International Institute for
Applied Systems Analysis
Schlossplatz 1
A-2361 Laxenburg, Austria

Tel: +43 2236 807 342
Fax: +43 2236 71313
E-mail: publications@iiasa.ac.at
Web: www.iiasa.ac.at

Interim Report **IR-03-076**

Fisheries-induced Trends in Reaction Norms for Maturation in North Sea Plaice

Rob E. Grift (rob.grift@wur.nl)
Adriaan D. Rijnsdorp (adriaan.rijnsdorp@wur.nl)
Sébastien Barot (Sebastien.Barot@bondy.ird.fr)
Mikko Heino (mikko.heino@imr.no)
Ulf Dieckmann (dieckmann@iiasa.ac.at)

Approved by

Leen Hordijk
Director, IIASA

December 2003

Contents

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 and higher body growth.

About the Authors

Rob E. Grift
Netherlands Institute for Fisheries Research, Animal Science Group
Wageningen UR. P.O. Box 68, 1970 Ijmuiden, The Netherlands
and
Adaptive Dynamics Network, International Institute for Applied Systems Analysis
Schlossplatz 1, A-2361 Laxenburg, Austria

Adriaan D. Rijnsdorp
Netherlands Institute for Fisheries Research, Animal Science Group
Wageningen UR. P.O. Box 68, 1970 Ijmuiden, The Netherlands

Sébastien Barot
IRD-LEST, 32 Avenue H. Varagnat, 93143 Bondy Cedex, France
and
Adaptive Dynamics Network, International Institute for Applied Systems Analysis
Schlossplatz 1, A-2361 Laxenburg, Austria

Mikko Heino
Institute of Marine Research, P.O. Box 1870, Nordnes, N-5817 Bergen, Norway
and
Adaptive Dynamics Network, International Institute for Applied Systems Analysis
Schlossplatz 1, A-2361 Laxenburg, Austria

Ulf Dieckmann
Adaptive Dynamics Network, International Institute for Applied Systems Analysis
Schlossplatz 1, A-2361 Laxenburg, Austria

Acknowledgments

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. We thank Niels Daan for stylistic edits and Jeff Hutchings and two anonymous referees for their constructive reviews.

Fisheries-induced Trends in Reaction Norms for Maturation in North Sea Plaice

Rob E. Grift (Rob@rivo.dlo.nl)
Adriaan D. Rijnsdorp (a.d.rijnsdorp@rivo.dlo.nl)
Sébastien Barot (Sebastien.Barot@bondy.ird.fr)
Mikko Heino (mikko.heino@imr.no)
Ulf Dieckmann (dieckman@iiasa.ac.at)

Introduction

Fishing is almost always selective and may therefore induce changes in exploited populations (Law 2000, Heino & Godø 2002). 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 & 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), Northeast Arctic cod *Gadus morhua* (Law & Grey 1989), North Sea cod *Gadus morhua* (Rowell 1993), North Sea plaice *Pleuronectes platessa* (Rijnsdorp 1993a) and grayling *Thymallus thymallus* (Haugen & 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 (Reznick 1993, Law 2000). 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 & 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 & 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 & Kaitala 1999) and resource availability (Siems & Sikes 1998). Since fecundity and the viability of eggs and larvae are often positively related to maternal size (Trippel 1999), there is a trade-off between current and future reproduction (Heino & 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 (Reznick et al. 1990, Hutchings 1993a, 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 & Millner 1996) are thus expected to be partially responsible for the significant decrease throughout the 20th 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) 20th 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.

We follow up on the earlier work by disentangling phenotypic and evolutionary changes in age and length at maturation in North Sea plaice. 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, a) and Georges Bank cod (Barot et al. 2002). This strategy allows for a refined test of the hypothesis that the observed

