Reaction norm analysis of fisheries-induced adaptive change and the case of the Northeast Arctic cod

Mikko Heino, Ulf Dieckmann and Olav Rune Godø

We present a probabilistic concept of reaction norms for age and size at maturation, and outline methods that can be used for their estimation in typical fisheries data. Such estimations are critical for calibrating size- and age-structured population models, for understanding phenotypic plasticity and life-history changes in variable environments, and for assessing genetic changes in the presence of phenotypic plasticity. We apply the method of reaction norm estimation to a set of measurements on Northeast Arctic cod collected between 1932 and 1998. This cod stock has shown a drastic reduction in age at maturation. In the 1930's, age at maturation was typically around 10-11 years, whereas nowadays seven years is more usual. This change has been attributed both to fisheries-induced genetic selection for earlier maturation, and to a compensatory response caused by faster individual growth rate. However, previous analyses have been unable to disentangle these hypotheses. Our analysis, based on estimation of maturation reaction norms, shows that both increase in growth rate and change in age- and size-specific tendency to mature have contributed to the observed trend towards earlier maturation. The latter component probably represents a fisheries-induced adaptive genetic change.

Key words: evolution, fisheries-induced change, age and size at maturation, phenotypic plasticity, reaction norms.

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1. Introduction

Fishing is a major source of food and other resources for humankind. Today most marine fish stocks are heavily exploited, and many are overexploited. Exploitation has well-understood and documented consequences on the target populations: as the result of increased mortality, stock numbers and biomass are decreased, and population's age structure is shifted towards the dominance of younger individuals. Often individual growth increases when stock biomass declines (Lorenzen and Enberg 2002), presumably as the consequence less intensive inter-specific competition — the so-called 'compensatory growth'. Furthermore, exploited populations show frequently a trend towards earlier age at maturation (Trippel 1995, Rochet 1998, Law 2000). The reasons for this phenomenon, however, remain poorly understood. At least two, non-exclusive hypotheses have been proposed. First, earlier maturation is a phenotypically plastic response. When growth rate increases, fish attain the size required for maturation earlier. This hypothesis presumes the presence of compensatory growth, and may be referred to as the 'compensatory response hypothesis'. The second hypothesis states that earlier maturation is an evolutionary response to increased mortality. Under high mortality risk, the expected number of spawnings becomes very small for late-maturing individuals, and natural selection favours early-maturing phenotypes, even if these have lower age-specific fertility.

One of the most drastic reductions in age at maturation has occurred in Northeast Arctic cod (*Gadus morhua*), one of the commercially most important fish stocks in the North Atlantic. In the 1930's, age at maturation was typically around 10-11 years, whereas seven years is nowadays more typical (Fig. 1). Average length at maturation has decreased in parallel with age at maturation. In common with other examples of life history changes in exploited populations, the reasons of the downward trend in maturation of Northeast Arctic cod remain unquantified and controversial. The evolutionary explanation was put forward more than two decades ago (Borisov 1978), and it is supported by insight from life history theory (Roff 1992, Stearns 1992) as well as by modelling specific for Northeast Arctic cod (Law and Grey 1989, Heino 1998). However, body growth has increased in this stock (Fig. 2), and fast-growing cod are known to mature at early age (Godø and Moksness 1987). Thus, phenotypically plastic change in maturation is also a plausible explanation, often considered more parsimonious than genetic change (e.g. Jørgensen 1990). The difficulty is that the predictions from both hypotheses are similar.

Disentangling phenotypic plasticity and genetic effects in maturation is a challenging task. One potential pathway is a careful analysis of various environmental effects on maturation, and assigning the residual trend to genetic change (Rijnsdorp 1993). Another possibility is to use reaction norms for age and size at maturation (Reznick 1993, Heino et al. 2002a,b). The idea that maturation reaction norms can be used to disentangle phenotypic plasticity and genetic effects in maturation can be traced back to Stearns and Crandall (1984) and Stearns and Koella (1986). Probabilistic extension of the original, essentially deterministic concept has made the reaction norm approach more operational (Heino et al. 2002a). However, attempts to utilize maturation reaction norms in analysing time series data have only now started.

The reaction norm for age and size at maturation is defined as the probability that immature fish mature during a given time interval and at a certain age and size (Heino et al., 2002a). A description of the entire reaction norm involves specifying these probabilities for all relevant ages and sizes. Notice that maturation probability is conditional on having reached a certain age and size. This conditioning is crucial for separating the description of the maturation process from describing the processes of growth and survival; the latter two determine the

probability of fish attaining a certain age and size. The tendency to mature, described by the reaction norm, is assumed to be under genetic control. Even though the estimation of maturation reaction norms will be subject measurement error and residual environmental effects, continual trends in the maturation reaction norm are strongly indicative of a genetic change.

In this paper we utilize maturation reaction norms for studying the temporal trends in maturation of Northeast Arctic cod in 1932-1998. Ideally, estimation of maturation reaction norms is based on representative samples of both immature and maturing (or first-time spawning) individuals. Unfortunately, representative measurements on immature cod are not available prior to 1984. However, estimation of maturation reaction norms is made possible by reconstructing the size distributions of immature cod (Heino et al. 2002b). With data on first-time spawning cod and reconstructed immature cod, we aim at disentangling genetic change and phenotypically plasticity in the long-term time series on Northeast Arctic cod.

2. Material and methods

We use life history data on cod that have been collected by the Institute of Marine Research (Bergen, Norway). The data on length and age of first-time spawners amount to 74,261 individually measured fish sampled from the commercial longline catches at the Lofoten spawning grounds in 1932-1998 during the main spawning season (January – April). This is the same dataset as the one used by Godø (2000), and more information on the sampling and data selection can be found in that paper. Sampled fish have been measured for total body length, and their age was determined by otolith readings. First-time spawners can be determined and distinguished from repeat spawners on the basis of otolith patterns and the maturity status of gonads (Rollefsen, 1933; Jørgensen, 1990). Notice that although the maturation process is initiated already in the summer before first spawning, we equate age at maturation and first spawning.

