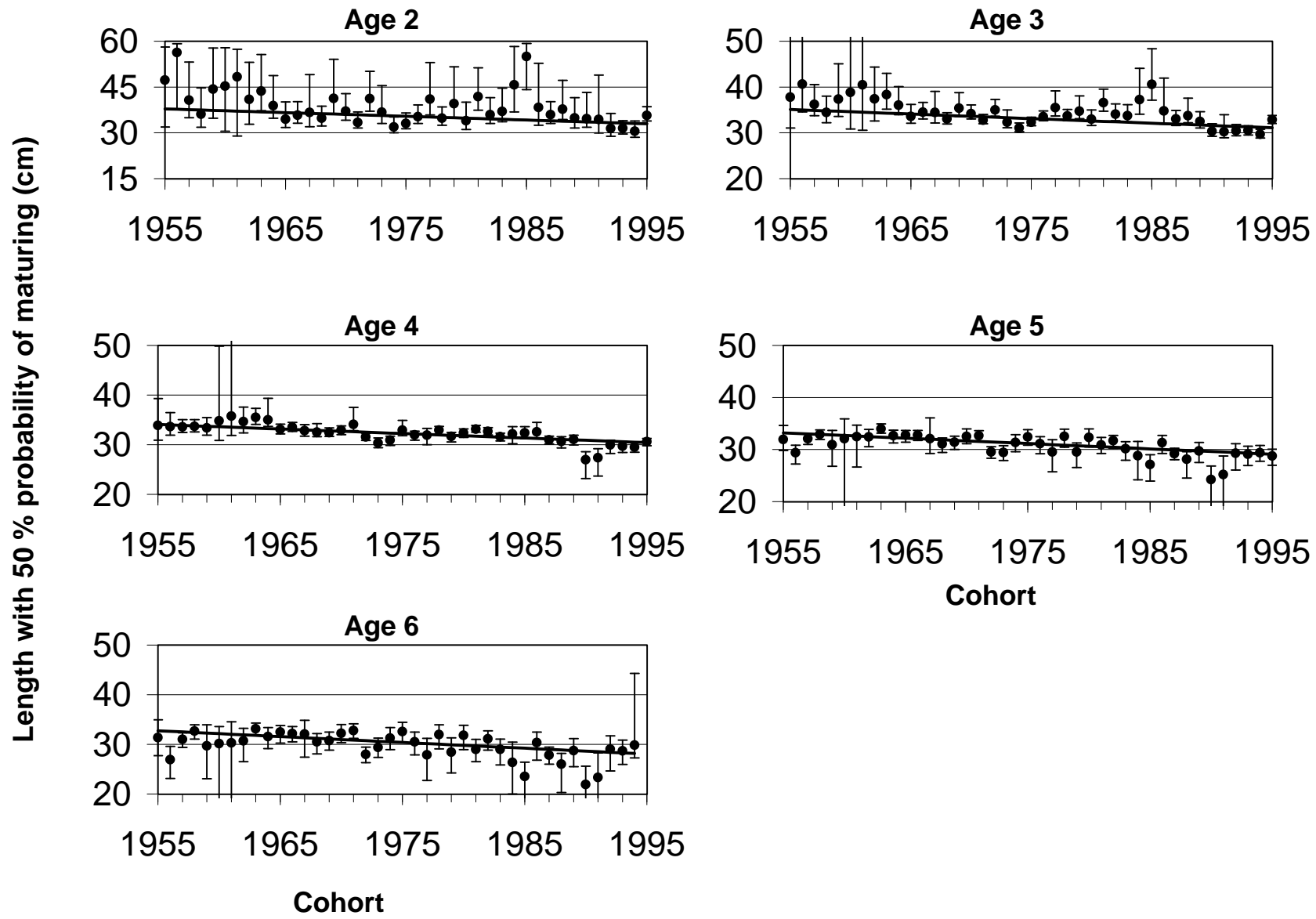


Figure 6.