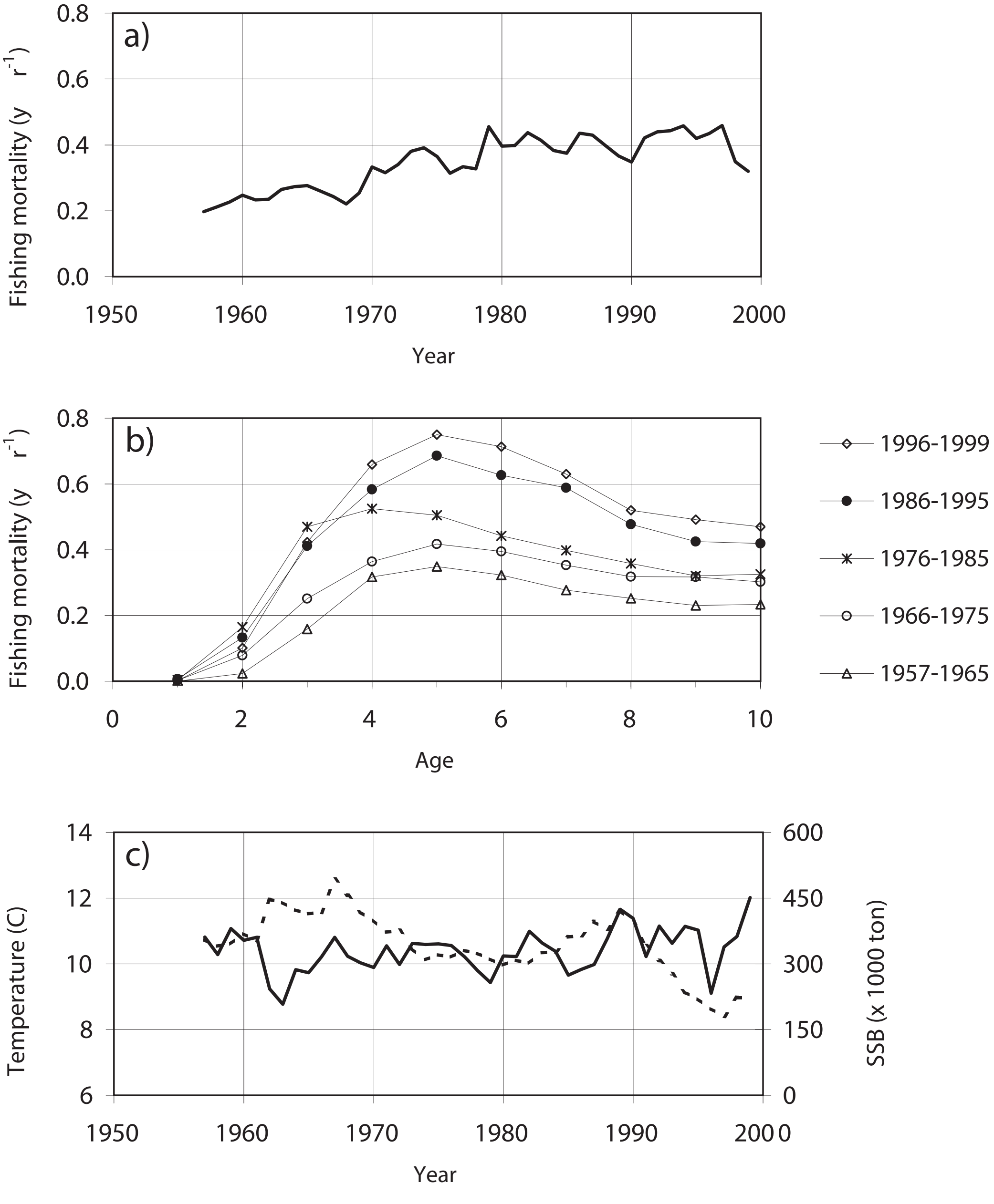

Figure 1. Trends in fishing mortality in North Sea plaice (averaged over ages 2-10, panel a) , the age-specific exploitation pattern (averaged over intervals of 10 years, panel b) and in water temperature (panel c, solid line) and spawning stock biomass (SSB, panel c, dashed line). Plaice stock parameters from ICES (2002). For comparison, the natural mortality rate of North Sea plaice is estimated at 0.1 yr^{-1}.

decrease in age and length at maturation is partly caused by fisheries-induced adaptive change. 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 19th century (Rijnsdorp & 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, due to a change in the selectivity of the fisheries, at present, fishing mortality does not decrease at higher ages, as it did in the 1930s (Rijnsdorp & Millner 1996). The selectivity probably changed 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 & Van Leeuwen 1992).

Data collection

Data on 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). In addition, 223 fish <27 cm were sampled since 1957. 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 each individual 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. (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 only data collected in the first quarter of each year were selected, because 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 were selected, because younger female plaice are not being caught commercially and because at age 7 all females were mature. We only used data from female plaice because males mature before they are representatively sampled; 96 % of male plaice in the market data is mature (n=22,700) whereas this percentages is 70 % for females (Table 1). After these selections, data on the length, age, and maturity status of 18,996 females, and for the analysis of yearly length increments, back-calculated lengths of 2,429 females were available. 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, $\mathrm{logit}(o)=\ln[o/(1-o)]$:

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

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

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 this process as being deterministic. If maturation were deterministic, it would occur with certainty once juvenile growth

Table 1. Numbers of female plaice of cohorts 1955-1995 of which data were used in the analysis. The fraction mature is the fraction of fish in the database that was mature in each age group.

	Length, age and maturity data						Back-calculated lengths
	Total	Age 2	Age 3	Age 4	Age 5	Age 6	Total
Total number	18,996	457	4,288	4,956	4,795	4,500	2,429
Average per cohort	463	11	105	121	117	110	59
Minimum per cohort	45	0	1	6	4	7	4
Maximum per cohort	1,479	94	488	441	417	447	257
Fraction mature	0.70	0.18	0.33	0.65	0.90	0.97	

trajectories intersect the reaction norm. 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. Some previous empirical studies attempted to separate growth from the maturation process (Hutchings 1993b, a, Rijnsdorp 1993a, Rowell 1993, Rochet et al. 2000), but could not conclusively disentangle these aspects.

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), differential losses of mature and immature fish (mortality) and by transitions of fish from one size class to another (growth). By contrast, the maturation reaction norm focuses on the process itself and thus is not affected by mortality and growth. A fish can only mature once, and therefore subsequent life does not influence the reaction norm. Moreover, since the 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 Northeast Arctic stock of cod; Rollefsen 1933) first-time and repeat spawners can be distinguished based on differential growth zones in their otoliths. For plaice such a distinction is not feasible, and the probability to mature at a certain age and size needs to be estimated with an alternative method based on ogives and growth rates. We follow this method developed by Barot et al. (2002). 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:

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

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, δs being the length gained between age $a-1$ and age a, and o is the fraction mature. 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 in the *previous* year. (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 age considered.)

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.

Estimation procedure

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 (Figure 2). Two further steps then consisted of: (4) estimation of confidence limits around the reaction norm using a bootstrap method, and (5) testing the significance of trends. Below, we describe each step in more detail.

(1) Ogives. Because the maturity status is a binary response variable 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 & Altman 1994). Because inclusion of non-linear terms increased the fraction of explained deviance by only 0.1 % only linear terms were used 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:

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

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. This model explained 44 % of the deviance (Table 2).

(2) Length increments. For each cohort and age, the mean length was determined from back-calculated lengths based on the otolith measurements. The yearly length increments (δs) were then estimated as the differences in mean length between two