Immature size distributions were reconstructed with a back-calculation method (Heino et al. 2002b) based on the observed size distributions of mature fish, maturity ogive, and the assumptions of linear immature growth and equal mortality among the juvenile and maturing individuals within an age class. We used the maturity ogive by Jørgensen (1990) for cohorts 1923-1937, and a maturity ogive made available by A. Ajiad and T. Jakobsen (pers. comm., IMR, Bergen) for the cohorts 1938-1990.

Only maturation ages from 5 to 12 years that are present in decent numbers and over reasonable periods of time were included in the analysis. Furthermore, samples of less than 25 first-time spawners of certain age and cohort were omitted because reconstruction of immature size distributions with very small samples is not robust. Notice that within a cohort, reconstruction allows obtaining immature size distribution for the last but one maturation age and earlier – therefore, maturation age 12 does not appear in the results.

Numerical robustness analysis has shown that the overall effect of the simplifying assumptions of the reconstruction method is unlikely to introduce a significant bias to the reconstructed size distributions (Heino et al. 2002b). However, violation of the assumptions may increase the amount of noise. In particular, even though the assumption that average growth trajectories are linear is justified in immature cod (Jørgensen 1992), deviations will occur when environmental conditions change rapidly (cf. Fig. 2). These deviations cause biases, which, when large enough, may lead to biologically inconsistent results that should be discarded. Therefore, the means and standard deviations of the size distributions of juveniles and

first-time spawners were compared to control for the quality of the reconstructed data. This allows detecting two types of inconsistencies that may arise in the reconstruction. First, juveniles were on average larger than those individuals that matured (nine cases). Second, bimodality, diagnosed as the standard deviations of the two distributions being non-overlapping (five cases). Altogether 14 cases (6.5%) were omitted as inconsistent, leaving data with 200 different combinations of age and year class. Problems in the data tend to occur in the more recent data: of the 14 omitted cases, eight were from the 80's and 90's. Most of these cases coincide with abrupt changes in growth (Fig. 2). The remaining cases can probably be ascribed to unrepresentative samples.

Reaction norms were estimated with logistic regression, which is a generalized linear model with logit link function and binomial error distribution (e.g. Collett 1991). The simplest biologically reasonable model involves only size as an explanatory variable:

$$\text{logit}(p) = c_0 + c_1 \text{ size}, \tag{1}$$

where p is the probability of maturing, logit(p) the logit-transformation $\log_e[p/\{1-p\}]$, and c_0 and c_1 are the two parameters to be estimated. In practice, the right hand side of the equation (1) will often include other explanatory variables such as age and cohort (see Heino et al. 2002a for biological interpretation of various logistic regression models for maturation reaction norms).

The data are treated as grouped binary data, that is, the response variable is the proportion mature individuals among the individuals in the sample unit. Williams' procedure is used to tackle with overdispersion (Collett 1991). We use likelihood ratio tests to compare models when parameters are included or removed from the model. The adequacy of models was judged by examination of residuals against explanatory variables, normal probability plots of residuals, and standard errors of parameter estimates.

Abundance estimates of Northeast Artic cod are available from 1946 onwards and have been obtained from "Virtual Population Analysis" runs as described by the ICES Arctic Fisheries Working Group (ICES, 2001). Abundance estimates of capelin (*Mallotus villosus*) in the Barents Sea are based on acoustic surveys. These data go back to 1974 (ICES, 2001). Both cod and capelin abundance estimates reflect the situation in the beginning of a year. Temperature data from 1932 onwards are taken from the Kola hydrographic section that runs north from the Kola Fjord along 33° 30' E and into the central Barents Sea. We have utilized annual averages based on monthly measurements for the 0-200 m depth interval. The observations are collected by the Knipovich Polar Research Institute of Marine Fisheries in Murmansk, Russia, and were made available through the Institute of Marine Research (see, e.g. Loeng, 1989). An index of annual growth of immature and maturing cod is available for 1932-1997 (M. Heino, F. Vinje, U. Dieckmann and O. R. Godø, unpublished). The index is based on the data on first-time spawning cod and is calculated by assuming that size at maturation is achieved through annual growth increments of equal size, assigning the obtained increments to years, and calculating yearly averages from values originating from different cohorts and ages at maturation.

3. Results

3.1 Preliminaries

Average size of first-time spawners and immature Northeast Arctic cod — the latter based on the reconstruction method — are illustrated in Figure 3. As expected, average size increases with age both for immature cod and for first-time spawners, with immature cod being on average 5cm shorter than first-time spawners. The youngest maturation ages (or 'maturation cohorts', sensu Beverton et al. 1994) display stable average size, but sizes of individuals maturing at ages 8-11 show clear upward trends. This observation is seemingly at odds with decreasing cohort-specific mean size at maturation. However, as indicated by the appearance of individuals maturing early and the disappearance of individuals maturing late, age distribution of first-time spawners is gradually shifting towards younger mean age, and consequently, smaller size. Therefore, the trends in Fig. 3 probably largely manifest increased growth rate. Meanwhile, the potential contribution of genetic changes to these trends remains uncertain.

