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Maturation Trends Suggestive of Rapid Evolution Preceded the Collapse of Northern Cod

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Contents

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Northern cod, comprising populations of Atlantic cod (*Gadus morhua*) off southern Labrador and eastern Newfoundland, supported major fisheries for hundreds of years[1]. In the late 1980s and early 1990s, however, northern cod underwent one of the worst collapses in the history of fisheries[2-4]. The Canadian government closed the directed fishing for northern cod in July 1992, but even after a decade-long offshore moratorium population sizes remain historically low[4]. Here we show that, up until the moratorium, the life history of northern cod continually shifted toward maturation at earlier ages and smaller sizes. Since confounding effects of mortality changes and growth-mediated phenotypic plasticity are accounted for in our analyses, this finding strongly suggests fisheries-induced evolution of maturation patterns, in the direction predicted by theory[5,6]. We propose that fisheries managers could use the method employed here as a tool that can provide warning signals about changes in life history before more overt evidence of population decline becomes manifest.

Commercially exploited fish stocks often show trends toward earlier maturation[7], which could involve fisheries-induced evolution[8-10]. Life-history theory predicts that increased mortality at potential ages and sizes at maturation selects for an earlier onset of maturation[5,6], and experiments with both wild and cultured fish show that the genetic variation needed for age at maturation to evolve clearly resides within populations[11,12]. However, another plausible explanation exists: earlier maturation may simply reflect phenotypic plasticity. Reduced stock biomass resulting from fishing can lead to increased resource availability and thus to accelerated growth for those fish remaining[13], and faster-growing fish generally mature at an earlier age than slower-growing fish[14]. Due to the difficulties involved in disentangling plastic and evolutionary components, the nature of phenotypic changes in exploited fish populations remains poorly understood[9].

For northern cod, the age at which the proportion of mature females reaches 50% has decreased from about 6 years in the mid-1980s to about 5 years in the mid-1990s (Fig. 1a). It is critical to realize, however, that this age at 50% maturity will depend not only on the maturation process itself, but also on conditions for growth and survival[15]. This makes interpretation of the reasons for changes in this quantity ambiguous. The collapse period was characterized by poor conditions for growth and a marked drop in the survival of fish at potential ages of maturation (Fig. 1b, c). Slower growth typically postpones maturation, which is the opposite of what was actually seen. Hence, it has been suggested that the collapse of northern cod was in fact a major selective episode favouring early-maturing genotypes relative to late-maturing genotypes[16]. Here, we aim to quantitatively test, for the first time, this "selective episode" hypothesis. We employ a novel method for estimating probabilistic reaction norms for age and size at maturation that overcomes the confounding effects of variation in growth and survival on maturation patterns[15] (see supplementary information). Reaction norms in general describe the different phenotypes produced by a genotype under different environmental conditions, and reaction norms for age and size at maturation in particular describe the maturation schedule of a genotype under different growth conditions[17]. Probabilistic reaction norms for age and size at maturation, then, describe the probability that immature individuals with given age and size will mature during a given time interval.

In other words, maturation probability is estimated conditional on the fact that these individuals have reached the considered age and size, the likelihood of which is influenced by growth and survival. Probabilistic maturation reaction norms are thus insensitive to variations in growth and survival (see supplementary information). Consequently, a trend in the maturation reaction norm strongly supports the hypothesis of evolutionary change having occurred in the maturation process itself[15].