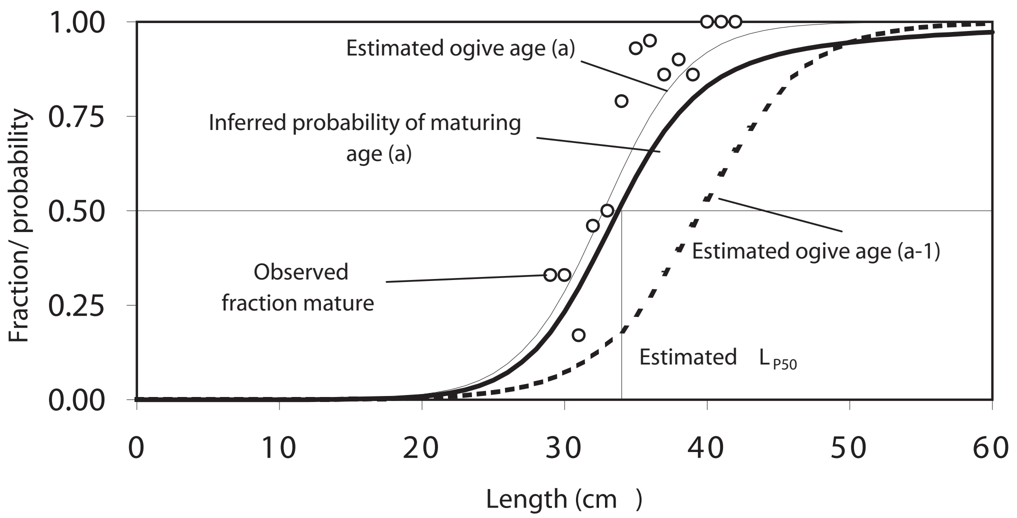

Figure 2. Illustration of how the probability of maturing is calculated. For a given age *a*, and based on the observed length-dependent fraction of mature fish (open circles) the maturity ogive (thin continuous curve) is estimated by logistic regression of the fraction of mature fish on length *s*. 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 (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.

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 (cumulative)	d.f.	χ^2	*P*
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

consecutive ages of a cohort. We assumed that length increments were similar for all individuals within an age group of a cohort.

(3) Probability of maturing. With the parameters obtained from Equation (4) and with the length increments from back-calculations, the probability of maturing for each cohort, age group, and length was 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) Confidence limits. Because estimates of the probabilities for maturing are based on several successive steps, confidence limits cannot be calculated directly (Barot et al. 2002), and a bootstrap method was used instead (Manly 1997). A new dataset was created by randomly sampling original data (observations of individual fish), stratified by age and cohort, with replacement. With the re-sampled data the reaction norm midpoints were calculated by the procedure described above, steps 1-3. The dataset was re-sampled 1,000 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 1,000 midpoints of each age and cohort (Manly 1997).

(5) Trend analysis. 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:

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

The estimated midpoints were weighted with the inverse of the variance of each midpoint. The variance estimates were obtained from the bootstrapping method.

Effect of temperature

The effect of water temperature in the years preceding maturation on the reaction norms was analysed using a logistic 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 the model, describing the average water temperatures two and three years prior to the year for which the probability of maturation was calculated. Because temperature showed a significant trend (an average increase of 0.02°C per year; p=0.007) this trend was removed to deal with autocorrelation. We wanted to analyse the short-term effect of temperature on the maturation process and thus removed the long-term trend. For each age group, the effect of length, cohort, and the two resulting temperature residuals, denoted $R_{T\text{-}2}$ and $R_{T\text{-}3}$, was then analysed:

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

where length is a variate and cohort is a factor. The effect of temperature on the probability to mature was quantified by predicting L_{P50} for the whole range of observed temperature residuals per cohort and age group, using the model parameters. A different midpoint at different temperatures reflects a change in the probability to mature due to a change in temperature. The temperature residual $R_{T\text{-}1}$ was not included in the model because previous analysis (Rijnsdorp 1993b) had shown that the temperature in the year of maturation is not expected to influence the probability.

Results

Growth rates at ages 1, 2, and 3 significantly increased in 1955-1995 (R^2=0.48; P<0.0001) whereas growth rates in age group 5 decreased (p=0.0011; Figure 3). No trend at age 4 and 6 was observed (p>0.25). The increase at ages 1-3 averaged 0.03-0.04 cm year^{-2}, whereas the decrease at age 5 was 0.01 cm year^{-2}. Superimposed on these trends, growth at age 2 showed a clear temporal structure, with dips around 1965 and 1985 and peaks around 1974 and 1995.

Both age and length at 50 % maturity showed a significant decline (R^2=0.30 for age, R^2=0.40 for length; p<0.0001; Figure 4). On average, A_{50} decreased by about one year over a 40 year period, whereas L_{50} decreased by about 1 cm. Both showed a similar temporal structure with peaks around 1966 and 1985 and a dip around 1974.

The maturation reaction norms of plaice had 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_{P10} and L_{P90} varies between 13 and 17 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. 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 probability to mature due to both the shift in the reaction norm, and due to increased growth rates is illustrated in Figure 6.

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 7); 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, particularly at age 2.

In contrast to the age at 50 % maturity (A_{50}), L_{P50} showed no clear temporal structure, except perhaps at age 3, at which small peaks in L_{P50} occurred around 1963 and 1985 (Figure 8). Beyond the significant downward trend, the temporal structure in A_{50} rather faithfully mirrors temporal changes in growth rates at ages 1, 2, and 3. By contrast, the reaction norm midpoints (L_{P50}) only show a downward trend, in combination with some short-term fluctuations. These fluctuations could be partly explained by short-term variations in water temperature (Figure 9). For all ages, the probability of maturing at a given length increased significantly (p=0.0022 for age 6; p<0.0001 for all other ages) with an increase of temperature two and three years earlier. At age 2, for example, L_{P50} was 2.2 cm lower when the average water temperature in the second and third quarters two years earlier was 1 °C higher.