Figure 4 shows probability of maturing at different ages, given that an individual is immature in the previous season. This probability is obtained directly from the maturity ogive with the equation $m(a)=[o(a)-o(a-1)]/[1-o(a-1)]$, where $m(a)$ denotes the probability of maturation at age a, and $o(a)$ is the proportion of mature individuals at age a (Heino et al. 2002b). The trend towards higher maturation probability within each age is obvious. However, interpretation of this finding is ambiguous because it is not possible to disentangle the effects of increasing size-at-age (cf. Figs. 2-3) and (potential) genetic change in the tendency to mature.

3.2 Reaction norm analysis of age and size at maturation

Maturation reaction norms for the cohorts 1932 and 1989 are shown in Fig. 5. These reaction norms are illustrated by their midpoints, defined as the size at which maturation occurs with a probability of 50%, and the lower and upper quartiles where maturation probability is 25 and 75%, respectively. The reaction norms overlap only for age 8. The 1989 reaction norm lies below the 1932 for this age. Thus, the size specific maturation probability has slightly increased, although the difference is not significant in this particular case.

Variability in the data makes independent estimation of both the shape and the position of the maturation reaction norms unrobust. Robustness of the analysis is improved by assuming that the reaction norms have a common shape across all cohorts. Therefore, the following logistic model was estimated for each maturation age:

$$\text{logit } (p) = c_0 + c_1 \text{ size} + c_{2,i} \text{ cohort}_i \,, \tag{2}$$

where cohort is treated as a factor (i.e., a categorical variable). This model allows the position, but not the shape, of reaction norm to vary freely among cohorts. The effects of size and cohort are statistically significant for all ages ($p<0.001$). However, the standard errors of parameter estimates are often high, and the estimated reaction norm midpoints show considerable variability (Fig. 6). Nevertheless, for ages 7-9 the trend towards higher probability of maturation at size is obvious.

Significance of the temporal trend is tested by treating cohort effect as a continuous variate. The following logistic model describes the data adequately:

$$\text{logit } (p) = c_0 + c_1 \text{ size} + c_{2,i} \text{ age}_i + c_3 \text{ cohort} + c_{4,i} (\text{size} \times \text{age}_i) + c_5 (\text{size} \times \text{cohort}), \tag{3}$$

where age is a factor. This model constrains the differential dependence of shape and position on cohort at different ages because the interactions "age × cohort" and "size × age × cohort" are not included. Including the interaction between age and cohort decreases the deviance significantly ($\chi^2=143.6$, d.f.=6, $p<0.001$), but the parameter estimates corresponding to the inter-

action term have large standard errors. Therefore, the model was not considered adequate, and the interaction was not included in the final model.

The effect of cohort on the maturation reaction norm is highly significant (Table 1) Thus, the tendency to mature at a certain age and size has changed. Significant autocorrelation in the residuals ($r=0.419$, $n=61$, $p=0.001$) suggests that the test for the trend can be too optimistic, but this does not alter our conclusions given the very low significance probabilities. The reaction norms have gradually been shifting downward, and the observed age range has moved towards younger ages (Fig. 7). The downward trend in the midpoints for different maturation ages is also clearly visible. The results indicate that the trend was initially weak, but has been getting stronger during the later decades. Correlation analysis of the residuals indicates that the variation around the main trend is influenced by feeding conditions of immature cod (Table 2): maturation probabilities are higher in years with low cod abundance and/or high capelin abundance. In contrast, temperature and growth have no effect.

Table 1. Analysis of temporal trend in the maturation reaction norms of Northeast Arctic cod. Statistical significance of the terms that include "Cohort" show the presence of temporal trend. Testing the significance of length effect is not possible because of the interaction term with age.

Term	χ^2	d.f.	p
Constant		1	
Length		1	
Age	423.3	6	<0.001
Cohort	478.9	1	<0.001
Length $\times$ Age	476.7	6	<0.001
Length $\times$ Cohort	373.3	1	<0.001
Residual		7548	

Table 2. Correlations of residuals with environmental variables. Residuals are deviance residuals from the model that includes linear cohort effect (equation 3). Relative capelin availability is the ratio of capelin abundance to biomass of immature cod.

Variable, year t	Residuals, year t-1			Residuals, year t		
	r	n	p	r	n	p
Temperature	-0.011	63	0.934	0.241	64	0.055
Biomass of immature cod	**-0.317**	49	0.026	-0.201	50	0.163
Biomass of mature cod	0.100	49	0.493	0.153	50	0.289
Capelin abundance	0.174	22	0.439	**0.460**	23	0.027
Relative capelin availability	0.349	22	0.112	**0.682**	23	<0.001
Growth	-0.018	63	0.886	0.138	64	0.278

3.3 Comparing the roles of phenotypic plasticity and changing maturation reaction norms

The significant trend in the maturation reaction norm shows that the tendency to mature at a certain age and size has changed. This, in turn, indicates that genetic changes in maturation characteristics have contributed to the observed phenotypic changes in maturation. Evidently, improved growth conditions must also have contributed to the change (see figure 2). Comparing the relative importance of these two effects on the observed changes in average age and size at maturation is intricate because they interact: the effect of growth change depends on the maturation reaction norm, and vice versa.