We estimated maturation reaction norms for female cod captured during offshore research surveys (1977-2002) off southern Labrador (Northwest Atlantic Fisheries Organization Division 2J) through the Northeast Newfoundland Shelf (Division 3K) to the northern half of the Grand Bank off eastern Newfoundland (Division 3L). Together, these three neighbouring areas encompass the distribution area of a stock complex commonly termed the “northern cod”. First, as an illustration, we show the reaction norms for female cod from Division 2J born in 1980 and in 1987. A female growing at a mean rate would intercept the 50% maturation probability contour, the so-called reaction-norm midpoint, of the 1980 cohort at an age of about 6 years, whereas this age had decreased to about 5 years for the 1987 cohort (Fig. 2). This illustrates how, for a given growth rate, a lower-positioned reaction norm corresponds to maturation at an earlier age and smaller size. (Note that, technically, the use of reaction-norm terminology is justified as long as a significant proportion of variation in growth is due to environmental variability rather than genetic variance. For northern cod in the 2J and 3K Divisions, body condition was decreasing in parallel with mean length at age during the late 1980s and early 1990s[18], which suggests an environmental influence on size at age.). More generally, we found that the maturation reaction norm of northern cod has shifted continually toward younger ages and smaller sizes throughout the 1980s and early 1990s (Fig. 3). From about 1993-1994 onwards, however, this trend appears halted, and may even have reversed. In most cases, linear regressions of reaction-norm midpoints, characterizing the age-specific body lengths at which the probability of maturing reaches 50%, on cohort confirmed the statistical significance of these trends (Fig. 4). Since probabilistic maturation reaction norms are independent of variations in survival and growth-mediated phenotypic plasticity, we conclude that our analyses strongly support the hypothesis that early-maturing genotypes were favoured relative to late-maturing genotypes during the collapse of northern cod[16]. Our results agree well with predictions from recent modelling of life-history responses to exploitation: harvesting on both immature and mature individuals – as was the case for northern cod[2,4] – is expected to displace the reaction norm for age and size at maturation toward younger ages and smaller sizes[6]. The positive trend in maturation reaction norms since about 1993 suggests that the moratorium caused a shift in selection regime favouring maturation at older ages and larger sizes. However, the moratorium period so far spans only a decade, northern cod still experience relatively low survival, and population sizes have not rebuilt[4]. We therefore shall have to await the results of future research surveys in order to confirm whether the trend in maturation schedule has indeed reversed.

We note that two other processes, in addition to local fisheries-induced evolution, might have contributed to temporal variation in maturation reaction norms. First, gene flow from populations with different genetically determined life histories might have affected the genetic composition of the stock considered. Despite the fact that cod around Newfoundland is structured into genetically recognizable units[19], there is dispersal among these units[20]: some immigration of genotypes with different maturation schedules therefore cannot be rejected. Second, it is also possible, in principle, that plasticity not mediated by growth, such as social suppression of maturation[21], could have influenced the reaction norms.

To complete the picture, we estimated rates of phenotypic evolution for the reaction-norm midpoints (body length at 50% probability of maturing) at age 6 years in the period before the initiation of the moratorium. Such rates can be expressed in two different units. *Haldanes* express evolutionary rates relative to generation length and phenotypic standard deviation of the population in question, whereas *darwins* simply describe the ‘raw’ rate of evolutionary change (see Methods). Estimated rates are as follows: −13,600 (95% confidence limits: −19,100, −8,320) darwins and −1.20 (−1.74, −0.63) haldanes in Division 2J; −18,810 (−24,410, −14,660) darwins and −1.50 (−1.93, −1.20) haldanes in Division 3K; −7,150 (−14,270, −670) darwins and −0.63 (−1.69, 0.26) haldanes in Division 3L. Estimates in darwins are high, but comparable with rates from other studies covering a similar temporal scale[22,23]. In contrast, estimates in haldanes are higher than most previously published rates[22-24]. This, however, is probably explained by estimates in haldanes being normalized relative to a trait’s phenotypic standard deviation[23]: since reaction-norm midpoints are estimated by removing growth-mediated environmental variation from the data, the corresponding phenotypic standard deviations are diminished accordingly, and the resulting estimates in haldanes are therefore bound to systematically exceed those for other quantitative traits sensitive to environmental variation.