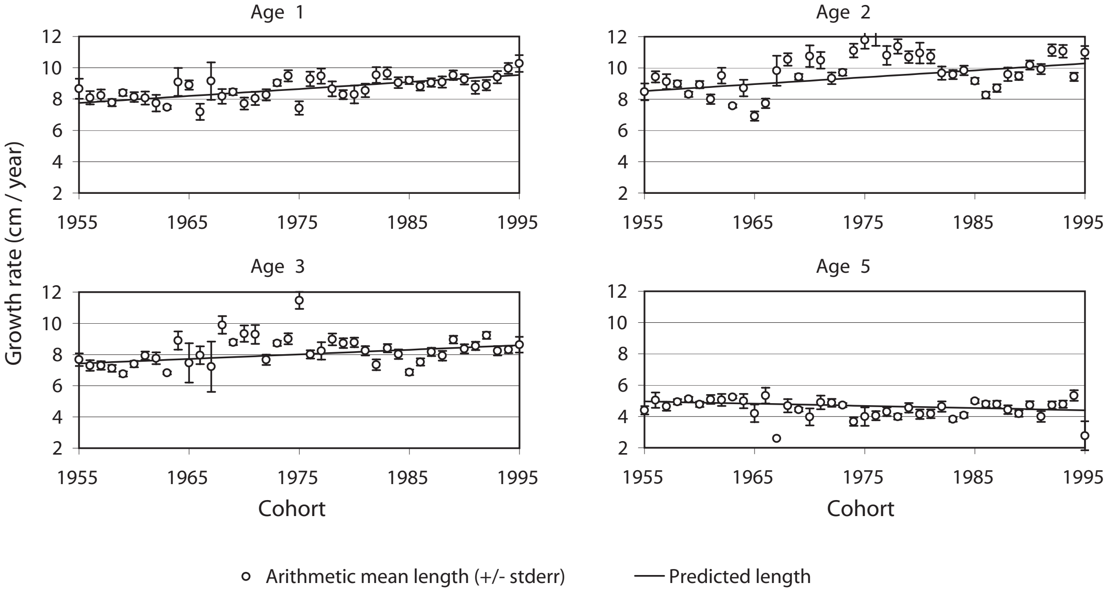

Figure 3. Trends in growth rates (lines) of ages 1, 2, 3, and 5. For these four ages the slopes of the regression lines were significantly different from 0 (linear model: Length ~ Age + Cohort × Age; where age is a factor and cohort is a variate; $p<0.005$; $R^2=0.48$; 11 d.f.; 12,725 observations). 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.

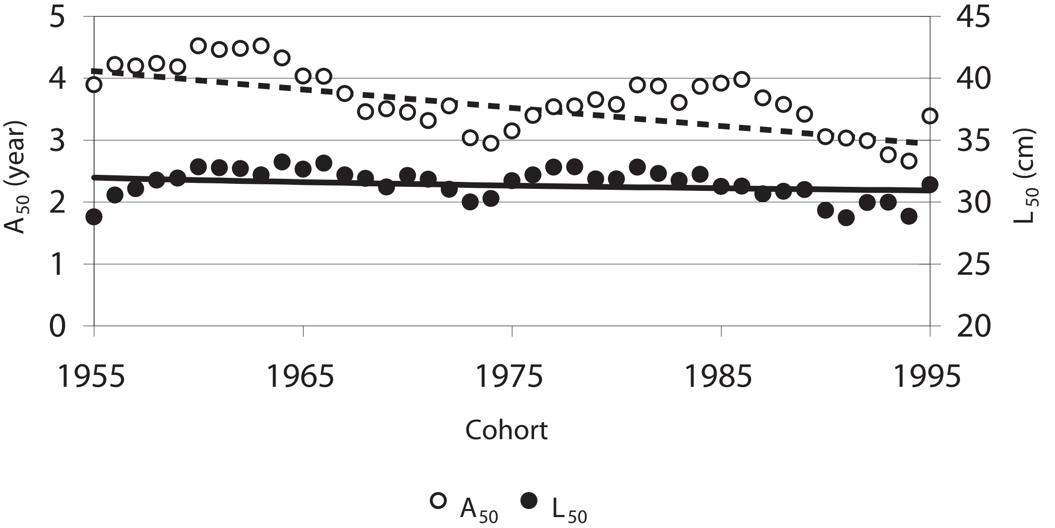

Figure 4. Trends in the age (A_{50}) and length (L_{50}) at which 50 % of fish are mature in each cohort. Data from logistic models with cohort either as a factor (open and filled circles; $R^2=0.34$ and 0.42 for age and length at maturation, respectively) or as a variate (dashed and continuous lines; $R^2=0.30$ and 0.40, respectively). In both cases, the decline of A_{50} and L_{50} with time (cohort) is significant ($p<0.0001$).