Insight can be gained with a simple modelling exercise. We use a model of maturation and growth dynamics described in an earlier paper (Heino et al. 2002b). In this model, a cohort of individuals are let to grow deterministically and mature stochastically, according to a speci-

fied probabilistic reaction norm. We emphasize that this model is meant to provide only qualitative insight, and that the description of dynamics is oversimplified (a more realistic approach is presented in Dieckmann et al. 2002). We study four different scenarios:

- Historical reaction norm and growth
- Present-day reaction norm and growth
- Change only in the reaction norm
- Change only growth regime

The latter two scenarios require information on the reaction norm at ages where maturation do not occur in the real data and thus cannot be estimated. Extrapolating the reaction norm to these ages requires that age be treated as a continuous variable. Furthermore, although maturation reaction norms for Northeast Arctic cod are slightly curved, models with a quadratic age term did not yield robust extrapolations. We therefore had to estimate reaction norms assuming a linear shape:

$$\text{logit} (p) = c_0 + c_1 \text{ size} + c_2 \text{ age.} \tag{4}$$

The reaction norms estimated with this model for the cohorts 1923-1927 ("historic") and 1986-1990 ("present-day") are shown in Fig. 8. The results of this exercise are presented in Table 3. Although the model predicts average age and length at maturation that are lower than observed (compared Figure 1 and Table 3), the total change is similar to the observed one. Reduction in age at maturation that occurs when only the reaction norm changes is almost as large as the reduction that occurs when both growth and reaction norm change, whereas the contribution from acceleration of growth is clearly smaller. With respect to length at maturation, the reduction that occurs when both growth and reaction norm change can attributed entirely to the change in reaction norm because accelerating growth has actually an opposite effect.

Table 3. Comparing the effects of changing growth and/or reaction norm on average age and length at maturation. "Historic" and "present" reaction norm and growth refer to the scenarios presented in figure 8. "Total change" is the difference in predicted values between the historic and present-day scenarios (i.e. historic reaction norm and growth vs. present reaction norm and growth). Percentages given in the "decomposition of the change" are relative to the total change.

	Age at maturation (yr)		Length at maturation (cm)	
	Growth regime			
Reaction norm	Historic	Present	Historic	Present
Historic	8.3	7.5	79.2	82.3
Present	6.3	5.8	60.0	64.3
Total change	-2.46		-14.94	
Decomposition of the change:				
Change only in growth	-2.0	33.9 %	3.1	-20.7 %
Change only in reaction norm	-0.83	81.4 %	-19.2	129 %
"Interaction"	0.38	-15.3 %	1.2	-7.9 %

Parameter values: standard deviation of length at age 4: 2.0cm; annual survival probability of immature and mature individuals σ=0.6; see figure 8 for growth and reaction norm; other parameters as in Heino et al. 2002b.

4. Discussion

We have shown in this paper that the reaction norm for age and size at maturation in Northeast arctic cod has changed significantly over the 20th century. This result indicates that the drastic reductions in age and length at maturation documented in this stock (Law & Grey 1989, Jørgensen 1990, Godø 2000) have a genetic basis, in addition to being partially attribut-

able to changes in growth regime. These results are similar to those obtained with reaction norm analysis in other fish stocks (Barot et al. 2002, Grift et al. 2002).

The results obtained here are in agreement with the predictions from the selection pressures that originate from shift in the mortality regime that occurred during the first half of the 20th century (Law and Grey 1989, Heino 1998, Ernande et al. 2002). Intensive harvesting has historically taken place in the spawning grounds. By delaying maturation, individual cod could postpone their exposure to increased mortality risk while gaining in terms of increased size and, after maturation, increased fecundity. This historical selection pressure for delayed maturation may even be responsible for the late maturation traditionally observed in this stock (Law and Grey 1989). Since around 1930, however, when the modern trawler fishery at the feeding grounds started, the harvest pattern has changed such that harvesting is largely non-selective with respect to maturity. This change resulted in strong selection for earlier maturation.

Although environmental effects that are not considered in the reaction norm analysis may confound the analysis presented here, it is probable that the change in reaction norms of the northeast Arctic cod has a genetic basis. However, phenotypic plasticity (in form of the so-called 'compensatory response', i.e., maturation at earlier age because of higher growth rate) also contributes to the change. Nevertheless, our modelling exercise indicates that most of the reduction in age at maturation can be attributed to change in the reaction norm (i.e., conceivable genetic change). Moreover, the reduction in length at maturation may be entirely caused by the change in maturation reaction norm.

Our results seem to confirm the concerns, based on both verbal arguments and models, that fisheries are causing genetic changes in the exploited fish stocks (Borisov 1978, Favro et al. 1979, Ricker 1981, Law and Grey 1989, Law and Rowell 1993, Rijnsdorp 1993, Rowell 1993, Heino 1998, Ratner & Lande 2001, Dieckmann et al. 2002, Ernande et al. 2002). Similar empirical evidence is currently becoming available in many fish stocks, as evidenced by this theme session. Genetic changes may not be easily reversed, even if they are considered undesirable from the human perspective. Managing fisheries-induced selection pressures is probably the most important new challenge that sustainable fisheries management is facing during this century.

