

Assessing changes in age and size at maturation in collapsing populations of Atlantic cod (*Gadus morhua*)¹

Esben Moland Olsen, George R. Lilly, Mikko Heino, M. Joanne Morgan, John Bratley, and Ulf Dieckmann

Abstract: By estimating probabilistic reaction norms for age and size at maturation, we show that maturation schedules of Atlantic cod (*Gadus morhua*) off Labrador and Newfoundland shifted toward earlier ages and smaller sizes during the late 1980s and early 1990s, when these populations underwent a severe collapse in biomass and subsequently were closed for directed commercial fishing. We also demonstrate that this trend towards maturation at younger ages and smaller sizes is halted and even shows signs of reversal during the closure of the fisheries. In addition, our analysis reveals that males tend to mature earlier and at a smaller size than females and that maturation age and size decrease with increasing latitude. Importantly, the maturation reaction norms presented here are robust to variation in survival and growth (through phenotypic plasticity) and are thus strongly indicative of rapid evolutionary changes in cod maturation as well as of spatial and sex-specific genetic variation. We therefore suggest that maturation reaction norms can provide helpful reference points for managing harvested populations with evolving life histories.

Résumé : L'estimation de normes probabilistes de réaction pour l'âge et la taille à la maturation nous permet de démontrer que les calendriers de maturation de la morue franche (*Gadus morhua*) au large du Labrador et de Terre-Neuve ont glissé vers des âges plus précoces et des tailles plus basses au cours de la fin des années 1980 et du début des années 1990; à ce moment, ces populations ont connu un effondrement important de leur biomasse, après quoi il y a eu interdiction de la pêche commerciale ciblée. Nous démontrons aussi que la tendance vers une maturation à des âges plus précoces et à des tailles plus petites s'est arrêtée et a même montré des signes de retour en arrière durant la période d'interdiction de la pêche. De plus, notre analyse démontre que les mâles tendent à atteindre la maturité plus jeunes et plus petits que les femelles et que l'âge et la taille à la maturation décroissent en fonction de l'augmentation de la latitude. Il est important de noter que les normes de réaction de maturation que nous présentons sont robustes vis-à-vis la variation de la survie et de la croissance (via la plasticité phénotypique) et qu'elles indiquent ainsi fortement l'existence de changements évolutifs rapides dans la maturation des morues, ainsi que des variations génétiques en fonction de l'espace et du sexe. Nous croyons donc que les normes de réaction de la maturation peuvent fournir des points de référence utiles pour la gestion de populations exploitées à cycle biologique en cours de modification.

[Traduit par la Rédaction]

Introduction

There is accumulating evidence that significant evolutionary changes may occur on contemporary timescales in natural populations, often within just a few years or decades

(Reznick et al. 1990; Hendry et al. 2000; Grant and Grant 2002). In some cases, such changes may be brought about by single episodes of particularly strong selection. For instance, the beak size of Darwin's finches (*Geospiza fortis*) on the Galapagos Islands evolved in response to a drought

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episode occurring within the timescale of one generation (Grant and Grant 2002). In the light of these findings, it has recently been argued that microevolution should be accounted for in the management of harvested populations and, more generally, in conservation biology (Stokes and Law 2000; Stockwell et al. 2003; Ferrière et al. 2004).

The populations of Atlantic cod (*Gadus morhua*) found off Labrador and Newfoundland in the Northwest Atlantic supported rich fisheries for hundreds of years (Templeman 1966; Hutchings and Myers 1995) but suffered a major decline in the early 1970s and a collapse in the late 1980s to early 1990s (Taggart et al. 1994; Myers et al. 1997). This collapse forced the Canadian government to close down much of the cod fisheries, and many coastal communities that used to depend on the cod experienced much economic and social hardship (Felt and Locke 1995). The moratorium on cod fishing has remained in effect in the areas that used to support the largest catches of cod (Lilly et al. 2003).

Evolutionary theory predicts that the heavy mortality imposed by industrial fisheries may cause evolutionary changes in exploited fish populations (Law and Grey 1989; Policansky 1993; Abrams and Rowe 1996). Especially, an increase in mortality at potential ages and sizes at maturation is expected to select for an earlier onset of maturation (Charlesworth 1994; Taborsky et al. 2003; Ernande et al. 2004). Specifically, it has been hypothesized that the collapse of the Canadian cod populations was a major selective episode strongly favouring early-maturing genotypes relative to late-maturing genotypes (Hutchings 1999).

Yet, detecting contemporary evolution in the wild is a major challenge. It requires that genetic changes are successfully identified among the total phenotypic variation. Expressed life history traits will be influenced not only by genetics but also by environmental variation through phenotypic plasticity. Harvested fish populations typically show trends towards an increased percentage of mature individuals at younger ages and smaller sizes, the Canadian cod populations being no exception (Trippel 1995). While these changes could reflect genetic responses to fishing mortality (Law and Grey 1989; Heino 1998; Heino and Godø 2002), they may also result, through phenotypic plasticity, from increased resource availability and faster growth of survivors after stock biomass has been depleted. Faster-growing individuals will often mature at an earlier age than slower-growing individuals (Alm 1959). Because of such confounding effects, the nature of phenotypic changes in exploited fish populations is not yet well understood (Law 2000).

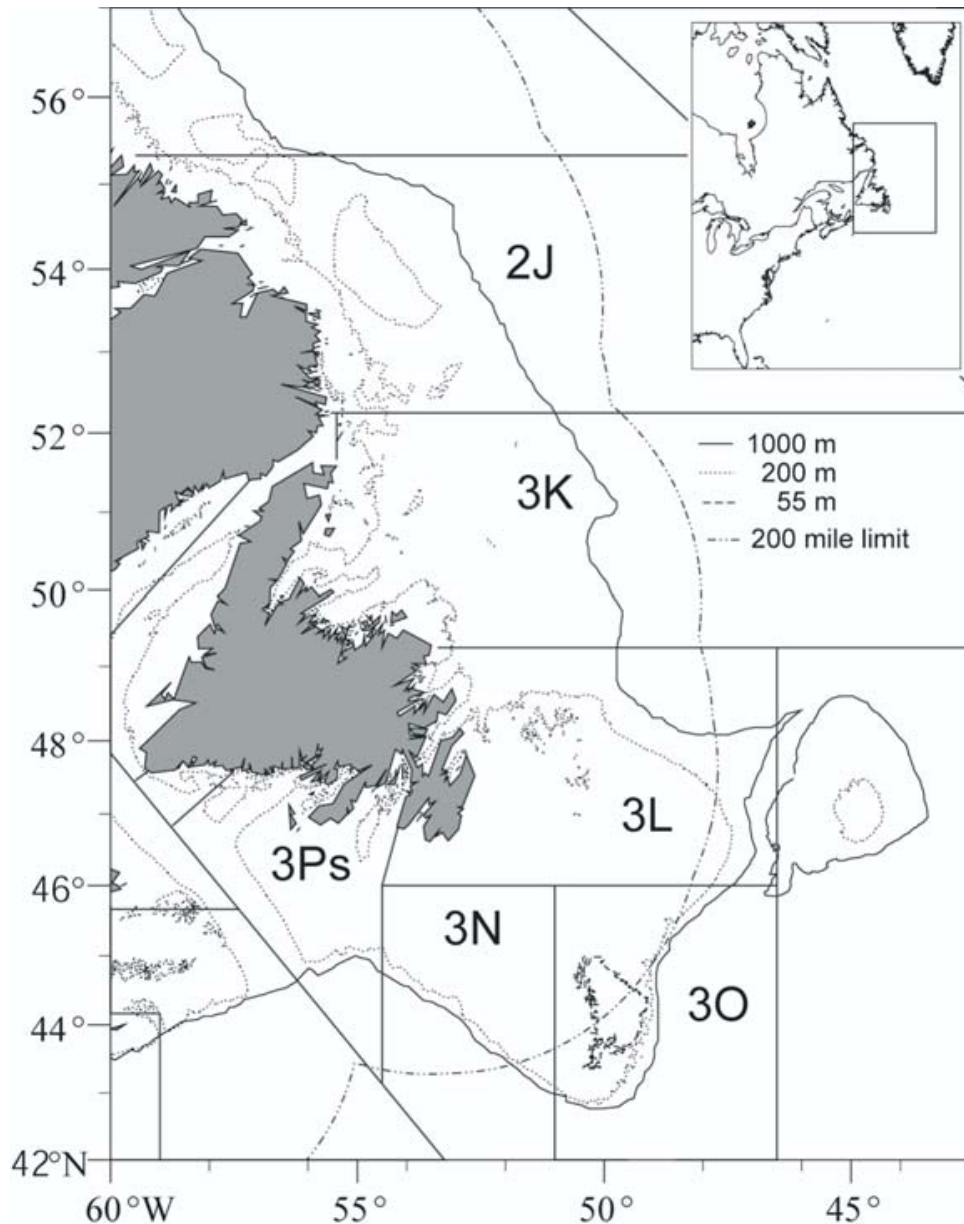
Maturation reaction norms can shed new light on the relative roles of environmental fluctuations and genetic changes as causes of variation in maturation patterns (Heino et al. 2002a). By definition, a reaction norm describes the phenotypes expressed by a genotype under different environmental conditions (Schmalhausen 1949). Stearns and Koella (1986) used variation in somatic growth as a surrogate for variation in environmental conditions when modeling reaction norms for age and size at maturation. A recently developed probabilistic extension of this reaction norm approach (Heino et al. 2002a) models the maturation process based on the probability that individuals having reached a given age and size mature in the next season. By construction, this probability is independent of variations in growth and survival that de-

