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Estimating reaction norms for age and size at maturation with reconstructed immature size distributions: a new technique illustrated by application to Northeast Arctic cod

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Reaction norms for age and size at maturation describe the probability of immature fish maturing at a certain age and size. Knowledge of such reaction norms is increasingly important, both for observing and understanding changes in maturation and for calibrating size- and age-structured population models. Estimating the reaction norms for age and size at maturation by logistic regression requires data on the size and age distribution of immature and maturing fish. To permit such estimation when measurements of the size and age distribution of immature fish are not available, the information can be reconstructed by means of a back-projection procedure. For the reconstruction, only the size and age distribution of maturing fish, or first-time spawners, together with the age-dependent proportion of mature fish, given in the form of maturity ogives, have to be known. The method of Gulland (1964) is used to generate maturity ogives in the absence of data on immature fish. The robustness of the estimation method is demonstrated by analysing artificial data generated with a known reaction norm. Application of the reconstruction method to a set of measurements on Northeast Arctic cod (*Gadus morhua*) collected between 1933 and 1944 illustrates how the approach allows new information to be extracted from real data.

Keywords: back-projection, logistic regression, maturation, phenotypic plasticity, reaction norm, reconstruction, size distribution.

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Introduction

Age and size at maturation are among the key life history traits that facilitate the adaptation of fish to environmental variability (Roff, 1992; Stearns, 1992). At an individual level, age and size at maturation influence growth rate, fecundity, and survival probability later in life. At a population level these effects interact, such that changes in maturation properties affect age and size distributions, population dynamics, and productivity. In particular, changes in maturation properties influence the potential yield from fish stocks. In the modern era of the precautionary approach, observing and understanding changes in the maturation properties of exploited stocks is critical to fisheries management.

Within each stock, individual fish typically follow different growth trajectories, maturity being attained by different individuals at different combinations of age and size (Alm, 1959; Stearns and Crandall, 1984). Moreover, because individual maturation is influenced also by the condition of the fish (Bernardo, 1993), involving factors such as recent growth history and the quantity of body reserves, it is common to find that, even within a given age- and size-class, some fish have matured while others

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have not. The process of maturation therefore calls for a probabilistic treatment. A convenient way to characterize the dependence of maturation on age and size is the so-called probabilistic reaction norm for age and size at maturation (maturation reaction norm, for short). This reaction norm describes the age- and size-dependent likelihood that an immature fish matures during the season considered (Heino *et al.*, 2002). The maturation reaction norm, estimation of which is equally valuable from both theoretical and applied perspectives, is introduced in the following section.

As explained below, estimating the maturation reaction norm requires information on both immature and maturing fish. Unfortunately, however, situations in which only data on mature (or maturing) fish can easily be collected are not uncommon in stock assessment: juveniles may have an inconspicuous lifestyle, or they may be spatially segregated from adults. The latter applies to species with a spawning migration, such as Northeast Arctic cod. For such species it would, at first glance, seem that estimating maturation reaction norms is precluded; fortunately this is not the case. In this paper we introduce a new technique by which such missing data can be reconstructed through a back-projection procedure. This procedure utilizes information on the size distribution of maturing fish, on age-based maturity ogives, and on growth curves of immature and maturing individuals. We show that the reconstruction method permits the robust estimation of probabilistic maturation reaction norms from stock data that lack information on immature size distributions.

The method aims at estimating the size distributions of juveniles when these have not been measured directly. However, it does require information on juveniles in the form of age-based maturity ogives. This apparent contradiction has two solutions. First, estimating age-based maturity ogives only requires information on relative juvenile abundance, not on their size distribution; consequently, age-based maturity ogives may well be known even if the size distributions of juveniles have not been measured. Second, if juvenile data are completely lacking, Gulland's (1964) method still allows estimation of age-based maturity ogives. [Gulland (1964) originally devised this method for Northeast Arctic cod; for subsequent applications, see Jørgensen (1990), Ajiad and Jakobsen (2001), and the section "Robustness of the reconstruction technique" later.]

The method is illustrated by estimating reaction norms for data on Northeast Arctic cod (*Gadus morhua* L.), commercially one of the most important gadoid stocks in the world. Mature Northeast Arctic cod undertake an annual spawning migration from the Barents Sea to the northern Norwegian coast, the main spawning locations being located in waters off the Lofoten Islands (Bergstad *et al.*, 1987). Representative samples of both immature and maturing cod are available from 1984 onwards when annual winter surveys were started. However, records of age and length of spawning cod around the Lofoten Islands go back as far as 1932. The goal of analysing temporal changes in age and size at maturation in this exceptionally long time-series prompted us to develop a method that would allow extracting more information from the available data. We demonstrate the estimation of probabilistic reaction norms and the underlying back-projection procedure by reconstructing the reaction norms for age and size at maturation for the Northeast Arctic cod cohorts of 1926–1931, which matured over the years 1933–1944.

Reaction norms for age and size at maturation

In general, reaction norms describe how one genotype can give rise to distinct phenotypes when exposed to different environmental conditions (Schmalhausen, 1949). In particular, 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 maturation reaction norm is defined here as the probability that immature fish mature during a given time interval and at a certain age and size (Figure 1; Heino *et al.*, 2002). A description of the entire reaction norm involves specifying these probabilities for all relevant ages and sizes. This probabilistic definition is a generalization of the essentially deterministic definition employed in earlier, mostly theoretical literature (Stearns and Koella, 1986; Roff, 1992; Stearns, 1992). Important features of the maturation reaction norm at each age are illustrated by its midpoint and width: the midpoint is defined as the size at which maturation occurs with a probability of 50%, and the width as the length of the size interval within which the probability of maturation rises from, say, 25 to 75% (Figure 1). It is important to realize that, at very early ages, fish may not be large enough to experience a maturation probability as high as 50%; yet, for illustrative purposes, the midpoint is still conveniently used for those ages.

The maturation reaction norm is here defined by the maturation probability of immature fish given that they have 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. By combining maturation reaction norms with the latter probabilities, one can predict, among other quantities, the fraction of a population or cohort that is maturing (or, alternatively, that is mature) at a certain age and size.