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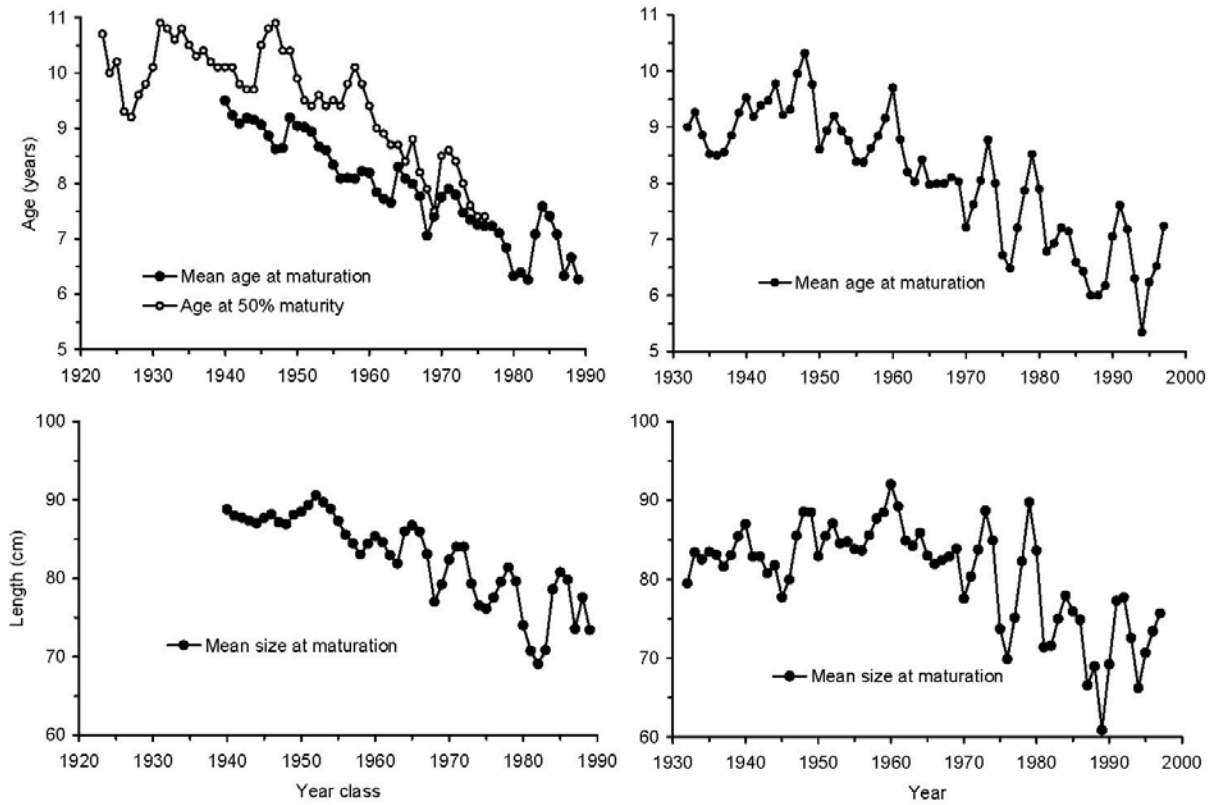
Figure 1. Age and length at maturation in Northeast Arctic cod. The time series are based on mature cod sampled at the spawning grounds during the period 1932-1998. Panels on the left show age and length at maturation for *cohorts* 1923-1989 according to Jørgensen (1990) and Godø (2000). The values are ages at which 50% of cohort is mature (Jørgensen) and cohort-specific average ages and sizes at maturation (Godø); see the original publications for the details on the underlying methods. Panels on the right show mean age and length at maturation for *years* 1932-1998, calculated as simple averages over all individuals sampled as first-time spawners in a given year.