termine the likelihood that individuals reach a given age and size (Heino et al. 2002a). Hence, the probabilistic reaction norm approach is useful for detecting changes in maturation, without being confounded by changes in growth and survival, and can thereby help to disentangle the effects of phenotypic plasticity and of genetic variation on maturation (see Materials and methods: Maturation reaction norms). The probabilistic maturation reaction norm terminology assumes that variation in growth is mainly environmentally determined (see Discussion).

For management purposes, it is important to be able to detect changes in life histories in exploited populations as early as possible. There are several reasons for this need. First, rapid evolutionary life history responses caused by experimental harvesting that mimics fishing (removal of larger individuals) have been shown to cause a significant reduction in harvestable biomass (Conover and Munch 2002). Second, in Atlantic cod and in many other species of fish, young females are known to breed for a shorter period, produce fewer egg batches, exhibit lower fecundity, and produce smaller eggs with lower fertilization and hatching rates compared with older spawners (Trippel 1998; Berkeley et al. 2004a). Third, it is important to understand the underlying causes of changes in life histories, in particular, whether these are mainly due to phenotypic plasticity or genetics. While plastic changes are in principle easily reversible, this may not be the case for genetic changes. Fourth, detecting life history changes at an early stage may aid managers by providing important additional clues about the status of a population. While population size is often the variable of focal interest for managers, it can be very difficult to detect changes in the abundance of populations in the wild. In oceanic fish populations, uncertainties in harvest statistics are typically large, and the same applies to population abundance surveys (Trippel 1995; Myers et al. 1997). An observed shift toward earlier maturation could then serve as a "stress" indicator (Trippel 1995).

In this study, we employ the new method of estimating probabilistic reaction norms for age and size at maturation of Atlantic cod populations found off Labrador and Newfoundland in the Northwest Atlantic. We characterize the maturation process in the years prior to, during, and after the dramatic collapse of these populations in the late 1980s and early 1990s, independently of temporal changes in growth and survival rates, and thereby provide new insights about the biology of these stocks as well as about the relative roles of environmental fluctuations and genetic changes as causes of changing maturation patterns. Previously, we have estimated maturation reaction norms for female cod from off southern Labrador and eastern Newfoundland (Olsen et al. 2004), finding evidence for maturation reaction norms having shifted toward earlier ages and smaller sizes during the stock collapse, which strongly suggests that an evolutionary response to high fishing pressure took place in this period. Here, we expand on these findings by comparing the maturation reaction norms of both female and male cod sampled from a broader geographic area. We also discuss how reaction norms for age and size at maturation may serve as biological indicators, or reference points, for the management of harvested populations.

Fig. 1. Study area off the coast of Labrador and Newfoundland in eastern Canada (inset) showing physiographic features and North-west Atlantic Fisheries Organization (NAFO) Divisions 2J, 3K, 3L, and 3NO and Subdivision 3Ps.



Materials and methods

Northern (2J3KL) cod

The designation “northern cod” refers to Atlantic cod found off southern Labrador (Northwest Atlantic Fisheries Organization (NAFO) Division 2J) through the Northeast Newfoundland Shelf (Division 3K) to the northern half of the Grand Bank off eastern Newfoundland (Division 3L) (Fig. 1). Northern cod is probably structured into several (sub)populations (Templeman 1966; Ruzzante et al. 1998; Beacham et al. 2002).

The collapse in the late 1980s and early 1990s reduced the cod abundance to about 2% of that in the early 1980s (Taggart et al. 1994; Myers et al. 1997; Lilly et al. 2003). There has been much controversy about the relative importance of fishing mortality, natural mortality, and emigration

as causes of the collapse. Some argue that fishing was by far the most important driving factor (Hutchings and Myers 1994; Hutchings 1996; Myers et al. 1996). Others suggest that a spectrum of environmental factors, both abiotic and biotic, changed during the period of stock collapse; these factors may have increased the natural mortality of cod as well as induced shifts in its geographical distribution (Baird et al. 1992; deYoung and Rose 1993; Kulka et al. 1995). Still, there is broad agreement that increased fishing mortality was an important factor in the collapse (Rose et al. 2000; Smedbol et al. 2002).

In July 1992, the Canadian government declared a moratorium on directed fishing of northern cod. This moratorium has remained in effect in the offshore but was lifted for a few years (1998–2002) to allow a small fishery in the inshore (Lilly et al. 2003). Despite the moratorium, northern

cod has not recovered, and its estimated population biomass remains at a historically low level (Lilly et al. 2003). There are several hypotheses as to why northern cod has not recovered; these include bycatches in fisheries directed at other species (Lilly et al. 2003), poor food availability (Rose and O'Driscoll 2002), increased predation from harp seals (Bundy 2001), various Allee effects (Frank and Brickman 2000; De Roos and Persson 2002; Rowe and Hutchings 2003), predation by other fish on cod eggs, larvae, and very early juveniles (Swain and Sinclair 2000; Walters and Kitchell 2001), and reductions in the reproductive potential of the spawning fish (Trippel 1995; Anderson and Rose 2001). The last hypothesis is inspired by the low number of spawning individuals and the truncated age distribution now characterizing the northern cod populations (Lilly et al. 2003).

Southern Grand Bank (3NO) cod

Cod in NAFO Divisions 3NO inhabit the southern Grand Bank of Newfoundland (Fig. 1). Like northern cod, the 3NO cod populations suffered a major decline in biomass in the late 1980s and early 1990s (Myers et al. 1997; Healey et al. 2003). The population structure of 3NO cod is not rigorously defined, and some seasonal mixing with cod in Subdivision 3Ps may occur (Healey et al. 2003). A moratorium on directed fishing of 3NO cod was imposed in February 1994 and has remained in effect since. Despite this effort, 3NO cod also has not recovered (Healey et al. 2003). It is suggested that bycatch of cod in other fisheries has increased to a point where it is impeding stock recovery (Healey et al. 2003).