Empirical evidence is mounting in support of contemporary evolution in natural populations[25]. Fishing for grayling (*Thymallus thymallus*) in Norwegian mountain lakes has been shown to induce evolutionary changes in grayling maturation comparable to what we observed for northern cod[22]. On the Galápagos Islands, body weight and beak size of Darwin’s finches (*Geospiza fortis*) evolved in the course of a single generation in response to a change in the natural mortality regime[26]. Field experiments with a small freshwater fish, the guppy (*Poecilia reticulata*), have documented rapid evolution of life-history traits in response to altered regimes of natural mortality[11].

We suggest that the reaction-norm approach employed here might help fisheries managers by providing warning signals about life-history changes likely to be caused by heavy exploitation. To corroborate this claim, we calculated reaction norms and regression parameters based only on the data that had been available at earlier points in time. Focusing on fish of age 6 years (which gave the most precise estimates before the moratorium), we estimated the confidence according to which the reaction norms of northern cod were exhibiting a decline: already by 1985 this probability had risen to above 95% for the 3K Division. The same level of confidence was reached for the 2J Division in 1986, and for the 3L Division in 1989. While eroding maturation reaction norms can thus signal extreme exploitation pressures, they are not to be misinterpreted as signs of imminent stock collapse. Yet, exploitation pressures so strong that they overturn a species' natural pattern of life-history adaptation certainly ought to be cause for concern.

There is growing anxiety about the consequences of fisheries-induced evolution, since such evolution may ultimately result in lower sustainable yields[9,27] and reduced stock stability. Our study provides new evidence that intense fishing may indeed lead to rapid evolution of key life-history traits in harvested populations. Furthermore, we show that relaxing the selection pressures – in this case through such a drastic measure as closing the fishery – may halt the trend, thus providing a basis for cautious optimism about practical options for managing fisheries-induced evolutionary change.

Methods

Sampling

Atlantic cod were caught in spatially stratified random bottom-trawl surveys during autumn and early winter, initiated in 1977 (Division 2J and 3K) and 1981 (Division 3L)[4]. Beyond the age of 2 years, this sampling is considered representative. Most cod were sampled in the autumn prior to their spring spawning in the next year. Therefore, age of cod is expressed as if they were sampled after their nominal birthday (January 1), that is, their age is incremented by 1. Data on 10,778 female Atlantic cod of ages 3 to 6 years were used in the statistical analyses; younger and older individuals were excluded due to low sample sizes at these ages[4].

Statistical analyses

Maturation reaction norms, given by the probability $m(a,s)$ of maturing at age a and body length s, were derived from maturity ogives, given by the probability $o(a,s)$ of being mature at that age and length, using the relation introduced in ref. 28: $m(a,s)=[o(a,s)-o(a-1,s-\Delta s(a))]/[1-o(a-1,s-\Delta s(a))]$, where $\Delta s(a)$ is the annual length increment from age a–1 to age a. This relation is exact if immature and mature individuals of a given age and size have the same survival and growth rates, and it has been shown that the estimation of m is relatively robust to violations of these assumptions[28]. Estimating a maturation reaction norm thus involved five steps: (1) estimation of the required maturity ogives, (2) estimation of the required annual length increments, (3) calculation of the probability to mature, (4) estimation of reaction-norm midpoints, and (5) estimation of confidence intervals around these midpoints. Maturity ogives o were estimated through logistic regression, with maturity state (juvenile or mature) as a binary response variable. Weighting observations by population abundance at length[28,29] had negligible effect and was not incorporated. Relatively small sample sizes prevented analysing the full interaction between cohort c, age a, and body length s, when treating both cohort and age as factors. Standard model selection led to the treatment of age as a linear effect while keeping cohort as a factor: $\mathrm{logit}(o) = \beta_{1c} + \beta_{2c}a + \beta_3 s$, with regression coefficients β_{1c}, β_{2c}, and β_3. The second term allows detection of age-dependent temporal changes in the probability of being mature. For each cohort, annual length increments $\Delta s(a)$ were estimated by calculating mean body length at age a and subtracting mean body length at age a–1[28]. Reaction-norm midpoints were estimated, separately for each age and cohort, as $-\beta_1/\beta_2$ through logistic regression of $m(a,s)$ on body length s: $\mathrm{logit}(m) = \beta_1 + \beta_2 s$, with regression coefficients β_1 and β_2[28]. These midpoints could be estimated for ages 5 and 6 years; most individuals at ages 3 and 4 years are immature[4]. Confidence intervals for the reaction-norm parameters were obtained through bootstrap techniques[28,30]. A bootstrapped sample was constructed for each cohort and age, with individuals being chosen at random with replacement from the original data set. The resampling was repeated 1,000 times, and the 2.5% and 97.5% percentiles were extracted as lower and upper confidence limits, respectively, around the reaction-norm midpoints.