From this fundamental disentanglement follow several specific properties of maturation reaction norms

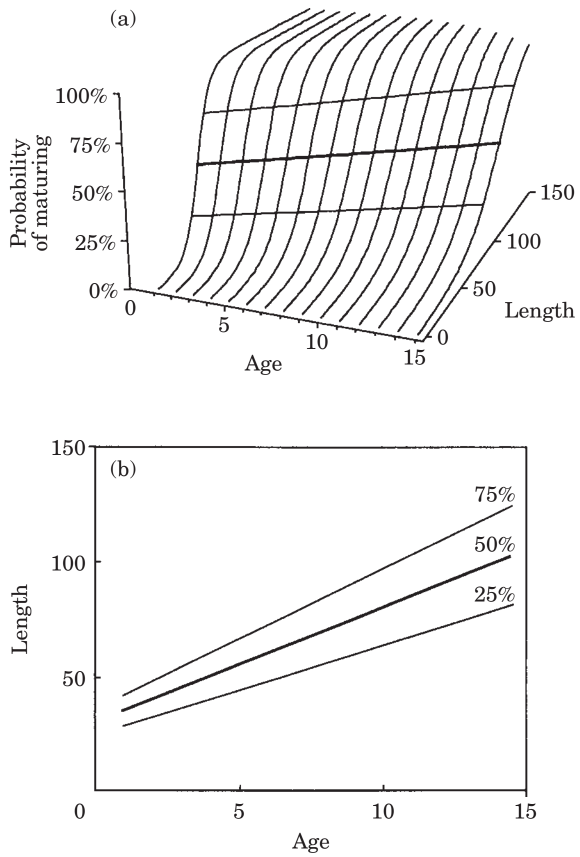

Figure 1. (a) The reaction norm for age and size at maturation describes the probability of immature fish reaching maturity at a certain age and size. (b) By projecting the points where maturation occurs with a probability of 50% onto the age-size plane, a two-dimensional illustration of the reaction norm is obtained.

that make their estimation valuable for both theoretical and applied purposes:

- The maturation reaction norm allows characterization of the maturation process in a manner that is not confounded by the processes of growth and survival (Heino *et al.*, 2002).
- Such descriptions are indispensable for age- and length-structured population models, and hence for stock assessment purposes (e.g. Frøysa *et al.*, 2002).
- Disentanglement allows stock data to be used to estimate how the fundamental biological processes of maturation, growth, and survival are affected by short- and long-term variations in environmental conditions.
- In turn, knowing the maturation reaction norm allows for prediction of how age and size at maturation will respond to changes in growth conditions (Stearns and Crandall, 1984).
- Finally, under the assumption that the maturation reaction norm is largely genetically determined, it can be used to disentangle phenotypic plasticity and genetic effects that influence maturation (Stearns and Crandall, 1984; Stearns and Koella, 1986; Rijnsdorp, 1993a, b). Looked at in this way, the maturation reaction norm can be used as a filter that removes the bulk of environmental variability from maturation data.

It is important to appreciate fully the differences between maturity ogives and the reaction norm for age and size at maturation. Maturity ogives describe the estimated proportions of mature individuals as functions of size, age, or both. In particular, no distinction is made between first-time and repeat spawners. The proportion of mature fish at age and size is influenced not only by the number of newly matured fish but also by losses through mortality and by transitions from one size-class to another through growth. In other words, the three biological processes described above become critically intertwined in maturity ogives. By contrast, the maturation reaction norm focuses on the maturation process alone. Because a fish can mature only once, life after maturation does not affect the maturation reaction norm. Also, as 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 that age and size leave the maturation reaction norm unaffected.

An intuitive way to determine the probability of maturing at a certain age and size is to estimate the proportion of newly matured fish among all individuals of that size that could potentially have matured during the time interval considered. However, it is much more efficient to utilize data on fish of all different sizes simultaneously, thus determining how size influences the probability of maturing within an age-class. Logistic regression is a powerful statistical tool for such analysis (Collett, 1991). A simple model to be fitted to the data then is

$$\text{logit}\,(p)=c_0+c_1 s \qquad (1)$$

where p is the probability of maturing, logit (p) the logit-transformation $\log_e[p/\{1-p\}]$, s the size, and c_0 and c_1 are the two parameters to be estimated. Logistic regression models can easily accommodate data with a more complex structure (see Heino *et al.*, 2002, for some examples). It is also possible to use other generalized linear models appropriate for analysing binary data (Collett, 1991). By contrast, other methods previously used to estimate maturation reaction norms without data on immature fish give results that are often seriously biased (Heino *et al.*, 2002). The bottom line is that, to determine probabilistic reaction norms, representative samples of both maturing and immature fish are required.

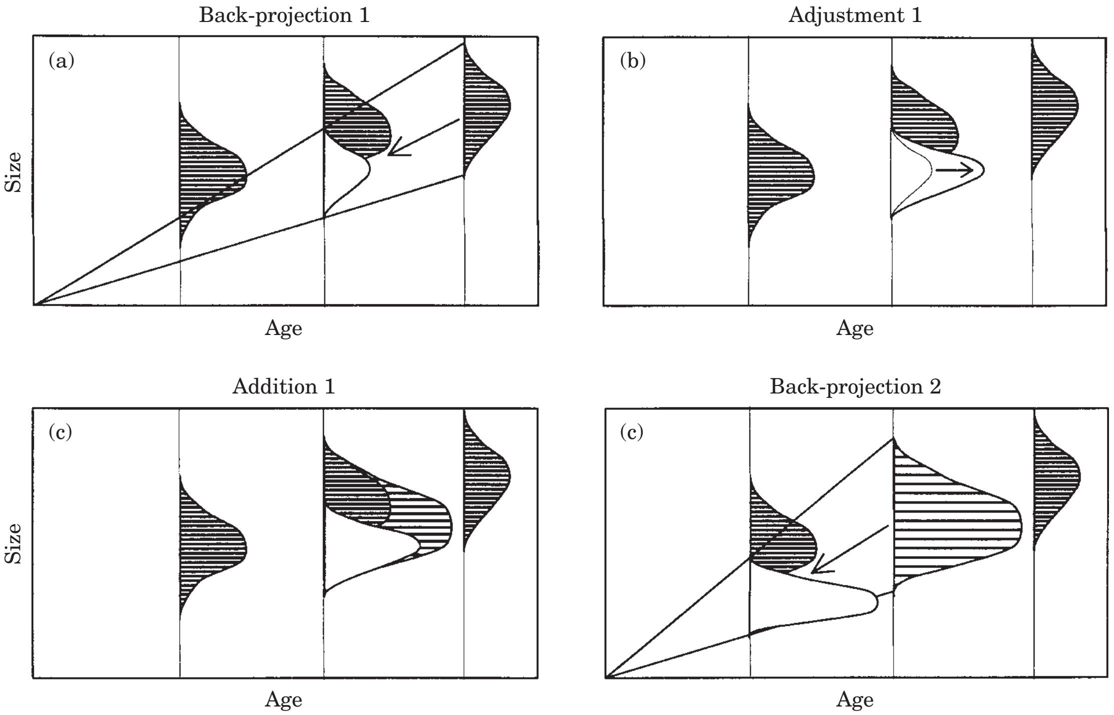

Figure 2. Illustration of the reconstruction process. (a) Original distribution data on maturing fish, and first back-projection based on growth model. (b) Adjustment of back-projected distribution according to the maturity ogive. (c) Merging of distributions for maturing and immature fish. This is the starting point for (d) the second round of back-projection.