St. Pierre Bank (3Ps) cod

Cod in NAFO Subdivision 3Ps is found south of Newfoundland on and around the St. Pierre Bank (Fig. 1). The population structure of 3Ps cod is not well defined, and the stock is considered a complex mixture of subcomponents. The abundance of 3Ps cod decreased substantially in the late 1980s and early 1990s, although the collapse was not as dramatic as for northern cod or for southern Grand Bank cod (Myers et al. 1997; Lilly et al. 2003). The 3Ps cod stock was under a moratorium from August 1993 to 1997, and population sizes have, in marked contrast with northern cod and southern Grand Bank cod, rebuilt to a considerable extent since the collapse (Brattey et al. 2003).

Analyzed data

We analyzed data on Atlantic cod caught in stratified random bottom-trawl surveys conducted annually by the Canadian Department of Fisheries and Oceans. Autumn surveys cover the distribution range of northern cod (2J3KL), while the data on cod from the southern Grand Bank (3NO) and the St. Pierre Bank (3Ps) are mainly from spring surveys. There is also a spring survey on northern cod from Division 3L. The autumn surveys are normally conducted during October to November and the spring surveys usually during April to May. The autumn survey was initiated in Divisions 2J and 3K in 1977 and in Division 3L in 1981. The spring survey was initiated in Divisions 3L, 3N, and 3O in 1971 and in Division 3Ps in 1972. Age and maturity sampling of captured cod was stratified by fish body length (Shelton et al. 1999; Lilly et al. 2003). Cod were aged on the basis of

otoliths that contain annual rings reflecting a fish's seasonal growth pattern (Rollesfsen 1933). Sex and maturity status were determined by visual inspection of the gonads. Body length was measured to the nearest centimetre. Age is here expressed as if the cod were sampled on their nominal birthday (1 January), which required adding 1 year to the ages from the autumn survey. Further details about sampling procedures and data are given in Lilly et al. (2003), Brattey et al. (2003), and Healey et al. (2003).

All cod of age 1 and 2 years were juvenile and were not included in the analyses. These youngest age-classes were also poorly represented in the samples owing to the sampling device used (Lilly et al. 2003). Note that the Engel trawl used for sampling the cod was changed in 1995, and the new Campelen trawl is more effective at catching the smallest cod (Lilly et al. 2003).

For 2J3KL cod, sample sizes of fish aged 7 years and older dropped to very low levels in the early 1990s (Lilly et al. 2003); robust estimates of the parameters describing growth and maturation at these ages could therefore not be obtained. Accordingly, analyses of maturation patterns were performed on 3- to 6-year-old fish. Most males in 2J3KL are mature at age 7, and most females in 2J3KL are mature at age 8 (Lilly et al. 2003). For 3NO and 3Ps cod, analyses were performed on 3- to 8-year-old fish. The statistical analyses were based on a total sample of 57 532 fish (Table 1).

The spring data from Division 3L were included mainly for comparison with the autumn survey in this area. This comparison will determine if sampling fish in the fall, several months before spawning, has an impact on the results. The cod considered in this study spawn mainly during a 3- to 4-month period in late winter and spring (Hutchings and Myers 1993; Myers et al. 1993), and it is possible that recruit spawners could develop gonads over the winter. Unless otherwise specified, Division 3L will hereafter refer to the autumn survey.

Maturation reaction norms

The probabilistic reaction norm for age and size at maturation is defined by the age- and size-specific probabilities with which an immature individual matures during a given time interval (Heino et al. 2002a). A description of the entire reaction norm involves specifying these probabilities for all relevant ages and sizes. For many purposes, it will be convenient to plot only the reaction norm midpoints, i.e., those combinations of age and size for which the estimated probability of maturing is 50%.

Maturation reaction norms should not be confused with other quantities, known as maturity ogives, traditionally used for describing a population's maturation status by estimating the proportion of mature individuals at a given age. The development of methods for estimating probabilistic maturation reaction norms was motivated by realizing that maturity ogives depend not only on the inherent maturation tendency of individuals (which is genetically coded) but also on the prevailing conditions for growth and survival (which affect the ogives both directly and through phenotypic plasticity). By contrast, the probabilistic reaction norm approach overcomes the potential confounding effects of growth and mortality, by estimating maturation probabilities conditional on individuals having reached a certain age and size. Variation

Table 1. Sample sizes for surveys of Atlantic cod (*Gadus morhua*) conducted annually by the Canadian Department of Fisheries and Oceans in Northwest Atlantic Fisheries Organization (NAFO) Divisions 2J, 3K, 3L, and 3NO and Subdivision 3Ps.

Division	Survey	Years	Ages (years)	Females	Males	Total
2J	Autumn	1977–2002	3–6	3 711	3 773	7 484
3K	Autumn	1977–2002	3–6	4 667	4 364	9 031
3L	Autumn	1981–2002	3–6	3 133	3 131	6 264
3L	Spring	1971–2002	3–6	4 077	3 962	8 039
3NO	Spring	1971–2002	3–8	6 822	6 764	13 586
3Ps	Spring	1972–2002	3–8	6 958	6 170	13 128
Total				29 368	28 164	57 532

Note: No data exist for spring 1974 in Subdivision 3Ps, spring 1983 in 3NO, and autumn 1984 in 3L.

in growth will thus only influence which parts of a reaction norm can be observed but is expected to leave the position of the reaction norm unchanged. A consistent shift in the position of the reaction norm itself is thus strongly indicative of an evolutionary change in maturation (Stearns and Koella 1986; Heino et al. 2002a). This view assumes that maturation reaction norms are under genetic control and may evolve in response to selection pressures (Via and Lande 1985; Stearns and Koella 1986). There is evidence for genetic variation in reaction norms in fishes, both for early life history traits (Haugen and Vøllestad 2000) and for sexual maturation (McKenzie et al. 1983).

The data available for this study do not distinguish between first-time and repeat spawners. To estimate the probability of maturing, we used a refinement of the probabilistic reaction norm method (Barot et al. 2004a) by which the probability of maturing at age a and size s , denoted by $m(a, s)$, is derived from the probability of being mature at age a and size s , denoted by $o(a, s)$, and from the mean annual growth increment at age a , $s(a)$:

$$(1) \quad m(a, s) = \frac{[o(a, s) - o(a - 1, s - \Delta s(a))]/[1 - o(a - 1, s - \Delta s(a))]}{[o(a, s) - o(a - 1, s - \Delta s(a))]/[1 - o(a - 1, s - \Delta s(a))]}$$

where $\Delta s(a)$ refers to the length gained from age $a - 1$ to age a . The function $o(a, s)$ is referred to as the age- and size-based maturity ogive. The above equation for $m(a, s)$ determines the probability of maturing as the frequency of fish that have matured (numerator) relative to the frequency of fish that could have matured (denominator). The equation is exact only when immature and mature individuals within a given age- and size-class have the same survival and growth rates. As demonstrated by Barot et al. (2004a), this estimation is relatively robust to a relaxation of this assumption.

Estimating maturation probabilities thus involves four steps: (i) estimation of maturity ogives, (ii) estimation of growth rates, (iii) estimation of the probabilities of maturing, and (iv) estimation of confidence intervals around the obtained maturation probabilities. Maturity ogives were estimated by fitting logistic regression models to the data (Collett 2003), with individual maturity state (juvenile or mature) as a binary response variable. We carried out separate analyses for each sex and NAFO Division (Divisions 3N and 3O were pooled to accommodate for their small samples sizes). We were not able to analyze the full interaction between cohort, age, and body length while using cohort and

age as factors. Barot et al. (2004a) showed that such a full model requires sample sizes of about 100 individuals per cohort and age-class to obtain robust estimates. Therefore, our ogive model had to be simplified. By inspecting parameter estimates and their errors, and through standard model selection (Collett 2003) based on different candidate models, we decided to model age as a variate (linear effect) while keeping cohort as a factor; also, the interaction effect between cohort and age could be retained in the model

$$(2) \quad \text{logit}(o) = \beta_0 + \beta_1 \cdot \text{length} + \beta_{2,c} + \beta_3 \cdot \text{age} + \beta_{4,c} \cdot \text{age}$$

where c denotes cohort. The cohort \times age interaction (fifth term) is needed for detecting age-dependent temporal changes in the probability of being mature. Growth was estimated as the difference in mean body length between two consecutive ages of a cohort. Reaction norm midpoints were estimated by fitting logistic regression models to the reaction norm estimates, $m(a, s)$, independently for each age and cohort

$$(3) \quad \text{logit}(m) = \beta_0 + \beta_1 \cdot \text{length}$$

and substituting 0.5 for m (Barot et al. 2004a).