Linear regression of reaction-norm midpoints on cohort was used to test for the significance of temporal trends in maturation schedules. Confidence intervals around the regression parameters were generated from bootstrap replicates. Evolutionary rates in darwins were estimated by regressing log(reaction-norm midpoint) on time (in millions of years) since the first available data point[23]. Evolutionary rates in haldanes were estimated by regressing the reaction-norm midpoints, rescaled by their pooled phenotypic standard deviation, on the number of generations since the first available data point[23]. Generation length was estimated as the mean age of mature females. Phenotypic standard deviation of reaction-norm midpoints was computed as the square root of the variance of the probabilistic maturation envelope around reaction-norm midpoints. This envelope variance, which comprises genetic variance in the reaction-norm midpoint as well as environmental variance generated by factors other than growth, is the variance of the distribution of body lengths obtained by taking the derivative of the probabilistic maturation reaction norm with respect to body length. Durbin-Watson tests showed that temporal autocorrelations were not significant ($P > 0.1$).

Age at 50% maturity, annual length increments, and annual survival rates were estimated for the descriptive illustration in Fig. 1. Age at 50% maturity in year y was estimated as $-\beta_{1y}/\beta_{2y}$ through logistic regression on age of the probability o of females at ages $a = 3,\ldots,6$ years to be mature in year y, using year as a factor: $\mathrm{logit}(o) = \beta_{1y} + \beta_{2y}a$, with regression coefficients β_{1y} and β_{2y}. Annual survival probabilities at age a in year y were obtained from survey catch data[4] as $C_{ay}/C_{a\text{-}1,y\text{-}1}$, where C_{ay} denotes the catch abundance per unit effort at age a in year y.

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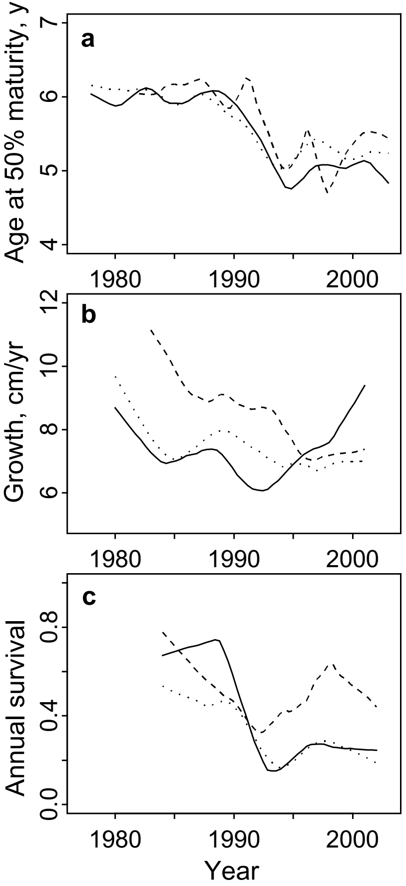
Supplementary information describing the probabilistic reaction norm method is available.