Reconstructing size distributions of immature fish

When data on immature individuals, needed to estimate maturation reaction norms directly, are unavailable, reaction norms can still be estimated provided that some other data can be relied on. Four groups of datasets are needed for this purpose: (1) age-specific size distributions of maturing fish, (2) age-based maturity ogives, (3) relative survival probabilities of immature, maturing, and mature fish, and (4) information about the growth pattern of immature fish. As mentioned already, in the absence of data on immature fish, a procedure proposed by Gulland (1964) can allow the estimation of sufficiently accurate maturity ogives from data on mature fish only. With these four groups of data at hand, it is possible to reconstruct unobserved size distributions of immature fish, so allowing for the robust estimation of probabilistic maturation reaction norms.

The basis of the reconstruction technique is easy to grasp and can be summarized as follows (Figure 2). Reconstruction is started from the year during which the last fish of the cohort considered have reached maturity. This is the first time at which the size distribution of immature fish in the cohort is known from the available data: none are left. (For that reason it is also not meaningful to estimate a probabilistic maturation reaction norm at this age.) The immature part of the cohort in the year before therefore only consisted of fish that would all mature one year later, and the size distribution of these maturing fish is known from the available data. Going backwards in time, the size distribution of these now maturing and previously immature fish in the year before can be estimated from their present size distribution and knowledge of the growth pattern of immature fish. The abundance in this distribution relative to that in the distribution of maturing fish, again known from the available data, is adjusted to be consistent with the maturity ogive. The two size distributions are then stored and added. The resulting distribution sum is back-projected again to give the size distribution of fish that were immature in the year before. This procedure is repeated until the earliest age of maturation has been reached.

The reconstruction technique described above is structurally similar to virtual population analysis (VPA) in that it is based on following a cohort backwards in time. However, while the technique used here is both age- and size-based, VPA is based on age alone. A second difference is that our analysis reconstructs distributions of immature fish only, whereas VPA focuses on all fish, irrespective of their maturation status. A third, correlated distinction is that our back-projection starts from the point in time at which the focal cohort has matured fully, whereas VPA starts from the moment when the cohort has completely died out.

For the sake of simplicity, we assume that growth trajectories of fish start from the origin and are linear before maturation; alternative growth laws can readily be implemented. This assumption does allow for growth variations among individual fish; it only implies that all fish within the same age- and size-class share a common growth history, which consists of identical annual size increments s(a)/a, where s(a) is the size at age a.

We use the following notation. The size distributions of immature and maturing fish at age are denoted by $n_I(s,a)$ and $n_{I\to M}(s,a)$ respectively. The sum of both size distributions, $n_I(s,a)+n_{I\to M}(s,a)$, is denoted by n(s,a). The total number of fish in these stages at age a is obtained by summing over all sizes, $N_I(a)=\Sigma_s n_I(s,a)$, $N_{I\to M}(a)=\Sigma_s n_{I\to M}(s,a)$, and $N(a)=\Sigma_s n(s,a)$.

The reconstruction procedure requires the ratio $m(a)=N_{I\to M}(a)/N(a)$ between the number of individuals of age a that mature at that age and the number of those that could mature at that age to be known. This ratio can be calculated from the maturity ogive o(a), which describes the probability of being mature at age a. Under the assumption that maturing fish have the same survival probability as mature ones, we obtain (see Appendix for the derivation)

$$m(a)=\frac{o(a)-o(a-1)[r(a-1)-o(a)(r(a-1)-1)]}{1-o(a-1)[r(a-1)-o(a)(r(a-1)-1)]}$$

where r(a) denotes the ratio, at age a, between the survival probabilities of mature or maturing individuals and of immature ones. The Appendix also presents the derivation of m(a) under the alternative assumption that maturing fish have the same survival probability as immature ones.

With these preliminaries in place, the reconstruction procedure is based on one initialization step and a subsequent cycle of three further steps:

(1) Reconstruction is started from the year during which the last fish of the cohort considered reached maturity (see Figure 2a). The observed size distribution of fish maturing at that age, $n_{I\to M}(s,a)$, equals the size distribution of all immature and maturing fish, n(s,a), because, by definition of that age, no immature fish remain.

(2) The shape of the size distribution of immature fish in the year before, $\tilde{n}_I(s,a-1)$, is obtained by projecting size distribution n(s,a) back in time. This is achieved by using the growth model backwards: the distribution is moved by one year in the direction towards the origin (see Figure 2a). Thus, at age $a-1$ the cohort consists of two subgroups: immature fish, for which the unadjusted size distribution can be obtained by back-projection, and maturing fish, for which the size distribution $\tilde{n}_{I\to M}(s,a-1)$ can be obtained directly from available data. However, the relative abundances of the two subgroups will be incorrect because of two unconsidered factors: mortality and the annually varying sampling intensity.

(3) The back-projected size distribution of immature fish is adjusted, either with information on mortality and sampling intensity, or with information extracted from the maturity ogive, as assumed here. The fraction of individual fish maturing at age $a-1$ is $m(a-1)=[N_{I\to M}(a-1)/(N_{I\to M}(a-1)+k\tilde{N}_I(a-1))]$, where $N_{I\to M}(a-1)$ is the real sample size of fish maturing at age $a-1$, and $\tilde{N}_I(a-1)=\Sigma_s\tilde{n}_I(s,a-1)$ is the unadjusted back-projected sample size of immature fish. After solving the equation above for the adjustment constant k, this constant can be calculated from known quantities. The adjusted size distribution of immature fish is then obtained as $n_I(s,a-1)=k\tilde{n}_I(s,a-1)$; see Figure 2b.

(4) The size distribution of all immature and maturing fish, $n(s,a-1)$, is obtained by adding the distributions of immature, $n_I(s,a-1)$, and maturing fish, $n_{I\to M}(s,a-1)$; see Figure 2c. This is the basis for the next round of back-projection in Step 2 (see Figure 2d). Steps 2–4 are repeated until the immature size distribution at the earliest age at maturation has been obtained.

An important task after the back-projection has been completed is to check whether the results obtained are biologically sensible. Two consistency checks should be applied: immature fish should be, on average, smaller than those maturing, and the combined size distribution of maturing and immature fish will usually be expected to be unimodal.

In the above procedure, two simplifying assumptions require attention. First, size-dependent effects on mortality are not considered in the described reconstruction. This simplification may bias the shapes of back-projected distributions and we therefore investigate potential implications in the following section. Second, the reconstruction procedure described here does not account for annual variations in growth conditions. Long-term fluctuations will have little influence on the results, but if growth conditions change abruptly from year to year, size distributions will not be reconstructed accurately. If exceptionally complete information is available, these two complicating factors could be controlled for in the reconstruction procedure. As this is often not the case, we need to provide an assessment of the sensitivity of the reconstruction with regard to these factors.

Robustness of the reconstruction technique

In this section we systematically evaluate how the reconstruction method works in practice: whether it produces sufficiently unbiased estimates, and whether it is satisfactorily robust against uncertainty and sampling errors in the data, as well as against relaxing the simplifying assumptions of the reconstruction method. The last paragraph summarizes the salient conclusions drawn from the evaluation.