As described above, probabilities of maturing are obtained through a sequence of statistical analyses. Since confidence intervals for the reaction norm parameters thus cannot be obtained directly, bootstrap techniques are used instead (Manly 1997). A bootstrapped sample was constructed for each cohort and age, where individuals are chosen at random with replacement from the original data set. The resampling was repeated 1000 times. We fitted linear regression models to the reaction norm midpoints to test for temporal trends in maturation. Confidence intervals around the regression parameters were derived from the 1000 bootstrap replicates, with the 2.5 and 97.5 percentiles being set as lower and upper confidence limits, respectively. All analyses were performed without weighting the observations by population abundance at length (Morgan and Hoenig 1997; Barot et al. 2004a), since preliminary analyses revealed that such weighting did not affect the conclusions about the data but tended to introduce more noise in the model estimates.

Survival and age at 50% maturity

Mainly for descriptive purposes, we present estimates of annual survival rates and of the traditional ogive-based measure of maturation, the age at 50% maturity. Annual survival

probabilities $S_{a,y}$ at age a in year y were estimated from survey catch data as

$$(4) \quad S_{a,y} = C_{a,y}/C_{a-1,y-1}$$

where $C_{a,y}$ is the catch abundance per unit effort at age a in year y (Brattey et al. 2003; Healey et al. 2003; Lilly et al. 2003). The change in survey gear that took place in 1995 (Engel trawl replaced with Campelen trawl) could potentially have influenced trends in survival; hence, the Engel data have been transformed to Campelen equivalents (for details, see Lilly et al. 2003). These Campelen equivalents were available for the years 1983–1994. Age at 50% maturity was estimated from logistic regression models with year as a factor and age as a variate:

$$(5) \quad \text{logit}(o) = \beta_0 + \beta_1 \cdot \text{age} + \beta_{2,y} + \beta_{3,y} \cdot \text{age}$$

Results

Survival, growth, and age at 50% maturity

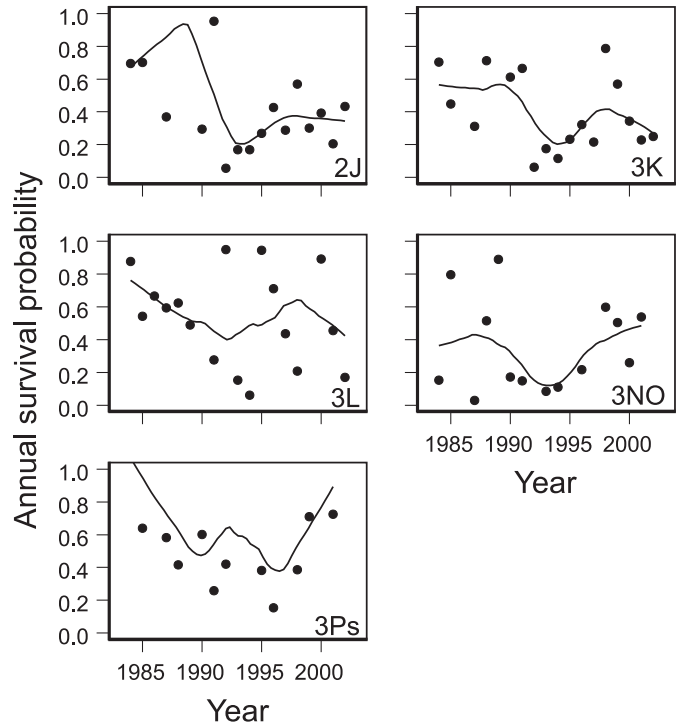
The estimates of annual survival probabilities are relatively noisy, but very low values are found in the early 1990s (Fig. 2). The estimates are generally higher again during the moratorium years (Fig. 2). Annual length increments, averaged for 4- to 6-year-old cod, lie between 4 and 12 cm·year⁻¹ (Fig. 3). The growth estimates are lower in the north (Divisions 2J and 3K) compared with the south (Divisions 3NO and 3Ps) (Fig. 3). There are no clear temporal trends in growth rates, but the lowest estimates are found in the early to mid-1990s (Fig. 3). In Divisions 2J, 3K, and 3L, the age at 50% maturity in females decreased from about 6 years in the 1980s to about 5 years in the mid-1990s (Fig. 4). In Divisions 3NO and 3Ps, the age at 50% maturity in females varied between 5.5 and 7 years in the 1970s and 1980s and decreased to about 4.5–5.5 years in the 1990s (Fig. 4). Male age at 50% maturity is about 1 year below female age at 50% maturity and shows a similar trend over time (Fig. 4). Our analyses agree with results that have been reported earlier in terms of instantaneous total mortalities, mean body length at age, and maturity ogives (Brattey et al. 2003; Healey et al. 2003; Lilly et al. 2003).

Maturation reaction norms

We were able to estimate maturation reaction norms for two or three ages for a given sex and division. For younger or older fish outside such an age bracket, data were either too sparse or too skewed towards juvenile or mature individuals. As an example, we show the reaction norms for female and male cod of the 1980 cohort in Division 3Ps. These reaction norms had negative slopes, meaning that the body length at which the cod reach a given maturation probability decreases with age (Fig. 5). Furthermore, the male reaction norms were positioned below the female reaction norms (Fig. 5), implying that for a given age and body length, a male has a higher maturation probability than a female. These patterns were qualitatively similar for most other cohorts for which reaction norms could be estimated (additional reaction norms are not shown but can be derived from Figs. 6 and 7).

Maturation patterns varied throughout the survey period. Most notably, there is a consistent temporal trend in all five

Fig. 2. Mean annual survival rates of 4- to 6-year-old Atlantic cod (*Gadus morhua*) from Northwest Atlantic Fisheries Organization (NAFO) Divisions 2J, 3K, 3L, and 3NO and Subdivision 3Ps fitted with a locally weighted regression smoother. The smoothing parameter (span) is set to 0.5. Point estimates exceeding 1 are not shown but were included when fitting the regression.