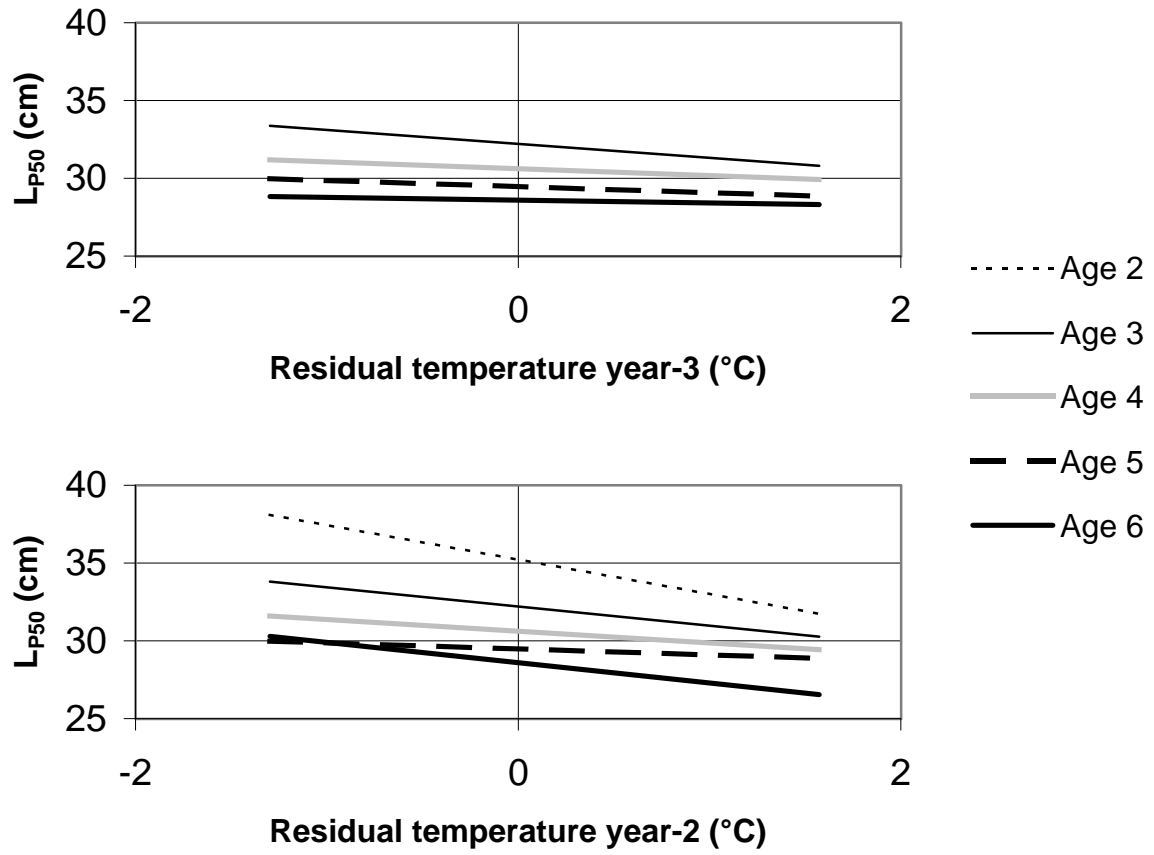


Figure 7.

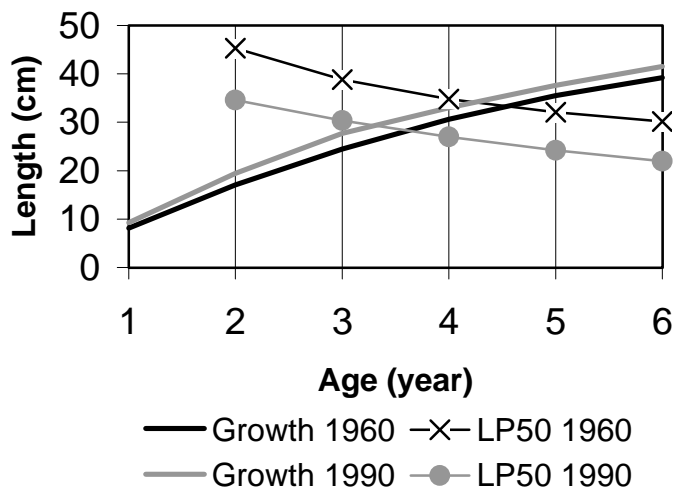


Figure 8.