To test for these features, a simple procedure is used to generate artificial maturation data for a known probabilistic reaction norm. Our example is motivated by existing data on Northeast Arctic cod; we can therefore assume that growth before maturation is approximately linear (Jørgensen, 1992), that cohort size is very large (unless otherwise stated, we chose $N_{cohort}=10^6$ at age 4) and that a large number of maturing fish are sampled at each age ($N_{sample}=250$ in the examples, unless otherwise stated). The latter figure was chosen to be representative of the typical sample size in the existing cod data. Typically, relative sampling intensity is lower for very abundant age-classes; we therefore did not consider variations of N_{sample} with age. Although the chosen value for N_{cohort} is smaller than in reality ($N_{cohort}=10^9$ might be more appropriate), the actual choice is immaterial as long as the cohort size is large enough to render demographic stochasticity insignificant. Data are generated by letting individuals grow deterministically and mature stochastically; maturation occurs while their growth trajectories pass through the given probabilistic maturation reaction norm.

Beyond its function for testing the robustness of the reconstruction method, the procedure below has an additional benefit: it illustrates how the maturation reaction norm can be used to build age- and size-structured models of stock dynamics. An appreciation of the need to extend classical age-structured stock models in this regard is currently mounting in the literature (Parma and Deriso, 1990; De Leo and Gatto, 1995; Frøysa *et al.*, 2002).

The generation procedure is based on two initialization steps and a subsequent cycle of six further steps:

(1) We start by considering a probabilistic reaction norm with age-independent coefficients c_0 and c_1 [see Equation (1)]. These coefficients describe a horizontal reaction norm of fixed width, the shape chosen to render conspicuous any discrepancies between the reconstructed reaction norm and the actual one.

(2) The size distribution of immature fish, $n_I(s,a)$, at the first age considered for maturation, a=4, is generated for a cohort of initially N_{cohort} fish by selecting sizes at random from a normal distribution with mean length 40 cm and standard deviation 4 cm. The size distributions of maturing, $n_{I\rightarrow M}(s,a)$, and mature fish, $n_I(s,a)$, at all ages are initially empty.

(3) Equation (1) describes the size-dependent probability of maturing for each fish in the distribution $n_I(s,a)$. Therefore, we can flip a coin, loaded according to this probability, and transfer those fish that mature from $n_I(s,a)$ to the size distribution $n_{I\rightarrow M}(s,a)$. All non-maturing fish are kept in the size distribution of immature fish, $n_I(s,a)$.

(4) To mimic the limited number of measurements available in real data, random samples of N_{sample} fish can be drawn from the distribution $n_{I\rightarrow M}(s,a)$. The resulting distribution $\tilde{n}_{I\rightarrow M}(s,a)$ is the output of the generation procedure; continuation of the procedure itself is based on the full distribution $n_{I\rightarrow M}(s,a)$.

(5) All fish in the size distribution $n_{I\rightarrow M}(s,a)$ are transferred to the size distribution of mature fish, $n_I(s,a)$.

(6) The two distributions $n_I(s,a)$ and $n_M(s,a)$ so obtained can then be used to calculate the maturity ogive, $o(a)=N_M(a)/[N_I(a)+N_M(a)]$ with $N_I(a)=\Sigma_s n_I(s,a)$ and $N_M(a)=\Sigma_s n_M(s,a)$. Alternatively, Gulland's (1964) method can be used in this step.

(7) Immature and mature fish survive with probabilities $\sigma_I(s)$ and $\sigma_M(s)$ respectively; the distributions $n_I(s,a)$ and $n_M(s,a)$ are therefore multiplied by these factors. Unless otherwise stated, below we assume $\sigma_I(s)=\sigma_M(s)=\sigma$. The actual value of σ is then inconsequential as long as it does not reduce cohort or sample sizes to an extent at which sampling errors become important.

(8) If there are still immature fish left in the cohort, they are allowed to grow according to linear growth trajectories that pass through the origin and through the point given by the current size and age of the considered fish; the resulting growth rate is s(a)/a. The growth rate of mature fish is assumed to slow relative to that of immature fish; their growth rates are set to $r_g s(a)/a$ (with $r_g=0.75$; this assumption is immaterial as long as mortality is size-independent). The resulting distributions $n_I(s,a)$ and $n_M(s,a)$ are then copied to the next age and the process returned to Step 3 until no immature fish remain in the cohort.

This procedure yields, for a given reaction norm, the size distributions $\tilde{n}_{I\rightarrow M}(s,a)$ of maturing fish at all relevant ages, as well as the maturity ogive o(a) of the cohort. Information about relative survival probabilities of immature, maturing, and mature fish, and about the growth pattern of immature fish is known from the onset. We thus have available the four groups of data required for the reconstruction method.