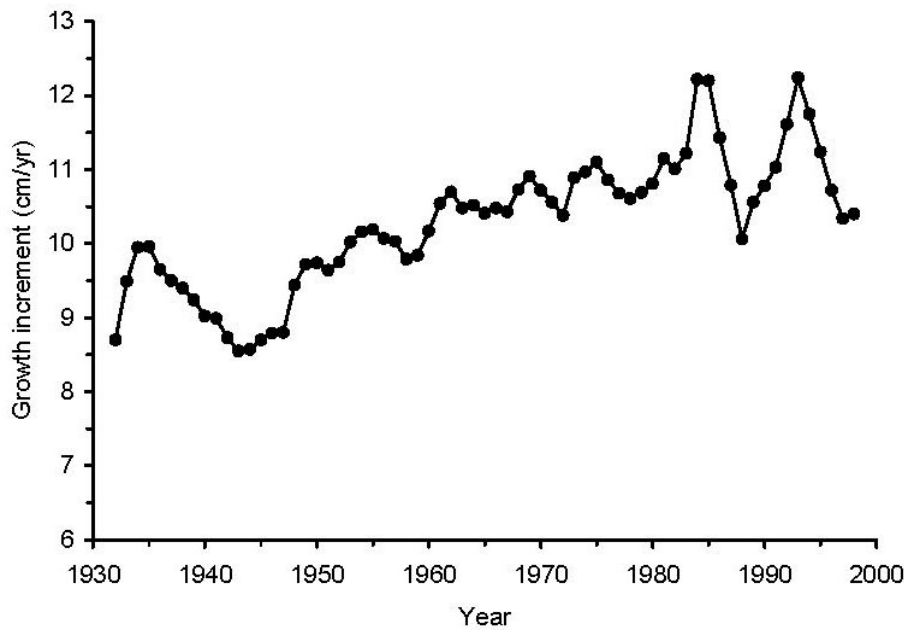
Figure 2. Index of annual growth of immature and maturing Northeast Arctic cod in 1932-1997 (M. Heino, F. Vinje, U. Dieckmann and O. R. Godø, unpublished).
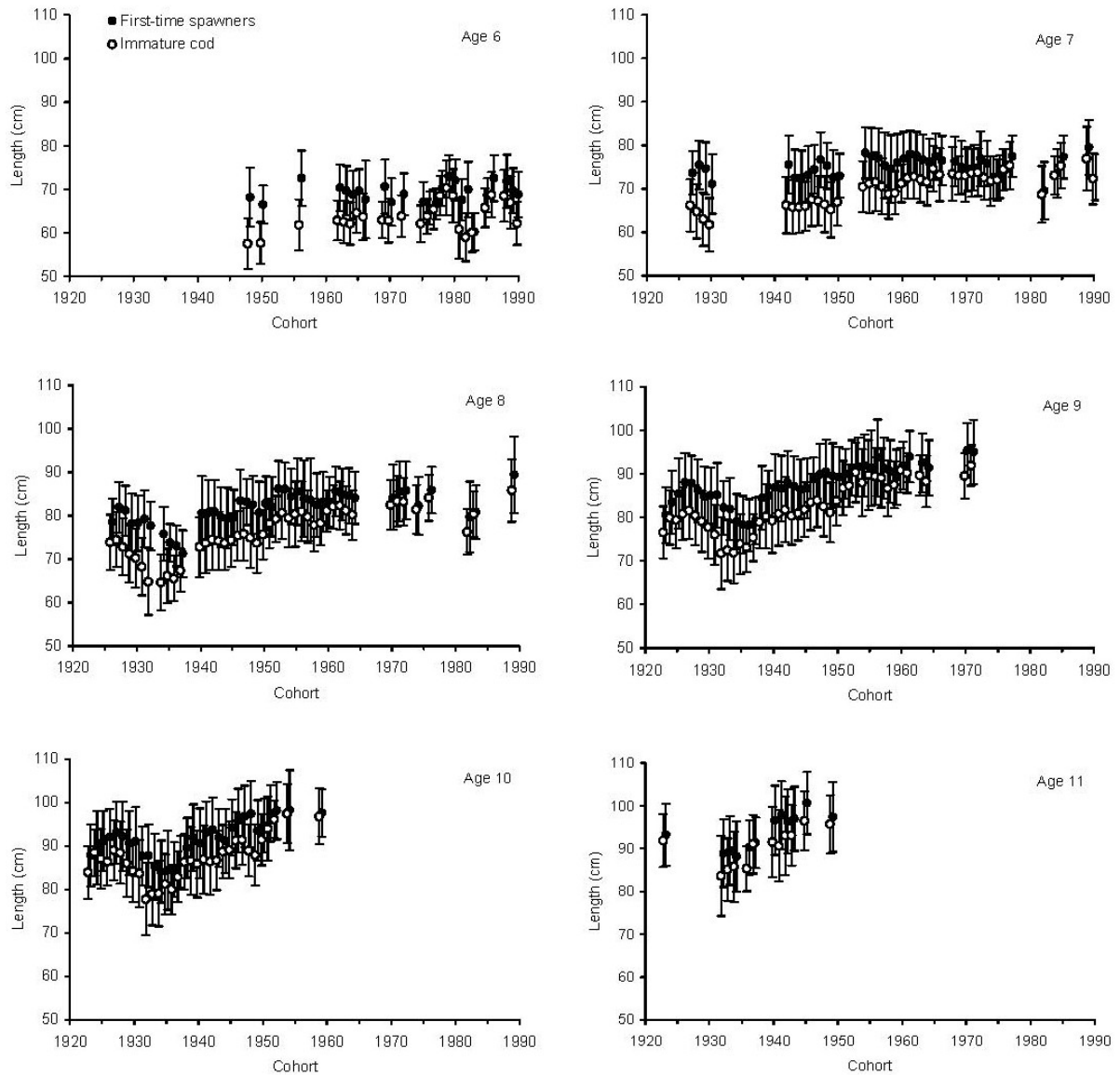
Figure 3. Average size of first-time spawners and immature Northeast Arctic cod in different matura-tion age groups. Vertical bars give the standard deviation. Age 5 is omitted from the figure because sufficient data was available only from three cohorts.
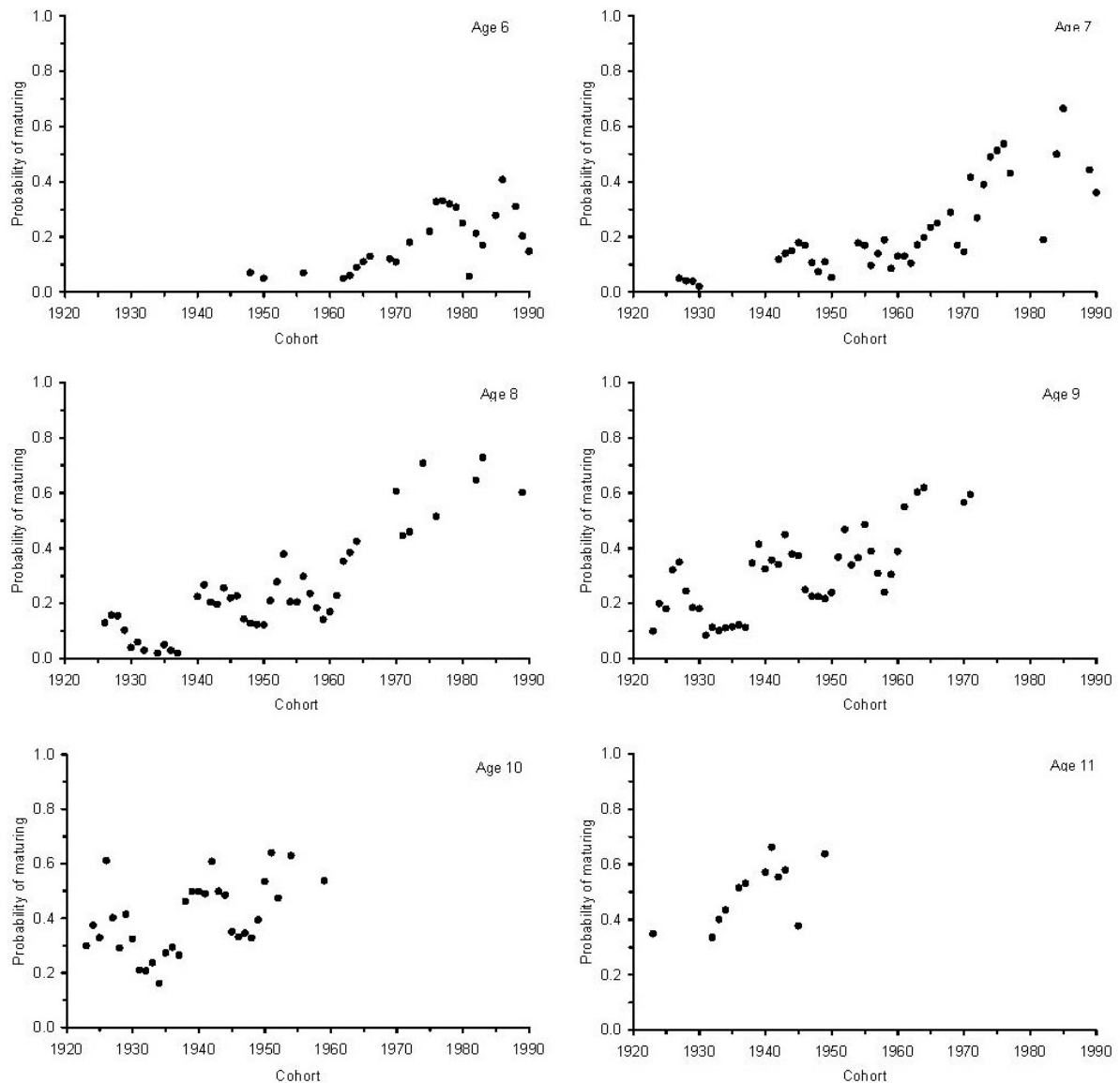
Figure 4. Age-specific maturation probabilities for immature Northeast Arctic cod estimated from the maturity ogive (see text for the estimation method).
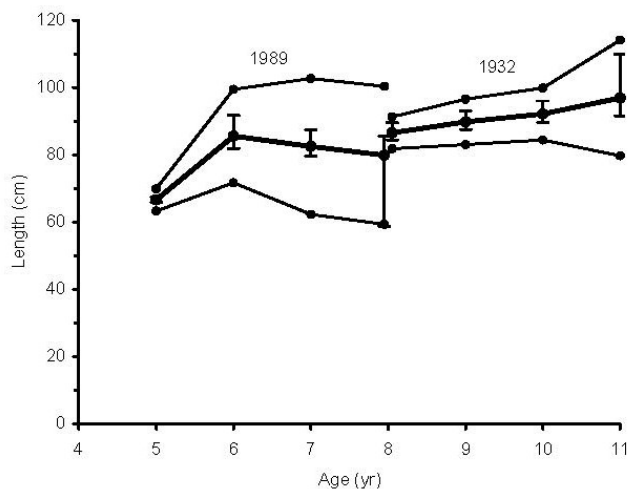