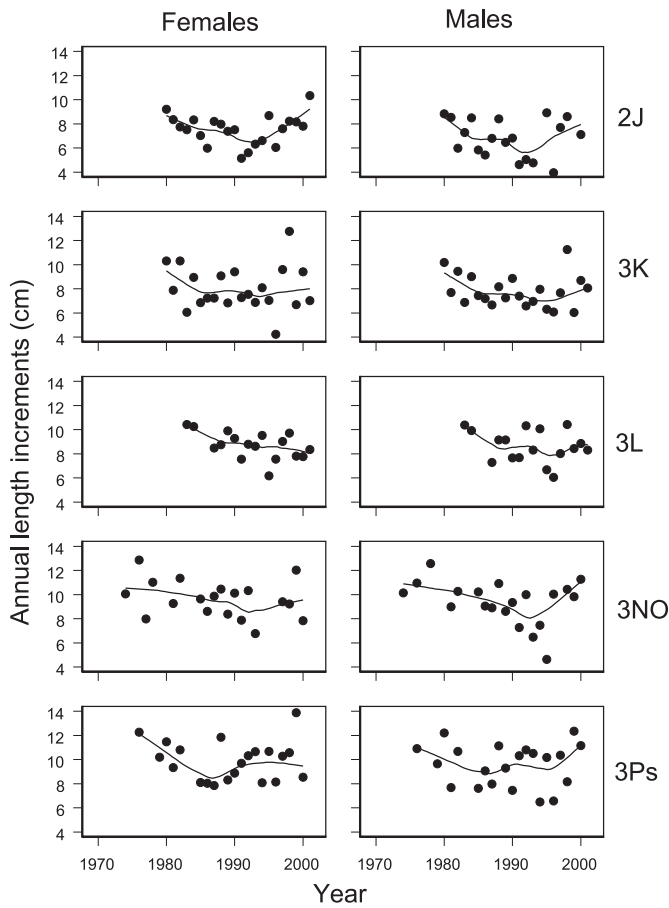


geographic areas (2J, 3K, 3L, 3NO, and 3Ps) and for both males and females: reaction norm midpoints (i.e., age-specific body lengths resulting in a 50% probability of maturing) decline by about 15–25 cm through the 1980s and early 1990s (Figs. 6 and 7; Table 2). This decline in reaction norm midpoints means that maturation at a given growth rate shifted toward earlier ages and smaller body lengths. Furthermore, there appears to be a moment in time, around 1993–1995, from which onwards there is no further decrease in reaction norm midpoints (Figs. 6 and 7; Table 2). We used the year in which each moratorium was introduced as a logical break point for analyzing these finer patterns in the data. For the period subsequent to the start of each moratorium, there is evidence for differences among the sexes in the trends in reaction norm midpoints. The females show a significantly positive slope in all geographic areas, although not always at age 6 years, owing to sparse data at that age (Table 2). Males show a significantly positive slope only in Divisions 3K and 3L, and their slopes are generally not as steep as for the females in the same areas (Table 2).

Together, Figs. 5–7 suggest that (independent of differences in growth and survival) males tend to mature at smaller body sizes and younger ages compared with females and that there is a spatial trend by which maturation probabilities increase with latitude for all ages and sizes. These patterns are best seen by comparing smoothed temporal trends in reaction norm midpoints at age 5 years for all divisions (Fig. 8).

Notice that changes in the observed sizes and maturity frequencies at each age occurring over winter could, in prin-

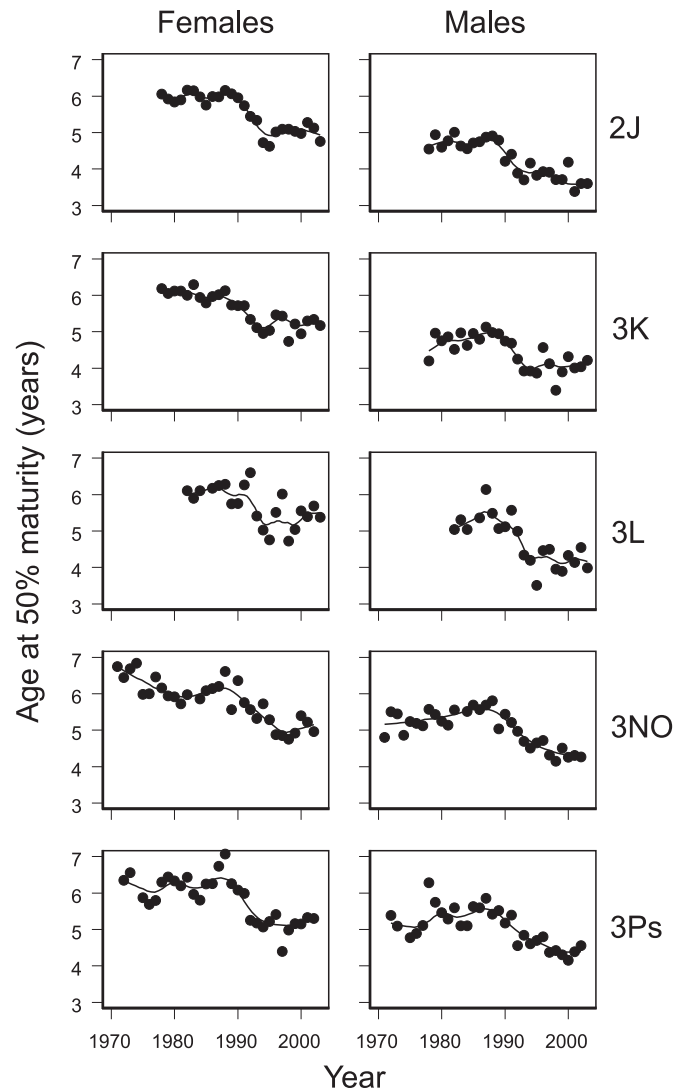
Fig. 3. Mean annual length increments of 4- to 6-year-old Atlantic cod (*Gadus morhua*) from Northwest Atlantic Fisheries Organization (NAFO) Divisions 2J, 3K, 3L, and 3NO and Subdivision 3Ps fitted with a locally weighted regression smoother. The smoothing parameter (span) is set to 0.5.



ciple, induce differences in reaction norm midpoints estimated from autumn versus spring surveys. Reassuringly, for Division 3L, for which we have data from both autumn and spring, this appears not to be the case: the estimated reaction norm midpoints are very similar (Fig. 9). Temporal overlap between the two surveys in 3L is reduced because, owing to the scarcity of data, reaction norm midpoints could not be estimated from spring data from about 1990 onwards.

From a management perspective, the following question is of high relevance: at what moment in time could the decline in reaction norm midpoints have been detected? We have explored this question by going back in time (in steps of 1 year from the year in which the moratorium was introduced), computing reaction norm midpoints and slopes from the restricted data that were available to managers at that time. We limited this analysis to 6-year-old females, as these exhibited relatively precise estimates for the period up to the moratorium. This retrospective analysis indicates that the negative slopes in reaction norm midpoints could have been detected in all areas by 1990. In some divisions, these trends could have been picked up even earlier: negative slopes could have been detected in the early 1980s in 3Ps, in the mid-1980s in 2J, 3K, and 3NO, and around 1990 in 3L (Fig. 10).

Fig. 4. Ages at 50% maturity of Atlantic cod (*Gadus morhua*) from Northwest Atlantic Fisheries Organization (NAFO) Divisions 2J, 3K, 3L, and 3NO and Subdivision 3Ps fitted with a locally weighted regression smoother. The smoothing parameter (span) is set to 0.3.



Discussion

This study provides evidence for contemporary life history evolution in one of the world’s leading food fish, the Atlantic cod. We show that the maturation schedule of Atlantic cod off southern Labrador and Newfoundland shifted towards earlier ages and smaller body sizes in the 1980s and early 1990s. This shift is demonstrated through changes in the reaction norm for age and size at maturation and thus is not confounded by concomitant changes in growth or survival. The same trend was shown independently for both female and male cod from five neighbouring geographic areas (NAFO Divisions 2J, 3K, 3L, and 3NO and Subdivision 3Ps). Our findings strongly suggest that the collapse of the cod populations off southern Labrador and Newfoundland, which took place during the late 1980s and the early 1990s, was a distinct selective episode that favoured early-maturing

Fig. 5. Maturation reaction norms of (a) male and (b) female Atlantic cod (*Gadus morhua*) of the 1980 cohort from Northwest Atlantic Fisheries Organization (NAFO) Subdivision 3Ps shown in terms of body lengths at which the probability of maturing equals 25%, 50% (reaction norm midpoint), and 75% (solid lines). Growth rates are depicted as arithmetic mean length at age (shaded lines) together with 5th and 95th percentiles (broken shaded lines).