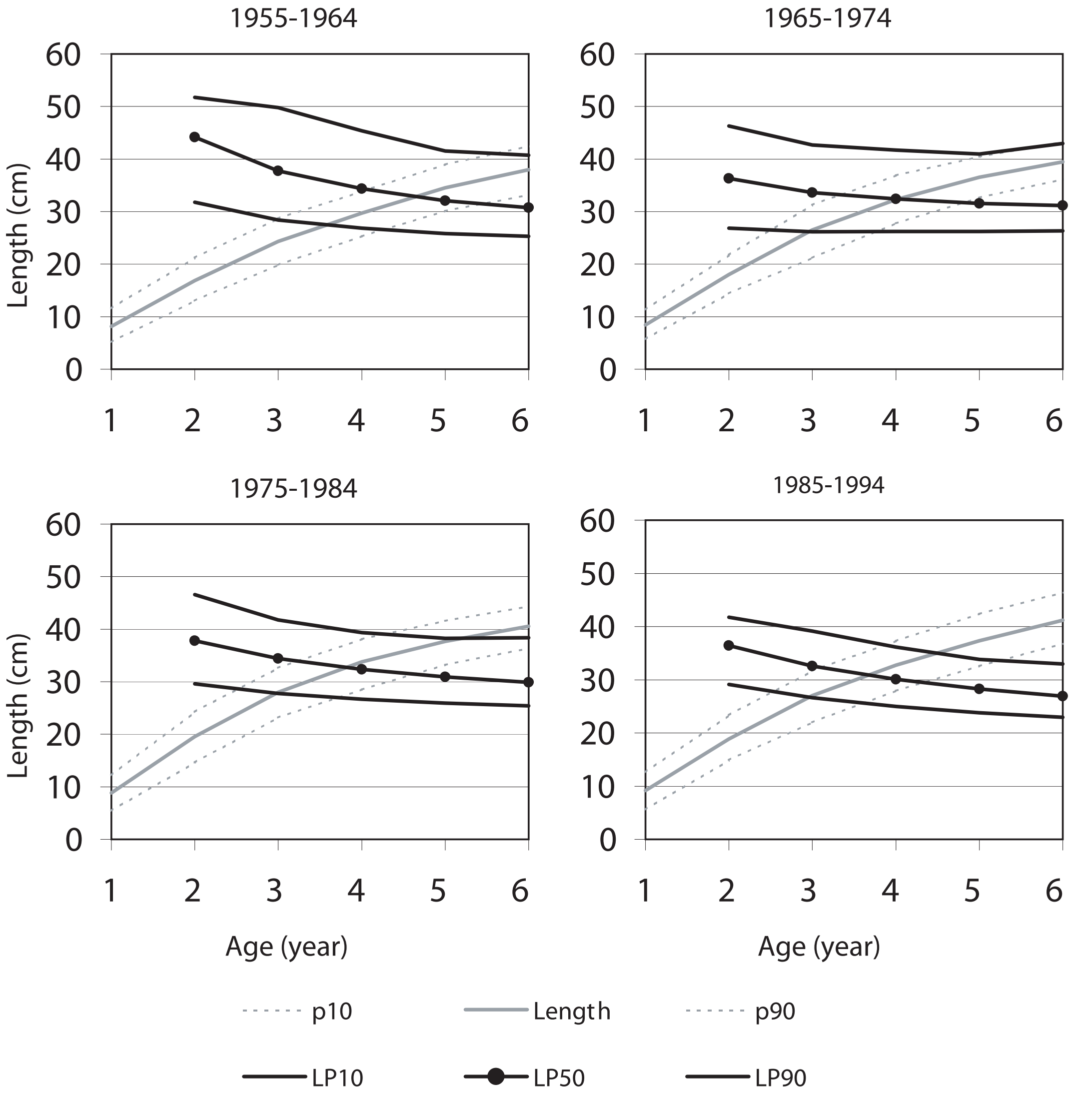

Figure 5. Maturation reaction norms and growth curves. The lengths at which the probability of maturing reaches 10, 50, and 90 % (L_{P10}, L_{P50}, and L_{P90}) are shown as continuous curves. Distributions of growth trajectories are depicted in terms of arithmetic mean length-at-age together with 10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

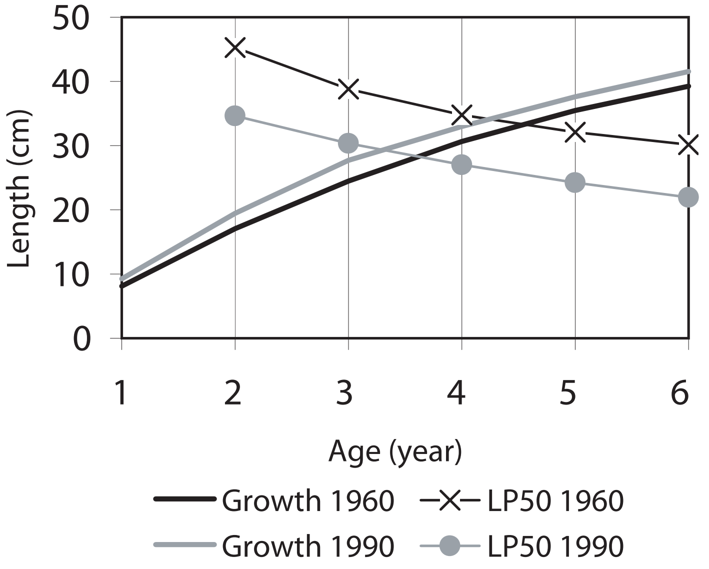

Figure 6. Reaction norm midpoints and growth curves for the cohorts of 1960 and 1990. From 1960 to 1990, the reaction norm has shifted downwards, while size-at-age has increased. For the cohort of 1990, growth curves thus hit the reaction norm at a lower age and smaller length, leading to earlier maturation at smaller length.