Fig. 5. Maturation reaction norms for Northeast Arctic cod cohorts 1932 and 1989. Thick lines with the 95% confidence limits give the midpoints of the reaction norms, i.e. the sizes where probability of maturing is 50%. The thin lines give the upper and lower quartiles.
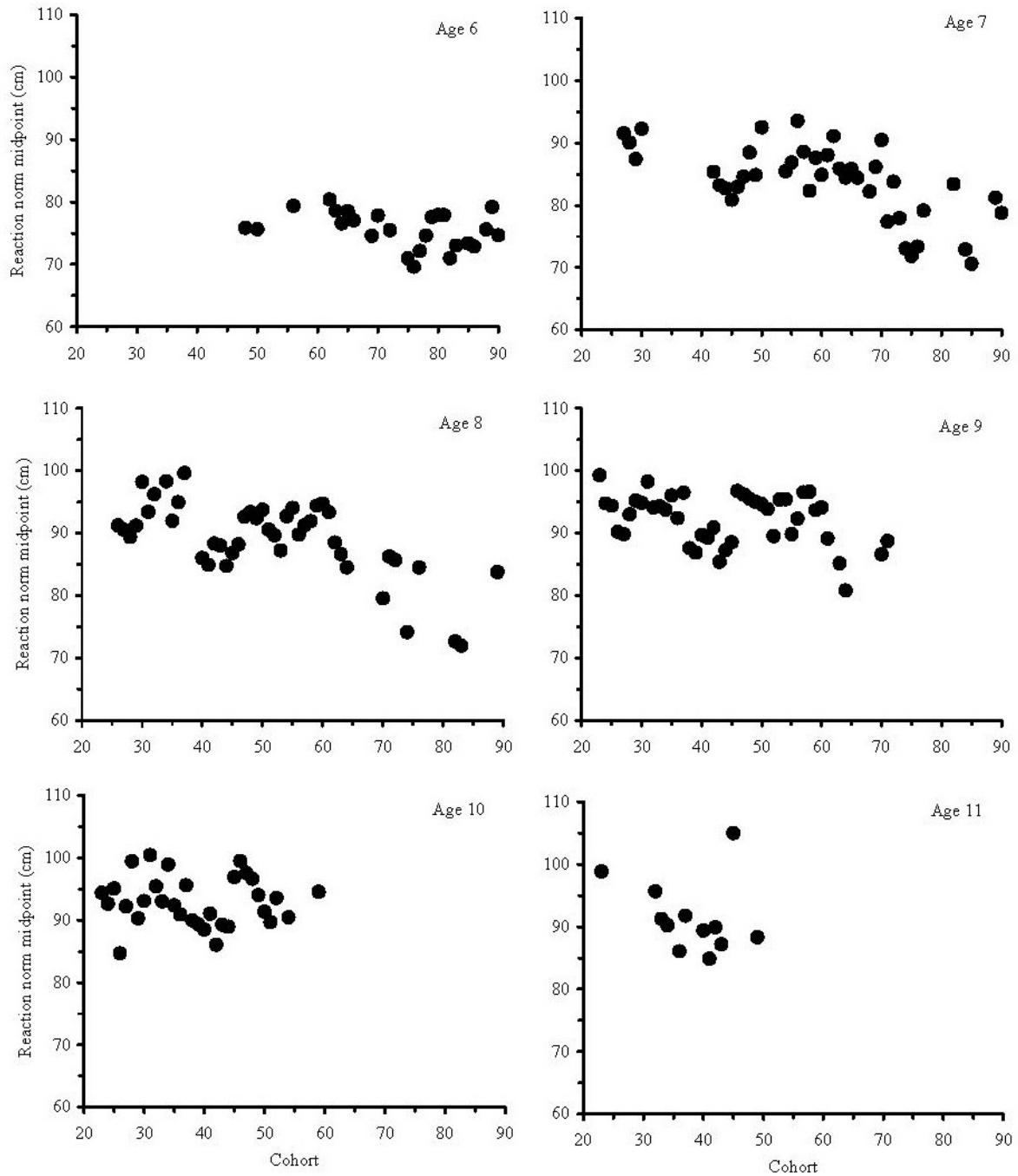
Figure 6. Reaction norm midpoints for age and size at maturation for Northeast Arctic cod as esti-
mated by the logistic model with cohort as a factor (equation 2). Age 5 is omitted from the figure be-
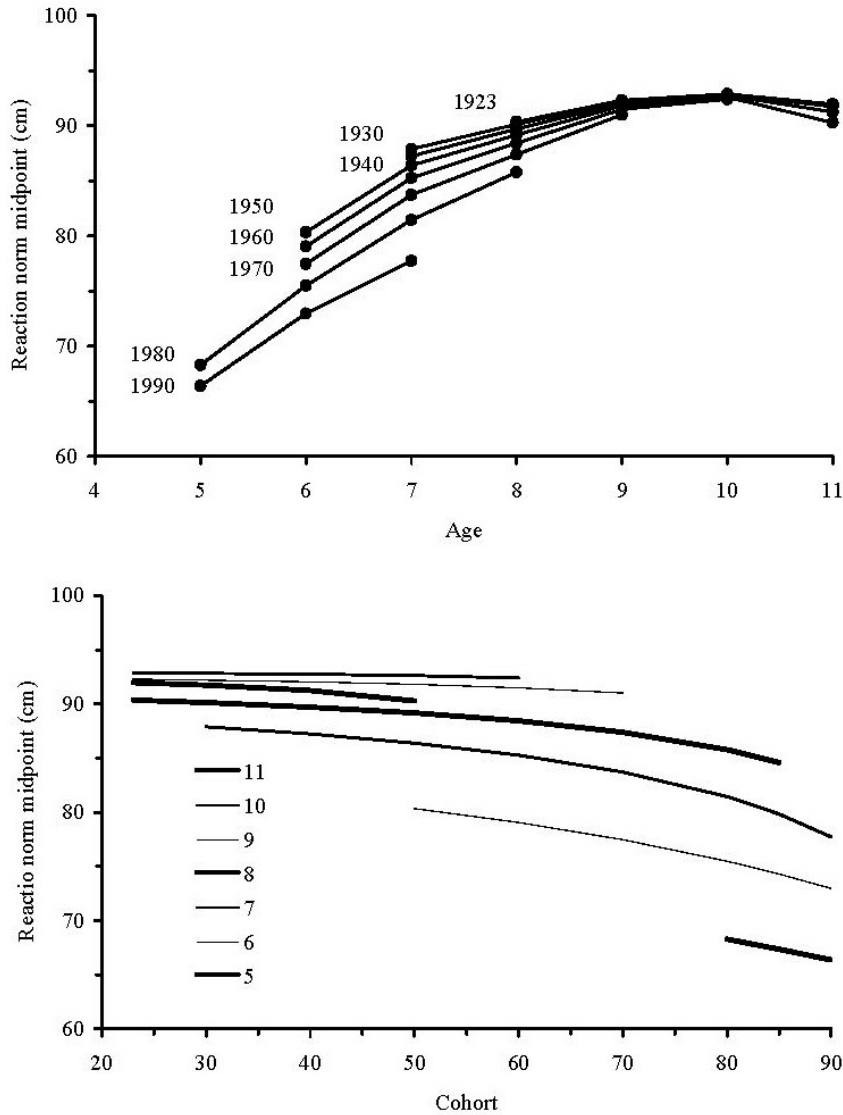cause sufficient data was available only from three cohorts.