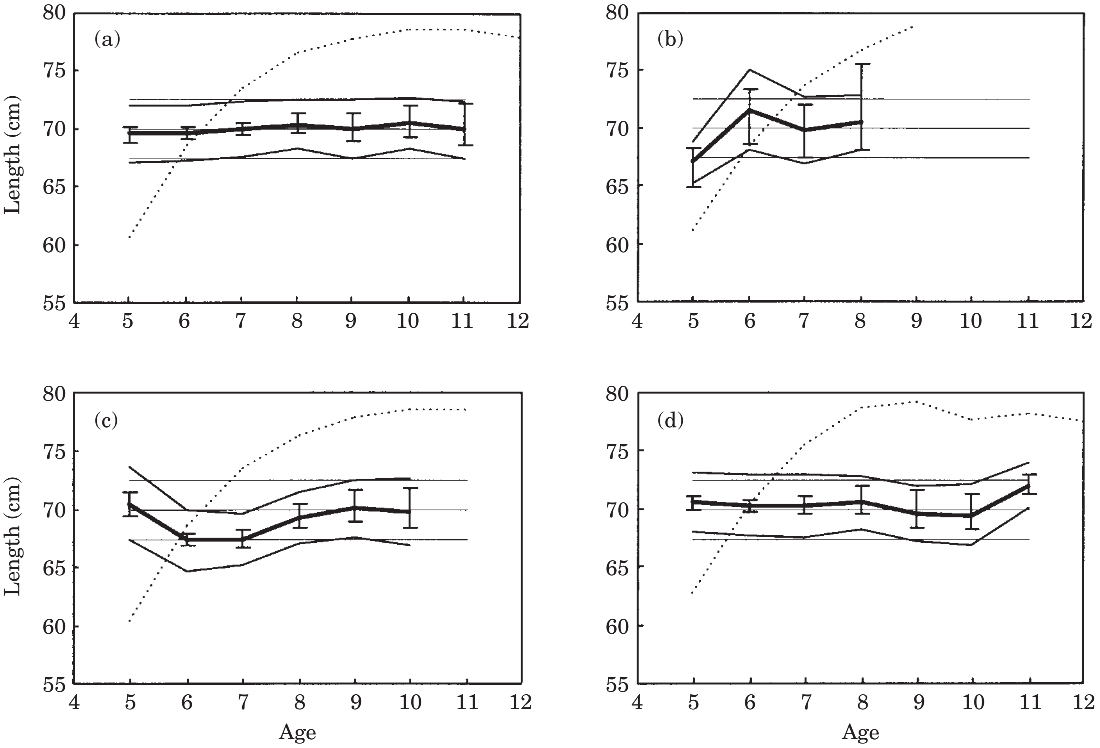

Figure 3. Examples of reconstructed reaction norms, illustrated by their midpoints (dark lines, shown together with 95% confidence intervals) and quartiles (light lines), as estimated from artificially generated data. The actual reaction norm is given by hairlines for the midpoint and the quartiles. Dashed curves describe the average size of maturing fish at different ages. (a) When growth conditions are constant, samples are large, and the maturity ogive is accurate, the reconstruction technique yields good results. (b) Very small samples or (c) a maturity ogive biased to the left change the shape of the estimated reaction norm in systematic ways. (d) By contrast, variations in annual growth increments introduce unsystematic fluctuations; years of good and bad growth conditions are reflected by ups and downs in the reaction norm. See Table 1 and its discussion in the text for more details.

Based on these data, we can attempt to reconstruct the size distribution of immature fish and the originally assumed reaction norm according to the techniques presented in the previous two sections. To allow for maximum sensitivity to potential biases in the reconstruction, the midpoints and widths of the probabilistic reaction norm are estimated separately for each age-class. Ages at which fewer than ten fish matured or at which the reconstruction yielded fewer than five immature fish were ignored.

If the cohort size is sufficiently large, the maturation dynamics of the cohort as a whole are essentially deterministic. If sample sizes are also sufficiently large, there is hardly any sampling error and the procedure above generates ideal data (in the sense that both the sampled size distributions at maturation and the maturity ogive are unbiased). Under such conditions, the estimated reaction norm is (and must be) practically identical to the actual reaction norm. However, such ideal data are not likely to be available in reality. Therefore, in the following sensitivity analysis, we conduct a sequence of robustness checks against two fundamental types of error in the estimation method: first, source data can be inaccurate and/or biased; second, simplifying assumptions in the reconstruction method may introduce errors.

Sampling errors can arise in source data because only relatively few maturing individuals are observed at each age. At large sample sizes of 250 fish, sampling error is negligible and estimated reaction norms are similar to the actual one, although the width of the reaction norm is slightly underestimated (Figure 3a and Table 1, Row A). Very small samples of, say, 25 fish, are subject to considerable sampling error, so introducing a systematic bias to the estimation: the estimated reaction norms have a positive slope and are slightly convex (Figure 3b and Table 1, Row B). Likewise, a small cohort size, introducing a higher degree of stochasticity to the maturation dynamics, tilts the reaction norm to attain a positive slope (Table 1, Row C).

The source data for the shape of the maturity ogive can be biased as well, potentially causing a strong bias in the estimated reaction norm. Ogives that are too flat or too steep result in estimated reaction norms with positive or negative slopes respectively (Table 1, Rows D

Table 1. Sensitivity of estimated reaction norms to different sources of error in data and reconstruction. The actual reaction norm used to generate data on the age and size of maturing individuals is horizontal, with an age-independent width. For each robustness test, four properties of the estimated reaction norm are assessed. (1) The reaction norm's midpoint describes, for each age, the size at which the probability of maturation reaches 50%; displayed figures are averaged over all ages. (2) The width of the reaction norm, measured for each age as the size interval within which the probability of maturation rises from 25 to 75%; again, displayed figures are averaged over all ages. (3) The given slope of the reaction norm is the linear coefficient obtained by linear age-midpoint regression. (4) The shape of the reaction norm is characterized by the quadratic coefficient obtained by quadratic age-midpoint regression. For the first three of these properties, mean values resulting from fivefold replication of the generation/reconstruction procedure are given together with their error, measured as the mean absolute difference between estimated and actual values; for the shape, only the sign of the curvature is displayed (convex=significantly positive, concave=significantly negative, linear=no significant curvature). The maturity ogive was flattened (Row D) by dividing the logit of the actual ogive by 1.5 (thus, the level of 50% probability remains unaffected, whereas a probability of 25% is increased to 32.5%). Likewise, a steeper ogive (Row E) was constructed by multiplying by 1.5. The maturity ogive was biased to the left (Row F) by adding an offset of 1 to the logit of the actual ogive (thus, in the distorted ogive a probability of 25% is replaced with 47.5% and one of 50% with 73.1%). Analogously, subtraction of 1 biases the ogive to the right. Annual variation in growth (Row H) was introduced by multiplying the expected deterministic growth increment by independent Gaussian random deviates with mean 1 and standard deviation 0.2. Higher mortality after maturation (Row I) was realized by assuming survival probabilities $\sigma_M(s):\sigma_I(s)=0.75:1$; for lower mortality after maturation (Row J) the ratio 1:0.75 has been used. Importantly, these differences are accounted for only in the generation procedure, whereas they are deliberately ignored in reconstructing the reaction norm and in calculating the maturity ogive by Gulland's (1964) method. A positive size-dependence in mortality (Row K) was introduced by $\sigma_I(s)=\sigma_M(s)=1-(s-s_{min})/l$ and a negative size-dependence (Row L) by $\sigma_I(s)=\sigma_M(s)=1-(s_{max}-s)/l$ with $l=100$ cm, where s_{min} and s_{max} are, respectively, the sizes of the smallest and the largest individuals in the age-class of the considered individual. To assess the cumulative effect of a likely combination of confounding factors (Row M), we assumed annual variation in growth (as described above), positive size-dependence in mortality (as described above), and an extra size-independent mortality risk of 10% for mature fish.

		Average midpoint		Average width		Slope		
Parameter		Mean	Error	Mean	Error	Mean	Error	Shape
Actual reaction norm		70.0		5.0		0.0		Linear
Estimated reaction norm								
A	Sample size 250	70.0	0.30	4.78	0.31	0.093	0.112	Linear
B	Sample size 25	70.1	1.30	4.92	1.19	0.786	0.786	Slightly convex
C	Cohort size 500, sample size 50	70.3	0.68	4.48	1.10	0.759	0.759	Linear
D	Ogive too flat	70.3	1.94	4.83	0.35	0.985	0.985	Linear
E	Ogive too steep	69.5	1.97	4.75	0.47	−1.221	1.221	Linear
F	Ogive biased to the left	69.1	1.14	5.10	0.45	0.284	0.284	Concave
G	Ogive biased to the right	70.7	1.04	4.62	0.47	0.075	0.075	Convex
H	Variable growth	70.5	1.13	5.29	1.01	−0.336	0.423	Linear
I	Higher mortality after maturation	70.6	0.68	4.79	0.43	0.102	0.102	Linear
J	Lower mortality after maturation	69.4	0.78	4.90	0.49	0.129	0.182	Linear
K	Positively size-dependent mortality	69.8	0.82	4.65	0.42	0.315	0.315	Linear
L	Negatively size-dependent mortality	69.7	0.43	5.09	0.50	−0.257	0.257	Linear
M	Combination of factors	69.8	1.15	5.22	0.87	0.242	0.523	Linear

and E). Ogives that are biased by a shift to the left (resulting in an overestimated fraction of mature individuals at any age) cause the estimated reaction norm to be concave (Figure 3c and Table 1, Row F), whereas a shift in the opposite direction results in convex reaction norms (Table 1, Row G).