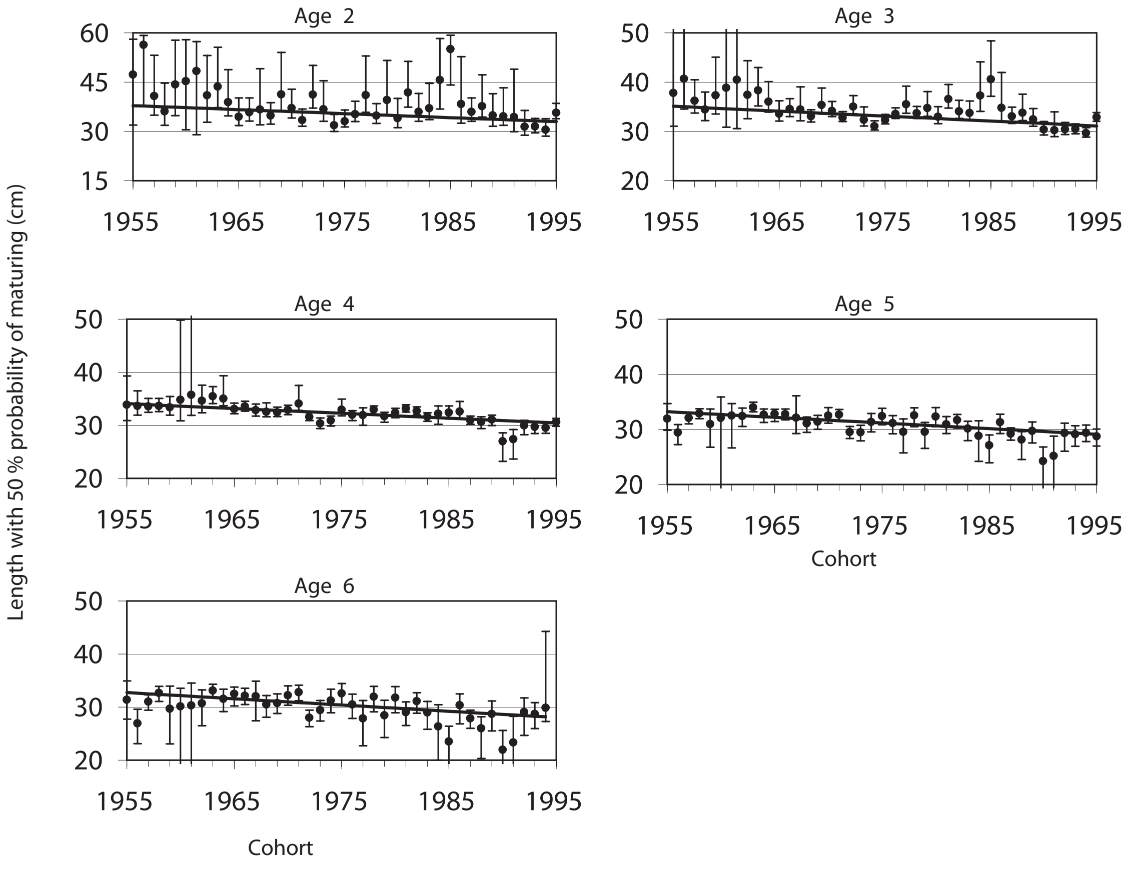

Figure 7. Reaction norm midpoints L_{P50} (filled circles) and 95 % confidence limits (error bars) for ages 2-6 of all cohorts. Trends in midpoints from the linear model in Equation (5) are shown by thick continuous lines. Notice that the scales of vertical axes vary with age.

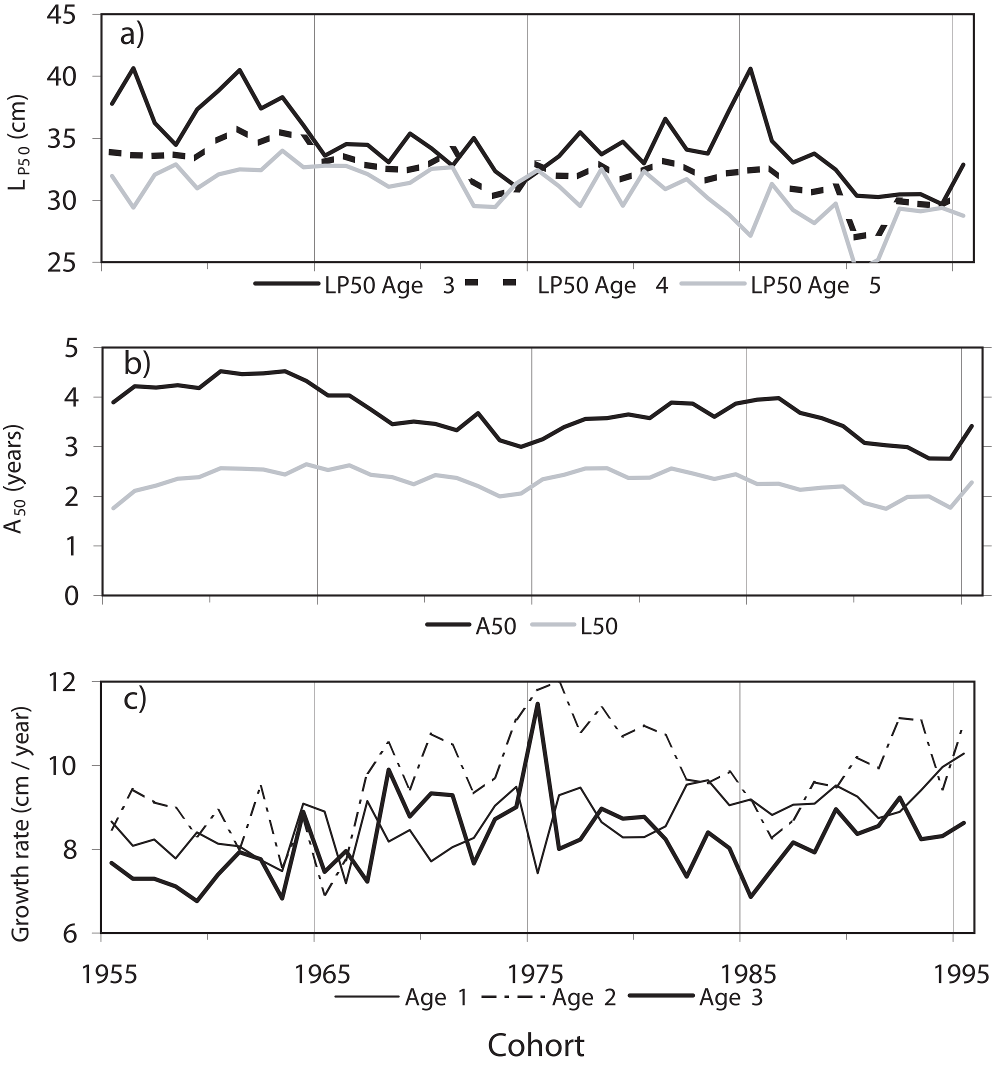

Figure 8. Trends in the North Sea plaice stock from 1955 to 1995. (a) Maturation reaction norm midpoints L_{P50} for three age groups. (b) Length L_{50} and age A_{50} at 50 % maturity. (c) Growth rates for three age groups.