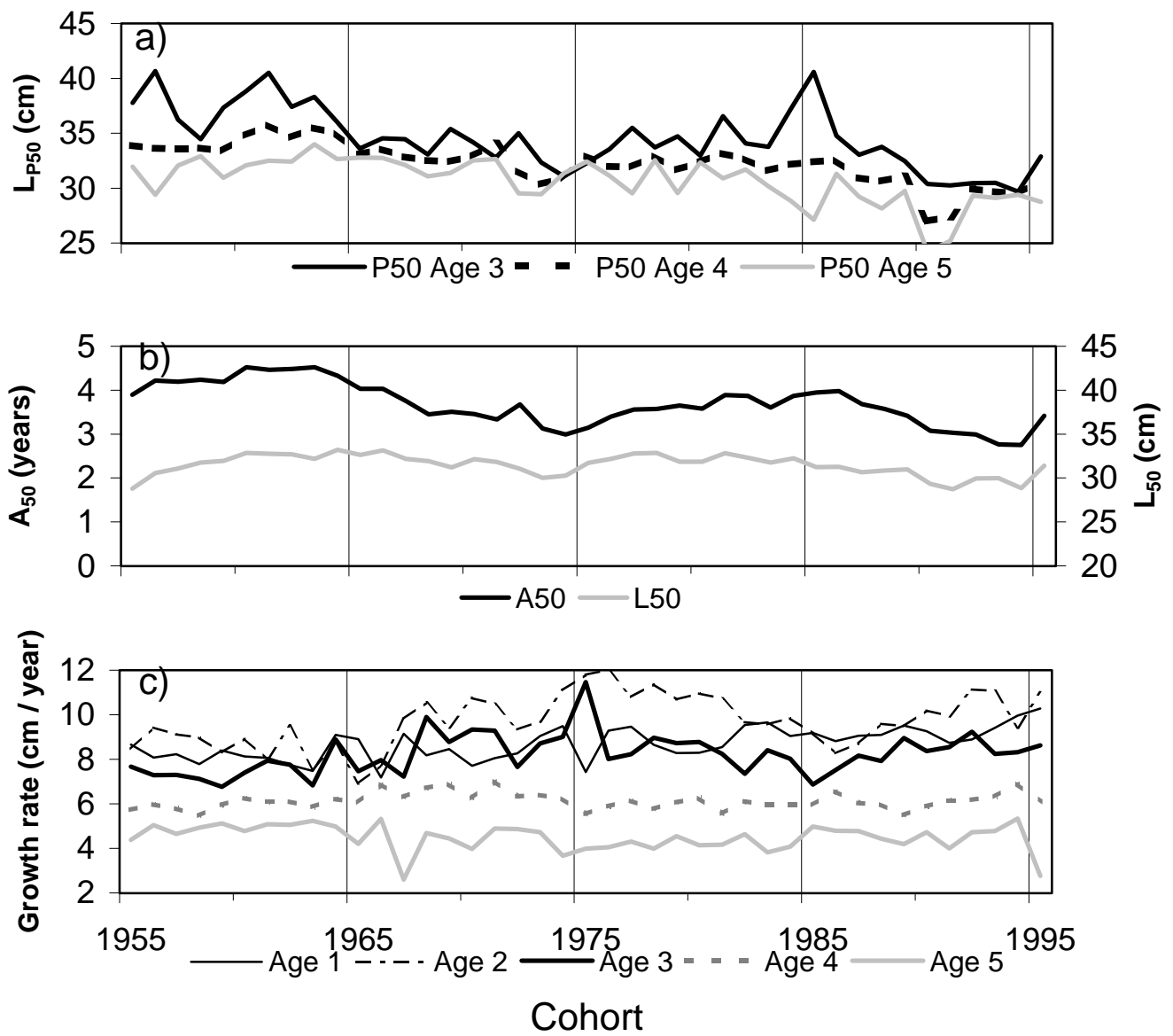


Figure 9.