Figure 7. Reaction norms for age and size at maturation for Northeast Arctic cod as estimated by the logistic model with cohort as a variate (equation 3). The upper panel illustrated the model-predicted reaction norm midpoints for different cohorts. The lower panel shows the temporal trend in the reaction norm midpoints for different ages.
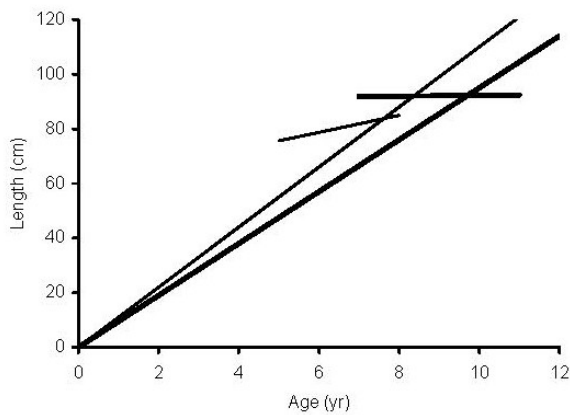

Figure 8. "Historic" and "present-day" reaction norms and growth trajectories used in Table 3. The historic growth trajectory (9.5 cm/yr, see figure 2) and reaction norm (cohorts 1923-1927: c_0= -10.5, c_1=0.116 and c_2=-0.0163) are shown with thick lines and the present-day growth trajectory (11 cm/yr) and reaction norm (cohorts 1986-1990: c_0= -5.63, c_1=0.0939 and c_2=-0.293) with thin lines.