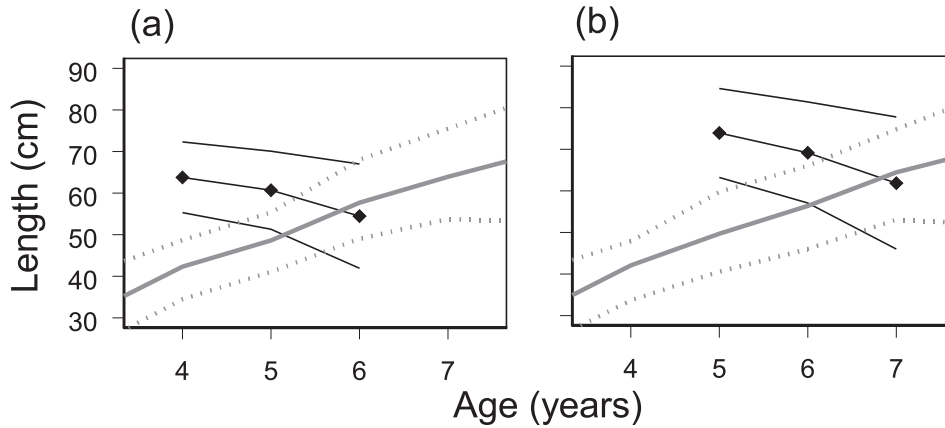


Fig. 6. Temporal trends in maturation reaction norm midpoints of female Atlantic cod (*Gadus morhua*) at ages 5 and 6 years from Northwest Atlantic Fisheries Organization (NAFO) Divisions 2J, 3K, 3L, and 3NO and Subdivision 3Ps. Some cohorts are missing owing to insufficient data.

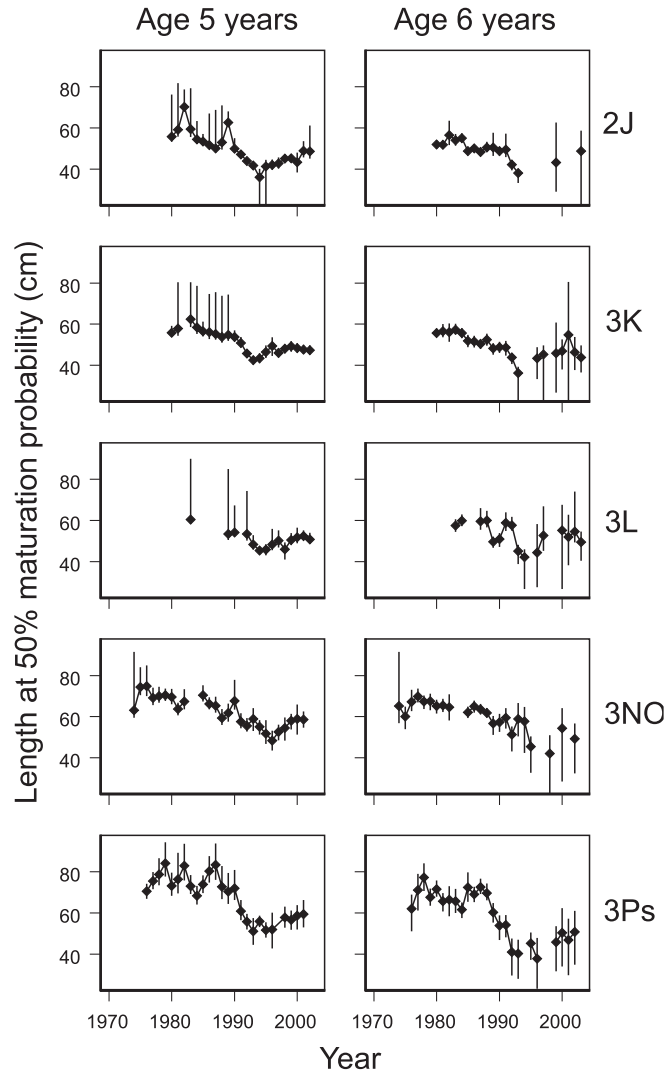


Fig. 7. Temporal trends in maturation reaction norm midpoints of male Atlantic cod (*Gadus morhua*) at ages 4 and 5 years from Northwest Atlantic Fisheries Organization (NAFO) Divisions 2J, 3K, 3L, and 3NO and Subdivision 3Ps. Some cohorts are missing owing to insufficient data.

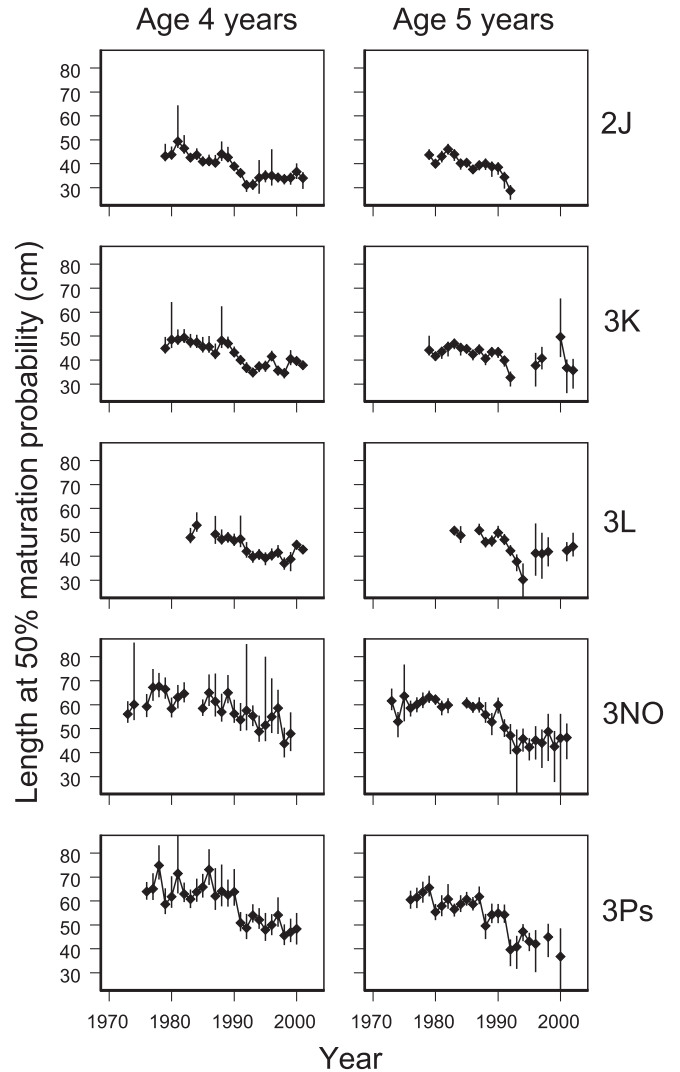


Table 2. Temporal trends in maturation reaction norm midpoints in Atlantic cod (*Gadus morhua*) from Northwest Atlantic Fisheries Organization (NAFO) Divisions 2J, 3K, 3L, and 3NO and Subdivision 3Ps.