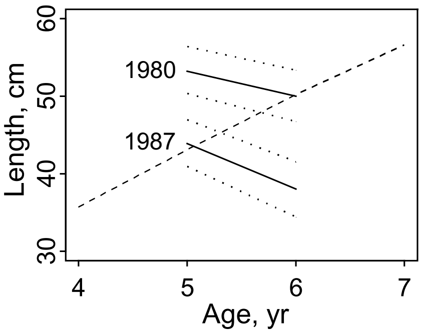
Figure 1 Background information on northern cod (*Gadus morhua*). Temporal trends in the traditional measure of maturation, the age at 50% maturity (a), annual length increments (b), and annual survival probabilities (c) of cod from Northwest Atlantic Fisheries Organization (NAFO) Division 2J (solid lines), 3K (dotted lines), and 3L (dashed lines). Maturity and length increments are from female cod, whereas survival estimates are not sex-specific. Length increments and survival are arithmetic and geometric averages, respectively, for 5 and 6 year old fish. Lines represent best fits using a local regression smoother.

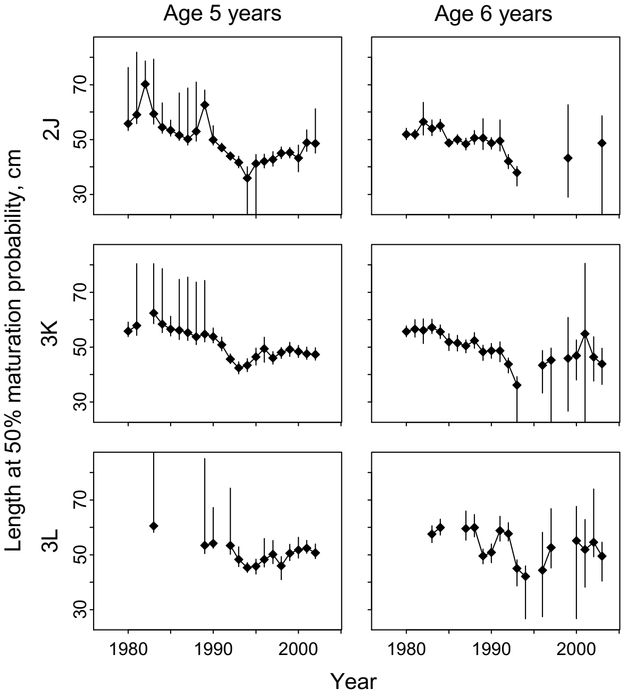
Figure 2 Cod maturation schedules. The reaction norms measure the probabilities for maturing at a certain size and age; here they are illustrated by lines connecting lengths of identical maturation probabilities at ages 5 and 6 years for female northern cod off southern Labrador (NAFO Division 2J) born in 1980 and 1987 (thick line: reaction-norm midpoints at 50% maturation probability, dotted lines: 25% and 75% maturation probabilities). The dashed line indicates the average growth trajectory.

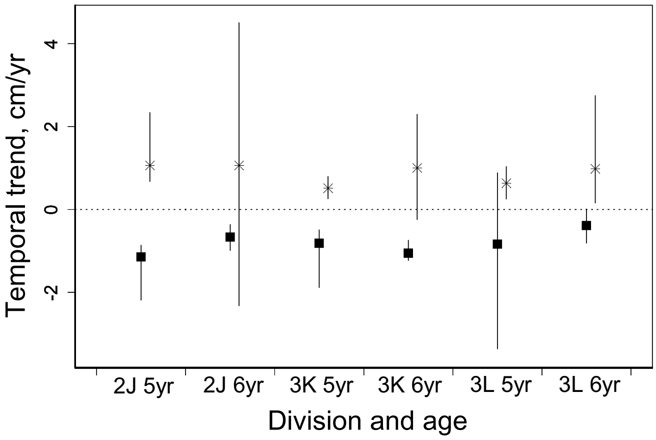
Figure 3 Temporal trends in cod maturation schedules. Midpoints of the maturation reaction norms, characterizing the age-specific body lengths at which the probability of maturing reaches 50%, for female northern cod (NAFO Divisions 2J, 3K, and 3L) of ages 5 years (left) and 6 years (right); vertical lines indicate 95% confidence intervals. Some midpoints are inestimable due to low sample sizes and lack of model fit.