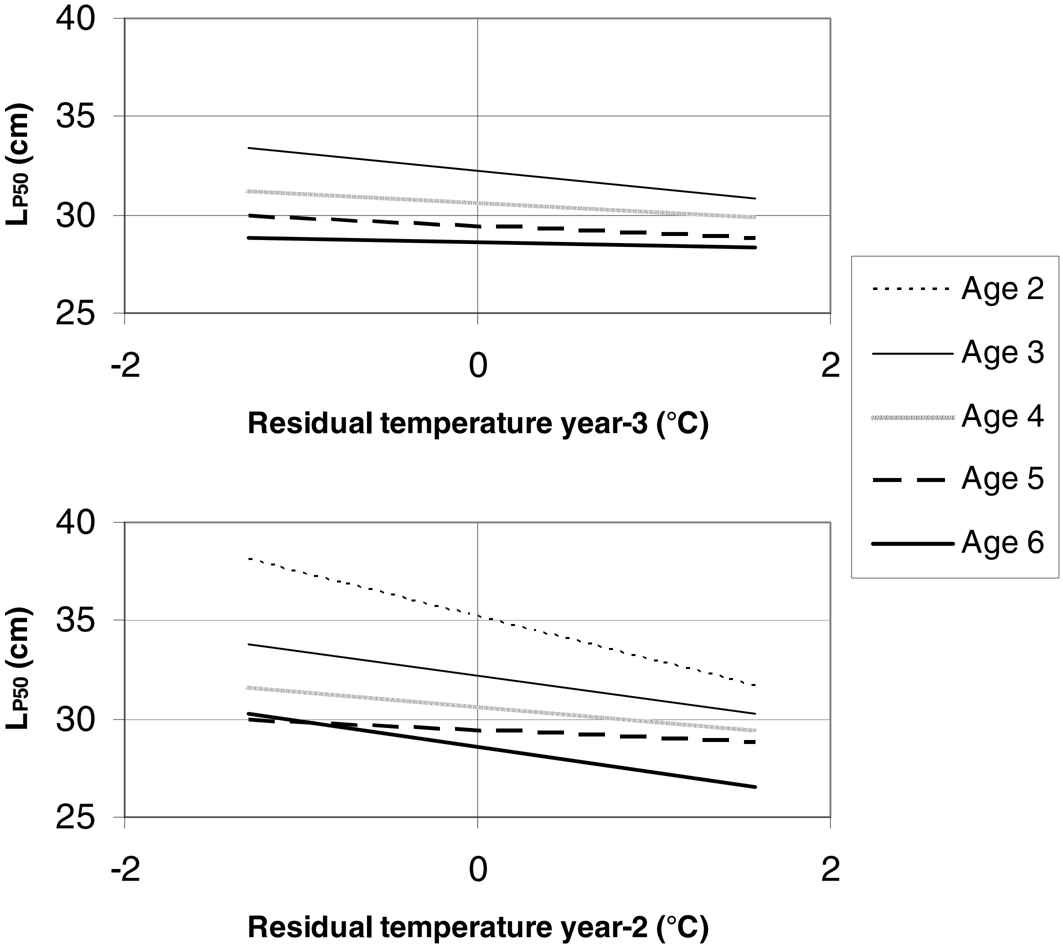

Figure 9. Effect of water temperature on reaction norm midpoints. The lines illustrate the effect of temperature (over the observed range of temperature residuals) on the change in the reaction norm midpoint L_{P50}. Data for cohort 1990.

Discussion

The significant gradual 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 over these 40 years. Through the phenotypic plasticity described by the reaction norm, the increased growth rates have led to an even earlier age at maturation, corroborating previous conclusions by Rijnsdorp (1993a) based on changes in maturity observed between the early and late 20th century.

In contrast to the traditional maturation metrics, age and size at 50% maturity, probabilistic reaction norms for age and size at maturation are not sensitive to variations in growth and mortality. This insensitivity has two reasons (Heino et al. 2002a,b). First, the reaction norm expresses maturation tendency as a probability conditional to having a certain age and size. Thus, the description of the maturation process is separated from the description of demographic processes that determine the likelihood of attaining a certain age and size. Second, reaction norms for age and size at maturation contain an ingrained measure of environment that is particularly relevant for maturation. The growth trajectory followed by an individual integrates all environmental factors that affect growth into a single object, size-at-age, which thus serves as a proxy of conditions favourable to the accrual of resources critical for growth and reproduction.

We consider fisheries-induced selection as the most likely explanation for the gradual change in the maturation reaction norms for North Sea plaice. However, with observational data only it is virtually impossible to proof that this is indeed the case.The downward trend in the reaction norms co-occurs with trends in temperature and in stock characteristics such as growth and spawning stock biomass (Figure 1). Could the trend in the reaction norms be explained by such trends? Above we have argued that reaction norms, by the very nature they are constructed, are not sensitive to variations in growth. Importantly, factors such as temperature and stock biomass are likely to influence growth and maturation similarly and therefore not to confound the analysis significantly. We have, nevertheless, uncovered a residual effect of temperature. However, the change in temperature over the study period is only about 0.9 °C and is insufficient to explain the trend. It remains to be explored whether there are density-related effects on maturation that are not manifested through growth.

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 and higher body growth. The short-term plastic responses could be partly explained by short-term variation in water temperature. High water temperatures are likely to favour earlier maturation either directly, via physiological effects, or indirectly, by indicating favourable environmental conditions. The positive effect of water temperature on the maturation process is in line with the results of Bromley (2000) who suggests that the higher temperature in the southern than in the northern North Sea causes maturation at earlier ages and smaller lengths of plaice. Our result that water temperature influences the probability to mature two to three years later corroborates the results of Rijnsdorp (1993b) that the maturation process of plaice may take up to three years: high growth rates three and two years prior to sampling were associated with higher fractions of mature plaice.

It remains unclear to which extent the increase in 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 (Imsland & Jonassen 2001, Conover & Munch 2002), it is unlikely that the short-term (decadal) fluctuations in growth rates we observed are a result of evolution (Rijnsdorp 1993a). Yet intensive size-selective fishing could have induced a longer-term evolutionary process selecting for lower growth rates, such that fish can delay their exposure to fishing (Ricker 1981, Kirkpatrick 1993, Conover & Munch 2002, Sinclair et al. 2002a, Sinclair et al. 2002b). For such selection to occur, survival benefits of smaller size must exceed the possible costs, e.g., lower fecundity (Heino & Godø 2002). Phenotypically, however, observed growth rates of plaice up to age 3 have increased, so that selection for low growth rates should have been over-compensated by much increased food abundance. Because 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 for investigating potential evolutionary responses 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 7 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). The growth rate of Atlantic silverside *Menidia menidia* evolved within just four generations in an experimental set-up in which fish were harvested size-selectively (Conover & Munch 2002). The selection differential for 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 the resulting biases should not be large and influence the interpretation of the results because the method has been shown to be robust in this respect (Barot et al. 2002). Growth rates of mature and immature female plaice differ significantly (Rijnsdorp 1993b), but differences are difficult to estimate. Because 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 because 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, because age and length at maturation of plaice show a slight longitudinal trend from south to north (Rijnsdorp 1989, Bromley 2000). We think, however, that these regional differences have no effect on our conclusion regarding evolutionary change in the stock, because the North Sea plaice stock can be considered as being genetically homogeneous (Hoarau et al. 2002).