Division	Age (years)	Regression slope, cm-year ⁻¹ (95% confidence interval)	
		Premoratorium	Moratorium
Female			
2J	5	-1.15 (-2.19, -0.87)	1.06 (0.68, 2.33)
2J	6	-0.67 (-0.99, -0.37)	—*
3K	5	-0.82 (-1.88, -0.50)	0.51 (0.26, 0.79)
3K	6	-0.97 (-1.23, -0.75)	1.00 (-0.24, 2.29)
3L	5	-0.84 (-3.36, 0.88)	0.63 (0.25, 1.03)
3L	6	-0.39 (-1.04, 0.07)	0.98 (0.16, 2.74)
3NO	5	-0.71 (-1.18, -0.56)	1.69 (0.63, 2.66)
3NO	6	-0.55 (-1.15, -0.40)	0.99 (-3.89, 11.55)
3Ps	5	-1.05 (-1.33, -0.78)	0.90 (0.19, 1.89)
3Ps	6	-1.34 (-1.68, -1.01)	1.25 (-0.84, 3.00)
Male			
2J	4	-0.80 (-1.20, -0.62)	0.25 (-0.50, 0.72)
2J	5	-0.82 (-1.07, -0.69)	—*
3K	4	-0.61 (-1.08, -0.43)	0.30 (0.057, 0.53)
3K	5	-0.49 (-0.73, -0.33)	-0.17 (-1.63, 1.07)
3L	4	-0.69 (-1.16, -0.12)	0.33 (0.04, 0.62)
3L	5	-0.60 (-1.19, -0.47)	1.02 (0.39, 2.13)
3NO	4	-0.38 (-0.70, -0.053)	-1.83 (-10.78, 0.23)
3NO	5	-0.65 (-1.31, -0.52)	0.43 (-3.12, 1.92)
3Ps	4	-0.70 (-0.96, -0.46)	-0.63 (-1.69, 0.36)
3Ps	5	-0.99 (-1.23, -0.81)	-1.24 (-4.57, 0.63)

Note: Regressions are shown for premoratorium years (including the year in which each moratorium was declared) as well as for subsequent years. The moratorium was initiated in July 1992 in Divisions 2J, 3K, and 3L, in February 1994 in Divisions 3NO, and in August 1993 in Subdivision 3Ps. The moratorium was lifted in 1997 in 3Ps; this is not taken into account in the analyses.

*Not estimable owing to sparse data.

genotypes relative to late-maturing genotypes. This conclusion is in agreement with earlier findings based on a subset of the data analyzed here (female northern 2J3KL cod; Olsen et al. 2004).

We note that age and size will typically not explain all variation in maturation, so that trends in the reaction norms could still be influenced by hypothetical trends in phenotypically plastic responses that are unrelated to growth, age, or size. First, a cod in good condition will likely have a higher probability of maturing than a similarly sized and aged cod in poor condition (Marteinsdottir and Begg 2002). Cod off southern Labrador and eastern Newfoundland (Divisions 2J3KL) experienced a decrease in body condition during the period of collapse, except for fish in parts of Division 3L (Bishop and Baird 1994; Krohn et al. 1997). The net effect of this would be to delay maturation, contrary to observations. It is not likely, therefore, that trends in body condition have caused the trends in reaction norms reported here for these areas. Second, the estimated reaction norms could be influenced by the social environment experienced by the fish. For example, in the southern platyfish (*Xiphophorus maculatus*), the presence of dominant males has been shown to suppress maturation of subordinate males (Sohn

1977). Since social suppression of subordinate, and likely smaller, adults would be released during a period of catastrophic population decline, this effect could account for some of the observed changes in reaction norms. Third, there could be a residual effect of temperature on the maturation reaction norms. For North Sea plaice (*Pleuronectes platessa*), it has been shown that the probability of maturing at a given age and length increased significantly with increased temperature 2 and 3 years prior to maturation (Grift et al. 2003). However, the collapse of the cod populations off Labrador and Newfoundland coincided with a prolonged period of low water temperatures (Drinkwater 2002). The net effect of this, as suggested by the study of North Sea plaice, would be to displace the reaction norms toward older ages and larger sizes, while the opposite was in fact observed.

We also wish to highlight a semantic issue that sometimes leads to confusion. The term maturation reaction norm implies, through its historical usage in the literature, that the variation of age and size at maturation along the reaction norm is mostly a phenotypically plastic response, in this case to variation in growth. Our usage of this term thus implies that variation along the reaction norm is mostly caused by environmental, as opposed to genetic, factors. While it is known that genetic variability in growth exists and that growth rates may thus evolve as a response to selective harvesting (Conover and Munch 2002; also see Sinclair et al. 2002; Munch et al. 2005), it is very unlikely that growth variation in a species exposed to an environment as unpredictable as that of Atlantic cod is primarily genetic. Even if this were different (perhaps for another species), the valuable descriptive properties of these reaction norms do not depend on their naming and thus not on the actual origin of growth variation. In the longer run, future research may aim to determine whether, and, if so, how, maturation evolution and growth evolution are interacting, both ecologically and genetically.

We found that the age-specific body length at which maturation probability reaches 50%, referred to as the reaction norm midpoint in this study, was smaller for male cod as compared with female cod. This implies that, for a given growth rate, male cod will tend to mature at earlier ages and smaller body sizes. This sex difference in maturation pattern conforms well to results based on the more traditional method of maturity ogives (Morgan 2000; Brattey et al. 2003), considering that there seems to be no major sex difference in growth. Also, the fact that females show a more pronounced reversal of maturation patterns during the moratorium years supports the suggestion that selection pressures have differed, and continue to differ, between the sexes. For female cod, a large body size offers an indisputable fitness advantage, in terms of both increased fecundity and improved offspring quality (Trippel 1998). For male cod, on the other hand, the benefits of large body size are less obvious. Tank experiments in which female cod had access to both small and large males revealed no positive association between male body size and reproductive success; in fact, many of the smaller males exhibited a higher success than their larger-sized competitors (Rakitin et al. 2001).

Our data indicate that from about 1993 to 1995, after the closing of the fisheries, the trends in the maturation norms are halted and, for females, even show signs of reversal. To

Fig. 8. Maturation reaction norm midpoints at age 5 years for (a) female and (b) male Atlantic cod (*Gadus morhua*) from Northwest Atlantic Fisheries Organization (NAFO) Divisions 2J (dashed line), 3K (dotted line), 3L (solid line), and 3NO (shaded line) and Subdivision 3Ps (dashed shaded line) fitted with a locally weighted regression smoother. The smoothing parameter (span) is set to 0.4. The arrows indicate how the maturation reaction norms are ordered with respect to increasing latitude.

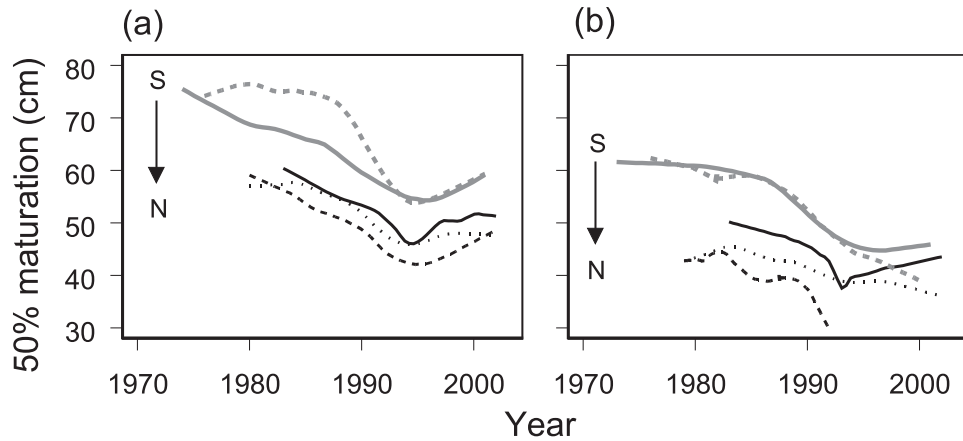
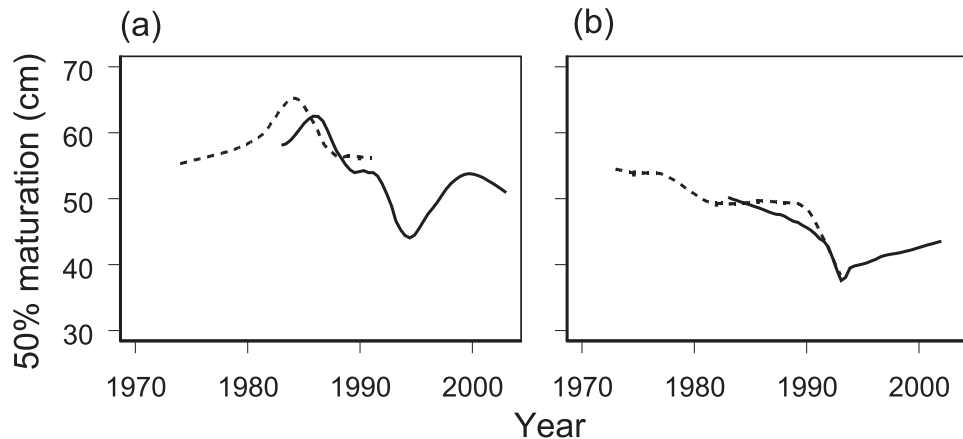


Fig. 9. Maturation reaction norm midpoints for (a) females at age 6 years and (b) males at age 5 years of Atlantic cod (*Gadus morhua*) from Northwest Atlantic Fisheries Organization (NAFO) Division 3L based on spring survey data (broken line) and autumn survey data (solid line) fitted with a locally weighted regression smoother. The smoothing parameter (span) was set to 0.4.