Figure 4 Statistical significance of temporal trends in cod maturation schedules. Slope parameters with 95% confidence intervals, estimated from linear regression on year of reaction-norm midpoints of female northern cod (NAFO Divisions 2J, 3K, and 3L) at ages 5 and 6 years (Fig. 3); including years with directed cod fishing (1979-1992, squares), and recent years since the offshore moratorium on directed cod fishing was established (1993-2003, stars).


a
Age at 50% maturity, yr
4
5
6
7
1980
1990
2000
b
Growth, cm/yr
6
8
10
12
1980
1990
2000
c
Annual survival
0.0
0.4
0.8
1980
1990
2000
Year


1980
1987
Length, cm
30
40
50
60
Age, yr
4
5
6
7


Age 5 years
Age 6 years
Length at 50% maturation probability, cm
2J
3K
3L
30
50
70
1980
1990
2000
Year


Temporal trend, cm/yr
4
2
0
-2
2J 5yr
2J 6yr
3K 5yr
3K 6yr
3L 5yr
3L 6yr
Division and age

The probabilistic maturation reaction norm method

A probabilistic reaction norm for age and size at maturation describes the probability that an immature individual matures during a given time interval (e.g., one season) in dependence on its age and body size[1]. Characterizing an entire reaction norm thus involves specifying these probabilities for all relevant ages and body sizes. For many purposes, it will be convenient only to plot the reaction norm midpoints, i.e., those combinations of age and body size at which the estimated probability of maturing is 50% (Fig. 1a). An individual will thus tend to mature around the point where its growth trajectory hits the reaction norm midpoint, and variability in growth trajectories will cause a population to "sample" a certain part of its maturation reaction norm.

Probabilistic reaction norms for age and size at maturation are useful for disentangling genetic changes in maturation from phenotypic plasticity and from merely demographic effects[1,2]. This property results, first, from the conditioning that is inherent in the definition of a reaction norm: the probabilistic reaction norm approach overcomes the confounding effects of changes in growth and survival by modelling maturation probability conditional on individuals having reached a particular age and size, whereas the processes of growth and survival only determine the probability of an individual actually attaining any particular age and size. Second, since size at age integrates all environmental factors that affect the growth trajectory of an individual, reaction norms for age and size at maturation account for an aspect of environmental variability that is of key importance for understanding maturation dynamics[3].

We illustrate the arguments above in figure 1, in which maturation reaction norm midpoints are displayed for four scenarios. The first scenario (Fig. 1a) may be considered as the original, historic, situation, while in the other three scenarios maturation has shifted towards earlier ages (Fig. 1b-d). The second scenario (Fig. 1b) illustrates how an improvement in the environmental conditions for growth will increase the slope of growth trajectories. This will, in turn, change which part of the reaction norm can actually be observed, while leaving the position of the reaction norm itself unchanged. *Consequently, the maturation reaction norm is robust to growth-mediated phenotypic plasticity*. A shift in the position of the reaction norm itself would therefore strongly suggest a genetic change in maturation. Such a shift is identifiable irrespectively of whether or not environmental conditions for growth change during the period of observation (Fig. 1c-d).

While maturation reaction norms provide a description of the maturation process from which both growth-mediated plastic and demographic effects have been removed, some environmental effects are bound to remain. The reason is that age and size cannot explain all variation in maturation in a population. For example, an individual in good body condition is likely to have a higher probability of maturing than an individual of the same age and body length that is in a poor condition[4]. However, this effect would only confound the conclusions on temporal trends if there were a trend in body condition that is not translated into size at age. Social effects on maturation[5] might also influence maturation reaction norms, but seem unlikely to play a significant role in most fish.

Using reaction norms for studying evolutionary change is based on two further assumptions. First, reaction norms are considered as heritable quantities. There is clear evidence in support of this assumption[6,7]. Second, the use of reaction norm terminology implies that the observed variation in growth is mostly due to environmental causes. This is, however, mainly a terminological issue. While there certainly is evidence for genetic variability in the growth rates of fishes[8], environmental variability of growth rates typically is substantial. Fortunately, the valuable descriptive properties of maturation reaction norms do not depend on the origin of growth variability.