Simplifying assumptions in the reconstruction method may also cause errors in the estimated reaction norms. For example, the reconstruction procedure assumes that growth conditions remain constant from year to year; in the wild, annual growth increments will obviously vary. Annual variability of growth conditions results in a "jagged" appearance of estimated reaction norms, with ups and downs corresponding to ages at which growth had accelerated or decelerated (Figure 3d). Fortunately, however, there turns out to be only a small systematic bias towards reaction norms that are negatively sloped and slightly too wide (Table 1, Row H).

Further robustness checks address cumulative errors arising from combined effects of inaccuracies in the source data and simplifying assumptions in the reconstruction procedure. A particular type of bias in the maturity ogive may occur if the ogive is estimated according to the method proposed by Gulland (1964). This method calculates the maturity ogive as $o(a)=\Pi_{a'=a+1}^{\hat{a}}[1-f(a')]$, where $\hat{a}$ is the earliest age at which all fish are mature and $f(a)=N_{I\rightarrow M}(a)/N_M(a)$ is the frequency of newly mature fish among mature ones at age a (Equation 3 of Jørgensen 1990). This procedure assumes equal survival probabilities of immature and mature fish. As shown by Jørgensen (1990), the estimated ogive becomes biased when the survival probabilities are unequal. If the ratio r(a) between the survival probabilities of mature or maturing and immature fish is known, a correction proposed by Jørgensen (1990) can be used to remove the bias. Unfortunately, however, information on r(a) is often very inaccurate or lacking altogether. It is therefore important to assess the cumulative error caused by ignoring such differences in survival, first in estimating the maturity ogive, and then in reconstructing the maturation reaction norm. For this purpose, we generated data assuming that mature fish had a survival probability that was either higher [$\sigma_M(s):\sigma_I(s)=1:0.75$] or lower [$\sigma_M(s):\sigma_I(s)=0.75:1$] than that of immature fish. As a consequence of this deliberate inaccuracy, the ogive is biased by a shift to smaller or larger sizes (for increased or decreased survival probabilities after maturation respectively), but the absolute bias is <9% at all ages. Equal survival was also assumed in reconstructing the reaction norm. Remarkably, the cumulative effect of this simplification on the estimated reaction norms is only minor (Table 1, Rows I and J).

Mortality rates may be affected by both maturation status and size. In particular, size-dependent mortality results in different average survival probabilities for mature and immature fish. As illustrated by the examples in the previous paragraph, ignoring this difference causes a bias in the maturity ogive when it is estimated according to Gulland's (1964) method. Again deliberately disregarding this inaccuracy, we obtain the maturity ogive by Gulland's method and use it in the reconstruction procedure, which also ignores size-dependence. In spite of these simplifications, a moderate size-dependence of mortality rates (with an absolute change in survival of 10% for each 10 cm of size difference) turns out to have only a small influence on estimated reaction norms: if mortality risk increases with size in the maturing age-classes (a common case in fisheries), the reaction norm is tilted counter-clockwise, whereas negative size-dependence tilts the reaction norm clockwise (Table 1, Rows K and L). Thus, moderate survival differences between immature and mature fish (arising either from the life-history transition itself, or indirectly from size-dependent mortality) are not critical for estimating ogives and reconstructing reaction norms.

In estimation tasks for real data, many different inaccuracies of the type investigated above will be present simultaneously. We therefore also evaluated the robustness of the reconstruction technique to a combination of confounding factors that could likely apply to Northeast Arctic cod: mortality risk increasing with size (among the ages and sizes considered here), lower survival after maturation, and annual variations in growth increments. As shown above, these factors, when considered in isolation, cause biases in opposing directions. Therefore, even when these confounding factors are combined, the resulting systematic bias is mild (Table 1, Row M).

In conclusion, the reconstruction technique introduced here turns out to be robust against different types of error in source data and against the relaxation of some simplifying assumptions. Mostly, the inaccuracies result in slightly tilted reaction norms. By contrast, the position and width of maturation reaction norms are not greatly affected. In particular, the assumed linear shape of the actual reaction norms is well recovered in all examples shown, except when samples are very small or when maturity ogives are strongly biased by horizontal shifts.

Example: the Northeast Arctic cod

Using the techniques described above, the reaction norms for age and size at maturation are estimated for data on Northeast Arctic cod. The data originate from a database at the Institute of Marine Research (Norway) and are based on commercial longline catches. We analyse the first six cohorts fully represented in that database; these are the cohorts of 1926–1931, which reached maturity in the years 1933–1944 (Table 2). Age of 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). The maturity ogive for these cohorts has been determined by Jørgensen (1990), utilizing the method of Gulland (1964). The growth of immature cod closely follows linear trajectories (Jørgensen, 1992), so conforming to the simple growth model assumed for illustrating the reconstruction procedure.

Mortality of Northeast Arctic cod is likely to increase after maturation because mature fish migrate each spring from the Barents Sea to their spawning grounds off the Norwegian coast around the Lofoten Islands, where they are subjected to intensive fishing. For the period studied, no rigorous estimates of mortality on the spawning grounds are available, so we assume that the extra mortality is likely to have been in the range 10–25%. On the basis of the robustness analysis above, we can expect that ignoring an extra mortality of such magnitude will not bias the estimated reaction norms significantly.

Figure 4 illustrates the original data as well as the reconstructed size distributions for the cohort of 1926. Age 11 is taken as the age at which all fish have reached maturity. The original data also include five older cod; omission of these fish has little influence on the results. The estimated reaction norm is shown in Figure 5a. The estimated probabilistic reaction norm turns out to be humped, with a width that stays roughly constant with age. There is considerable uncertainty at age 7, owing to

Table 2. Summary of age and length data on first-time spawners of the Northeast Arctic cod cohorts of 1926–1931. Samples of fewer than ten fish have been omitted.