The 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), and therefore the management regime imposed. First, fisheries-induced evolution is likely to decrease potential yield (Law & Grey 1989, Hutchings 1993b, Stokes & Law 2000), and, second, finding practical 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) because 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 & 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. Although spawning stock biomass may increase, because more fish are mature, an increased spawning stock biomass does not necessarily lead to higher recruitment, because 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.

References

Barot S, Heino M, O'Brien L, Dieckmann U (2002) Estimating reaction norms for age and size at maturation without first-time spawner data. Report No. IR-02-011, IIASA, Laxenburg

Borisov VM (1978) The selective effect of fishing on the population structure of species with long life cycle. Journal of Ichthyology 18:896-904

Bromley PJ (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 HI (2000) Application of evolutionary theory to fisheries science and stock assessment-management. Marine Ecology Progress Series 208:299

Conover DO (2000) Darwinian fisheries science. Marine Ecology Progress Series 208:303-307

Conover DO, Munch SB (2002) Sustaining fisheries yields over evolutionary time scales. Science 297:94-96

Haugen TO, Vøllestad LA (2001) A century of life-history evolution in grayling. Genetica 112-113:475-491

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

Heino M, Godø OR (2002) Fisheries-induced selection pressures in the context of sustainable fisheries. Bulletin of Marine Science 70:639-656

Heino M, 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 AD, Van Der Veer HW, Stam WT, Olsen JL (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 JA (1993a) Adaptive life histories effected by age-specific survival and growth rate. Ecology 74:673-684

Hutchings JA (1993b) Reaction norms for reproductive traits in brook trout and their influence on life history evolution affected by size-selective harvesting. In: Stokes TK, McGlade JM, Law R (eds) The exploitation of evolving resources. Springer Verlag, Berlin- Heidelberg, p 107-125

ICES (2002) Report of the working group on the assessment of demersal stocks in the North Sea and Skagerrak. Report No. ICES CM 2002/ACFM:01, ICES, Copenhagen

Imsland AK, Jonassen TM (2001) Regulation of growth in turbot (*Scophthalmus maximus* Rafinesque) and Atlantic halibut (*Hippoglossus hippoglossus* L.): aspects of environment × 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: Stokes TK, McGlade JM, Law R (eds) The exploitation of evolving resources. Springer Verlag, Berlin- Heidelberg, p 145-154

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

Law R, Grey DR (1989) Evolution of yields from populations with age-specific cropping. Evolutionary Ecology 3:343-359

Manly BFJ (1997) Randomization, bootstrap and monte carlo methods in biology, Chapman & Hall, London

Murawski SA, Rago PJ, Trippel EA (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 TJ, Rashid Sumaila U, Walters CJ, Watson R, Zeller D (2002) Towards sustainability in world fisheries. Nature 418:689-695

Reznick DN (1983) The structure of guppy life histories: the tradeoff between growth and reproduction. Ecology 64:862-873

Reznick DN (1993) Norms of reaction in fishes. In: Stokes TK, McGlade JM, Law R (eds) The exploitation of evolving resources. Springer Verlag, Berlin- Heidelberg, p 72-90

Reznick DN, Bryga H, Endler JA (1990) Experimentally induced life-history evolution in a natural population. Nature 346:357-359

Reznick DN, Shaw FH, Rodd FH, Shaw RG (1997) Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). Science 275:1934-1936

Ricker WE (1981) Changes in the average size and average age of Pacific Salmon. Canadian Journal of Fisheries and Aquatic Sciences 38:1636-1656

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

Rijnsdorp AD (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 AD (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 AD (1993c) Selection differentials in male and female North Sea plaice and changes in maturation and fecundity. In: Stokes TK, McGlade JM, Law R (eds) The exploitation of evolving resources. Springer Verlag, Berlin- Heidelberg, p 19-36

Rijnsdorp AD, Buys AM, Storbeck F, Visser EG (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 AD, Millner RS (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 AD, Van Leeuwen PI (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 AD, Van Leeuwen PI (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 AD, Van Leeuwen PI, Visser TAM (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 MJ, Cornillon PA, Sabatier R, Pontier D (2000) Comparative analysis of phylogenetic and fishing effects in life history patterns of teleost fishes. Oikos 91:255-270

Roff DA (1991) The evolution of life-history variation in fishes, with particular reference to flatfishes. Netherlands Journal of Sea Research 27:197-207

Rollefsen G (1933) The otoliths of the cod. Fiskeridirektoratets Skrifter Serie Havundersøkelser 4:1-18

Rowell C (1993) The effects of fishing on the timing of maturity in North Sea Cod (*Gadus morhua* L.). In: Stokes TK, McGlade JM, Law R (eds) The exploitation of evolving resources. Springer Verlag, Berlin- Heidelberg, p 44-61

Royston P, Altman DG (1994) Regression using fractional polynomials of continuous covariates: parsimonious parametric modelling. Applied Statistics 43:429-467

Siems DP, Sikes RS (1998) Tradeoffs between growth and reproduction in response to temporal variation in food supply. Environmental Biology of Fishes 53:319-329

Sinclair AF, Swain DP, Hanson JM (2002a) Disentangling the effects of size-selective mortality, density, and temperature on length-at-age. Canadian Journal of Fisheries and Aquatic Sciences 59:372-382

Sinclair AF, Swain DP, Hanson JM (2002b) Measuring changes in the direction and magnitude of size-selective mortality in a commercial fish population. Canadian Journal of Fisheries and Aquatic Sciences 59:361-371

Stearns SC (1992) The evolution of life histories, Oxford University Press, New York

Stearns SC, Koella JC (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 TK, Law R (2000) Fishing as an evolutionary force. Marine Ecology Progress Series 208:307-309

Trippel EA (1999) Estimation of stock reproductive potential: history and challenges for canadian Atlantic gadoid stock assessments. Journal of Northwest Atlantic Fishery Science 25:61-81