The maturation reaction norm method described here is geared toward data collected at regular time intervals. For many fish stocks, annual seasonality and the schedules of research surveys result in such regularity. However, for other populations, the maturity status of individuals may be recorded at irregular intervals, or even continually. In such cases, it will be advantageous to switch from maturation probability to maturation rate as the dependent variable of probabilistic reaction norms.

Maturation reaction norms must not be confused with a more traditional descriptive measure of the maturation status of a population, the proportion of mature individuals as functions of age, body size, or both (commonly referred to as maturity ogives in fisheries science and the basis for the estimates of age at 50% maturity reported in Figure 1a)[1]. All these proportions are influenced, not only by maturation, but also by growth and survival. Consequently, maturity ogives cannot be used to characterize the maturation process directly, and, since they are also affected by processes of growth and survival, maturity ogives alone cannot provide more than circumstantial evidence for evolutionary changes in a population's maturation process.

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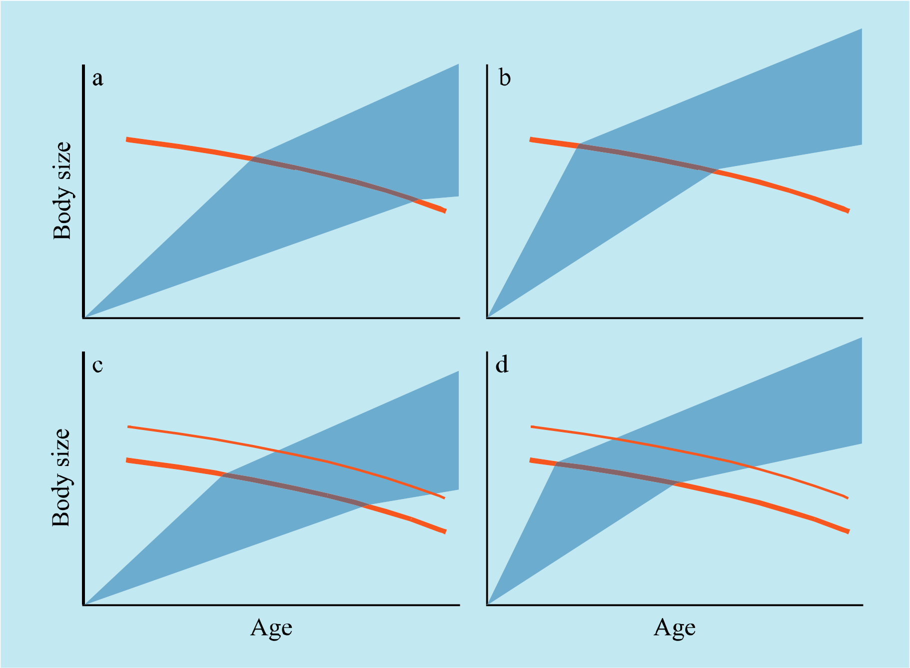

Figure 1 Probabilistic reaction norms for age and size at maturation. Thick orange curves shows reaction norm midpoints, that is, combinations of age and size at which the probability of maturing is 50%. In each of the four scenarios shown, maturation is likely to occur in the vicinity of this curve. Growth trajectories (spread across the dark blue area) determine which part of the reaction norm will be observed (a-d). An increase in growth rates (from a to b) leads to earlier maturation along a different part of the reaction norm, but will not change the observed position of the reaction norm itself (b). By contrast, a genetic change (from a to c or d) toward maturation at younger ages and smaller sizes results in a shift of the reaction norm: the observed midpoints (thick orange curves) therefore differ from the initial ones (thin orange curves). Importantly, the corresponding shift in the position of the reaction norm can be detected both in the absence (c) and in the presence (d) of concomitant environmental change in growth rates. Adopted from ref. 9.