	Age 7		Age 8		Age 9		Age 10		Age 11		Age 12		Age 13	
Cohort	Mean ± s.d.	n	Mean ± s.d.	n	Mean ± s.d.	n	Mean ± s.d.	n	Mean ± s.d.	n	Mean ± s.d.	n	Mean ± s.d.	n
1926	73.0 ± 5.3	10	78.5 ± 5.4	170	87.9 ± 6.8	295	92.0 ± 6.4	204	95.0 ± 6.1	67				
1927	73.7 ± 5.0	80	81.9 ± 5.8	267	87.8 ± 6.3	430	93.1 ± 7.1	211	97.9 ± 7.7	29	100.3 ± 7.2	18		
1928	75.5 ± 5.6	145	81.2 ± 5.7	530	86.1 ± 7.2	592	92.2 ± 8.0	110	97.1 ± 8.0	119	98.3 ± 8.0	11		
1929	74.7 ± 6.0	174	78.2 ± 6.8	643	84.8 ± 6.8	271	90.6 ± 7.3	523	94.6 ± 8.5	78	91.7 ± 5.1	13		
1930	71.1 ± 6.8	135	78.3 ± 6.4	194	85.0 ± 6.5	758	91.0 ± 8.0	307	92.6 ± 7.8	94	96.0 ± 9.3	17	101.6 ± 7.6	15
1931	74.5 ± 8.3	16	79.3 ± 6.5	159	85.1 ± 7.4	131	87.6 ± 6.7	91	92.0 ± 8.5	45	96.6 ± 8.3	24	101.4 ± 14.1	13

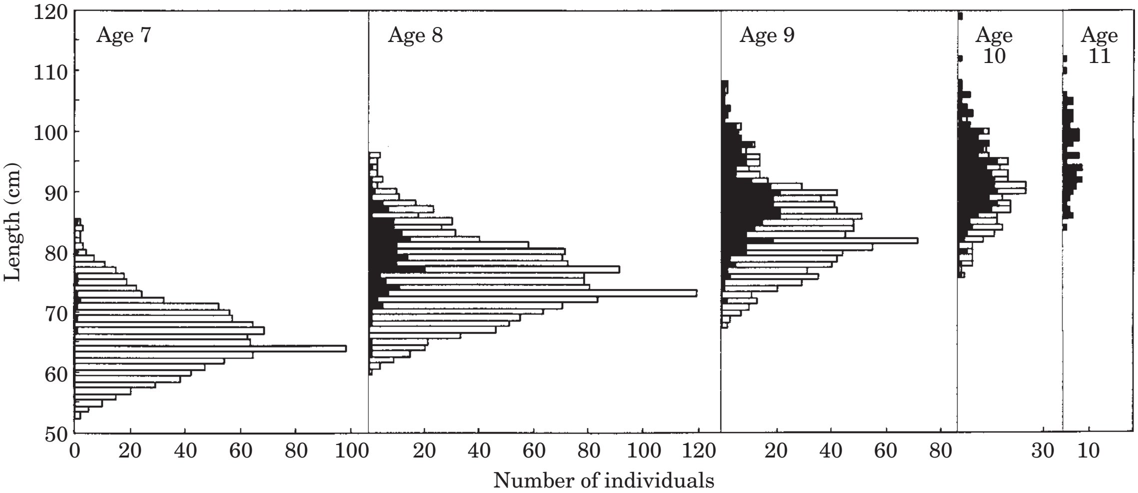

Figure 4. Original size distributions of first-time spawners in the Northeast Arctic cod cohort of 1926 (black bars), together with the reconstructed size distributions of immatures (white bars) for ages 7–11.

the very small number (10) of mature fish at that age. In contrast to the reaction norm for age and size at maturation, the relationship between mean age and mean size at maturation is roughly linear, with a positive slope (Figure 5a).

Reaction norms reconstructed for the cohorts of 1927–1931 are essentially similar. There is more scatter at the latest age of maturation (Figure 5b), probably a reflection of a small sample size at late ages of maturation. In just two cases (the cohorts of 1930 and 1931) it would have been possible to estimate the reaction norm at age 12. For these, however, there was no statistically significant relationship between maturation and size, so none of the reaction norms in Figure 5b extend beyond age 11.

Discussion

If data on the size distribution of immature fish are not available, it may still be possible to reconstruct such data if maturation probabilities at different ages are known. Reconstructed data on immature fish can then be used to estimate the reaction norm for age and size at maturation. Although the validity of the reconstruction method should be evaluated critically for any particular case study, the sensitivity analyses presented here have demonstrated that estimation results are expected to be satisfactory even when fairly noisy source data are available.

Logistic models are commonly utilized in fisheries science when estimating the fraction of mature fish as a function of either age or size in the form of maturity ogives (Rijnsdorp, 1993a, b; Rowell, 1993; Chen and Paloheimo, 1994; Morgan and Colbourne 1999; O'Brien, 1999; Bromley, 2000; Haugen, 2000). Despite the superficial similarity between maturation reaction norms and maturity ogives, there is a fundamental difference: the maturation reaction norm is concerned with the process of *maturing* or attaining maturity, whereas the maturity ogive addresses the issue of *being mature*. The latter is naturally influenced by maturation, but also by two other fundamental biological processes, growth and survival. In other words, the maturity ogive is the result of an interaction between growth, survival, and maturation, the last of which is directly described by the probabilistic maturation reaction norm.

The maturation reaction norm characterizes how age and size at maturation respond to variations in the growth regime that a fish experiences before maturation. However, unlike classical reaction norms, the maturation reaction norm makes no explicit reference to measures of environmental conditions. Instead, the growth trajectory followed by a fish integrates all environmental factors that affect growth into a single object, size-at-age. It is important to realize that the reaction norm terminology is warranted only if variability in growth and maturation are attributable mainly to environmental variation. In particular, if much variability in age and size at maturation can be ascribed to genetic variability in growth or maturation dynamics, then the reaction norm for age and size at maturation may be a reflection of this population variance rather than characterizing phenotypic plasticity.

For Northeast Arctic cod, interpretation of the reconstructed maturation probabilities as a reaction norm is justified, assuming that the stock is genetically sufficiently homogeneous. Evidence is currently inconclusive whether or not significant genetic substructure exists in Northeast Arctic cod (Møller, 1968; Mork *et al.*, 1985).

As mentioned before, spawning cod migrate to their spawning grounds off the northern coast of Norway, mostly around the Lofoten Islands. Genetic differentiation in the stock is likely to be counteracted by mixing on the spawning grounds, despite the extended and environmentally heterogeneous feeding range of the stock. Highly plastic maturation has probably evolved because cod eggs and larvae are randomly distributed by currents to different parts of the Barents Sea, where they experience different temperature and feeding regimes. From the perspective of juvenile cod, the growth environment is unpredictable, despite their great mobility later in life. Although some population variance undoubtedly will contribute, the reaction norms estimated in the preceding section would be expected mainly to reflect plastic responses to environmental variance.

Estimating reaction norms through logistic regression requires that first-time spawners can be identified, whether or not the estimation is based on reconstructed or actually observed immature fish. First-time spawners of Northeast Arctic cod can be identified on the basis of otolith patterns (presence or absence of the spawning check) and the maturation status of their gonads (Rollefsen, 1933). Otolith or scale patterns can be used to distinguish first-time spawners in a number of other fish species, including herring (Runnstrøm, 1936), flatfish (Devold, 1938), and salmonids (Scott and Scott, 1988; Wootton, 1998). If first-time spawners cannot be distinguished from repeat spawners, an alternative estimation approach can be used that utilizes age- and size-based maturity ogives; this requires data on immature fish but no separation between first-time and repeat spawners (Barot *et al*., 2002).