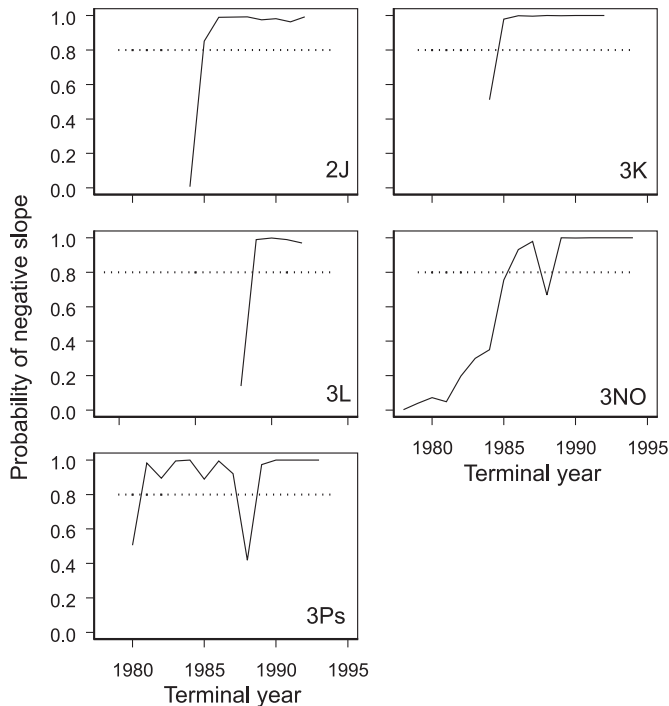


some extent, the signs of reversal are a surprising result because, in theory, genetic change caused by fishing will not be easily reversed: selection for early maturation appears to be much easier, and faster, than for late maturation (Law and Grey 1989). Still, field experiments on freshwater fish have documented rapid evolution towards delayed maturation when predation pressure was relaxed (Reznick et al. 1990). It is possible that the fitness benefits of large size in female cod (as discussed above) are stronger than until now considered in models. Also, it is possible, in theory, that immigration of genotypes with different maturation schedules could have influenced the recent trends in maturation reaction norms. Importantly, the period since initiation of the moratoria has been only a decade; to better understand whether the conjectured trend in maturation schedules is borne out, we shall have to await the results of future research surveys.

We also found evidence for a geographical trend by which the age-specific body length at 50% maturation probability decreased with increasing latitude (also see Morgan et al. 1994). This north–south gradient was substantial, and opposite to the effect of the latitudinal gradient in growth on the

timing of maturation. We therefore suggest that our results reveal countergradient variation in maturation tendency (Conover and Schultz 1995): the capacity for early maturation (as determined by the cod's genetics) appears to be greatest in areas with the least opportunity for early maturation (as determined by the phenotypically plastic consequences of differential growth). For instance, in the early 1980s, the reaction norm midpoints of 6-year-old females from off southern Newfoundland (Subdivision 3Ps) were around 70 cm as compared with only 50 cm for females from off southern Labrador. This finding suggests that genetic differences, consistent with the selective pressures of local adaptation, exist in the maturation schedules of cod from different parts of the Newfoundland–Labrador region. Tagging studies and population genetic studies corroborate that local population structure exists within this region (Templeman 1966; Ruzzante et al. 1998; Beacham et al. 2002). It thus seems likely that locally adapted life histories in Atlantic cod can evolve, despite the fact that cod is a highly mobile species inhabiting a marine environment without any obvious barriers to dispersal. As pointed out by Berkeley et al. (2004b)

Fig. 10. Probability of a negative trend in reaction norm mid-points estimated for 6-year-old female Atlantic cod (*Gadus morhua*) when analysis is retrospectively restricted to only part of the available time series up to and including the given terminal year. The last terminal year shown corresponds to the year in which the moratorium was initiated. Broken lines show, for reference, the 80% level of the probability of a negative trend. The probabilities were calculated as the proportion of 1000 bootstrap replicates yielding a negative slope.



and Hutchings (2004), managers should thus take into account that marine exploited species may have a complex spatial population structure and life histories that are evolving on a contemporary time scale.

Maturation reaction norms have also been estimated for other heavily exploited populations of Atlantic cod, from Georges Bank as well as the Gulf of Maine (Barot et al. 2004b) in the northwest and from the Norwegian Sea as well as the Barents Sea (Heino et al. 2002a, 2002b, 2002c) in the northeast. Similar findings have been obtained for North Sea plaice (Grift et al. 2003; also see Rijnsdorp 1993) and American plaice (*Hippoglossoides platessoides*) (Barot et al. 2005). These studies provide evidence for adaptive changes in maturation schedules that point in the very same direction as those documented in this study of Labrador and Newfoundland cod.

We suggest that monitoring maturation reaction norms for age and size at maturation may aid decision making in the management of exploited marine resources in general and of Atlantic cod in the Newfoundland–Labrador region in particular. First, estimates of age- and length-specific maturation probabilities are needed to parameterize age- and length-structured population models (Frøysa et al. 2002) and hence provide important input for a broad spectrum of population assessment purposes. Second, information on trends in the maturation process may serve as a helpful warning signal with regard to changes in population size and recruitment

potential. With the collapse of the cod populations off Labrador and Newfoundland in mind, Hutchings and Myers (1995) argued that the sustainability of any fishery clearly depends on quantifying a wide range of biological indicators of population health. Specifically, Trippel (1995) suggested that the age A_{50} at which 50% of fish are mature holds promise as one such stress indicator. We build on this argument and put forward maturation reaction norms as a biological indicator with important advantages over A_{50} . A reduction in A_{50} is ambiguous in that it may reflect either fisheries-induced selection favouring early maturation or maturation facilitated by faster individual growth in response to declining stock size. Both of these possibilities imply that fishing heavily impacts the population, which hence may be considered as being stressed. However, A_{50} may also decline if maturation is merely facilitated by a temperature increase or when the survival of mature fish increases. Neither of these scenarios represents a cause of concern for the management of a stock. By contrast, estimation of maturation reaction norms reveals changes in the maturation tendency itself, as shown here for the cod populations off Labrador and Newfoundland in the 1980s. A more robust indicator of population health may therefore be the length L_{P50} (Grift et al. 2003) at which the probability of maturing reaches 50% for a given age. The methodology described and utilized here enables estimation of L_{P50} .

In summary, this study shows that maturation of Labrador and Newfoundland cod shifted towards earlier ages and smaller body sizes during the severe collapse of these populations in the late 1980s and early 1990s. The use of reaction norm methodology removes confounding effects of growth or survival and thus provides stronger evidence for changes in the underlying maturation process than previous analyses could.

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