Age at maturation in Northeast Arctic cod has declined strongly over the 20th century (Jørgensen, 1990; Godø, 2000). The causes of this decline are still under debate. It has been suggested that the trend is primarily a compensatory response to reduced stock size (Jørgensen, 1990): nowadays, cod mature earlier because they grow faster than they used to. An alternative hypothesis states that the decline may be partially caused by fisheries-induced selection that has resulted in genetic change in the maturation age (Law and Grey, 1989). An analysis of maturation reaction norms for this stock, made possible by the reconstruction method introduced in this paper, would provide valuable insight into the causes of the observed decline.

Accurate and unbiased estimation of the reaction norm for age and size at maturation is an indispensable prerequisite for a sound understanding of maturation dynamics. Such understanding is critical in modern fisheries resource management: the precautionary approach generates a strong demand for efficient tools that permit reliable assessment of the the short- and long-term consequences of human exploitation for the viability and productivity of harvested populations.

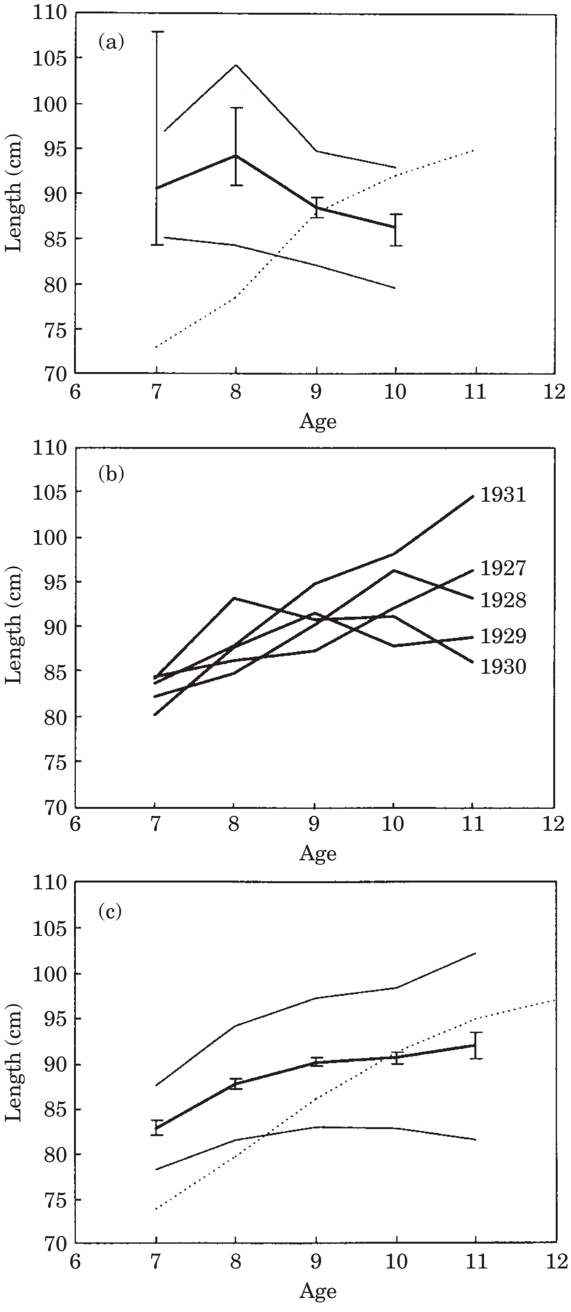

Figure 5. (a) The reaction norm for age and size at maturation for the Northeast Arctic cod cohort of 1926, based on the data depicted in Figure 4. The dark line shows the reaction norm midpoints at different ages (with 95% confidence intervals); the two light lines indicate the quartiles of the maturation reaction norm. The dashed line illustrates how the mean size at maturation varies with age at maturation. (b) Estimated reaction norms for the Northeast Arctic cod cohorts of 1927–1931. (c) Estimated joint reaction norm for those cohorts.

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Appendix: Calculating the fraction of maturing individuals from the maturity ogive

The maturity ogive describes how the fraction of mature fish varies with age, $o(a)=N_M(a)/N_T(a)$, where $N_M(a)$ is the abundance of mature fish at age a (including the newly matured ones of the year) and $N_T(a)$ is the total abundance of the cohort at age a. These abundances can be expressed in terms of abundances one year before, yielding

$$o(a)=\frac{\sigma_M(a-1)N_M(a-1)+\tilde{m}(a-1)\sigma_M(a-1)N_I(a-1)}{\begin{array}{c}N_T(a-1)[o(a-1)\sigma_M(a-1)+(1-o(a-1))\\(\tilde{m}(a-1)\sigma_M(a-1)+(1-\tilde{m}(a-1))\sigma_I(a-1))]\end{array}}$$

Here, $\sigma_M(a)$ denotes the survival probability of mature fish from age a to age a+1 (including fish maturing during that time interval), whereas $\sigma_I(a)$ denotes the survival probability of fish remaining immature. The abundance of immature fish at age a is $N_I(a)$ and $\tilde{m}(a)$ is the probability that an immature fish at age a starts maturation. Solving the above equation for $\tilde{m}(a-1)$, we obtain

$$\tilde{m}(a-1)=\frac{o(a)+o(a-1)[o(a)(r(a-1)-1)-r(a-1)]}{(o(a-1)-1)[o(a)(r(a-1)-1)-r(a-1)]},\quad(2)$$

where $r(a)$ denotes the ratio of the survival probability of mature or maturing fish and that of immature fish, $r(a)=\sigma_M(s)/\sigma_I(s)$.

After mortality takes place, the fraction $m(a)$ of fish maturing at age a will differ from the maturation probability $m\,(a-1)$ because of the differential survival of immature and maturing fish,

$$m(a)=\frac{(1-o(a-1))\sigma_M(a-1)\tilde{m}(a-1)}{\begin{array}{c}(1-o(a-1))[\tilde{m}(a-1)\sigma_M(a-1)\\+(1-\tilde{m}(a-1))\sigma_I(a-1)]\end{array}}.$$

Substituting $\tilde{m}(a-1)$ according to Equation (2) and simplifying yields

$$m(a)=\frac{o(a)-o(a-1)[r(a-1)-o(a)(r(a-1)-1)]}{1-o(a-1)[r(a-1)-o(a)(r(a-1)-1)]}.$$

Under the alternative assumption that maturing fish have the same survival probability as those remaining immature, the fraction $m(a)$ of fish maturing at age a can be calculated analogously, so

$$m(a)=\frac{o(a)-o(a-1)[r(a-1)-o(a)(r(a-1)-1)]}{1-o(a-1)}.$$

If there is no difference between the survival probabilities of immature and mature fish, $r(a)=1$, both expressions for $m(a)$ simplify to

$$m(a)=\frac{o(a)-o(a-1)}{1-o(a-1)}.$$