Life history consequences of overexploitation to population recovery in Northwest Atlantic cod (*Gadus morhua*)[1]

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Abstract: Changes to life history traits are often concomitant with prolonged periods of exploitation. In the Northwest Atlantic, 30- to 40-year declines of more than 90% of Atlantic cod (*Gadus morhua*) have been associated with significant reductions in age and length at maturity, changes most parsimoniously explained as genetic responses to fishing. Increased survival costs of reproduction associated with earlier maturity, resulting in higher natural mortality and shorter life span, negatively affect population growth rate and rate of recovery. Coupled with lower hatching rate among first-time spawners and smaller size at maturity, a modest reduction in age from 6 to 4 years can reduce annual population growth in Atlantic cod by 25%–30%, based on the output of a stochastic, age-structured life history model. Earlier maturity more than doubles the probability of negative population growth every generation. These results underscore the potential for fishing-induced changes to life history traits alone to generate slow or negligible recovery in marine fishes, exacerbating negative impacts on population growth resulting from ecosystem-level alterations to interspecific competition and predation.

Résumé : Des changements de caractéristiques démographiques accompagnent souvent les longues périodes d'exploitation. Dans le nord-ouest de l'Atlantique, les déclins sur 30 à 40 ans de l'ordre de plus de 90 % de la morue franche (*Gadus morhua*) sont associés à des réductions significatives de l'âge et de la longueur à la maturité, des changements qui s'expliquent, de la manière la plus parcimonieuse, comme étant des réactions génétiques à la pêche. Les coûts accrus de la survie à la reproduction associés à la maturité plus précoce, qui entraînent une mortalité naturelle plus élevée et une longévité réduite, affectent négativement le taux de croissance de la population et le taux de récupération. En conjonction avec un taux d'éclosion réduit chez les poissons qui fraient pour la première fois et une taille à la maturité plus faible, une réduction modeste de l'âge de 6 à 4 ans peut abaisser la croissance annuelle de la population de morues franches de 25–30 %, d'après les résultats d'un modèle démographique stochastique avec structure d'âge. Une maturité précoce plus que double la probabilité d'une croissance de population négative à chaque génération. Ces résultats soulignent que les changements de caractéristiques démographiques induits par la pêche peuvent produire une récupération faible ou négligeable chez les poissons marins, exacerbant ainsi les impacts négatifs sur la croissance de population qui résultent des modifications qui se font dans la compétition interspécifique et la prédation à l'échelle de l'écosystème.

[Traduit par la Rédaction]

Introduction

Exploitation affects life history. Changes to age and size at maturity, longevity, and quite possibly fecundity and egg size are the product of phenotypic and genetic responses to fishing (e.g., Rochet 1998; Law 2000; Hutchings 2002). Perhaps the most common phenotypic response is a reduction in age at maturity effected by faster rates of growth associated with reductions in population density (Policansky 1993). Hypothesized genetic responses to exploitation have also included changes to age and size at maturity, growth rate, and fecundity per unit body mass (Rijnsdorp 1993; Conover and

Munch 2002; Grift et al. 2003). Phenotypic responses by a life history trait are a product of phenotypic plasticity, the precise nature of the response being reflected by an individual's (genotype's) norm of reaction for that trait, which describes how a phenotype responds to environmental change (Hutchings 2004). Genetic responses are the product of fishing activities that render some individuals, because of phenotypic differences in heritable traits such as body size and growth rate, more vulnerable to exploitation than others. The higher the rate of fishing mortality and the greater the number of generations over which a population has been fished, the greater the likelihood that genetic responses to

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exploitation have occurred (Law 2000; Hard 2004). At the population level, one of the challenges in distinguishing phenotypic and genetic responses to fishing is the complication that fishing might differentially affect norms of reaction (Rijnsdorp 1993; Heino et al. 2002; Olsen et al. 2004). In other words, genetic responses are not restricted solely to changes in the average values of a trait but can also be reflected by changes to the ways in which individuals respond to environmental change (Haugen 2000; Hutchings 2004).

Phenotypic and genetic changes to life history traits are of interest to conservation biologists and resource managers because of the inextricable links that exist between these fitness-related characters and population growth rate. The former, manifested ultimately by age-specific schedules of survival and reproductive investment, are the primary determinants of individual fitness, usually represented either by r (intrinsic rate of increase) or by λ (finite rate of increase) (Roff 2002). The geometric mean of these individual fitness measures determines the growth rate of the population, r_{pop} and λ_{pop}, parameters positively associated with sustainable rates of harvesting, persistence, and rate of population recovery (Lande 1993; Myers et al. 1999).

The present study represents an exploratory analysis of the consequences of fishing-induced changes in life history to population growth in Atlantic cod (*Gadus morhua*), a species that has experienced precipitous declines throughout its geographical range. Since the early 1970s, North Sea cod have declined almost 90% (International Council for the Exploration of the Sea 2004); among stocks in the Northwest Atlantic, five have experienced even greater reductions, with declines over three-generation time intervals (roughly 30 years) as high as 99% (COSEWIC 2003) (Table 1). The reductions in population density concomitant with such declines are almost certainly sufficient to produce phenotypic change to life history traits. However, if fishing mortality during these declines was not random with respect to heritable phenotypic traits, one would expect some changes to life history to represent genetic responses to fishing. From a recovery perspective, empirical data across a broad spectrum of marine fishes have revealed that recovery by demersal species is significantly impaired by reductions in excess of 90% (Hutchings 2000).

I begin by describing changes to age and size at maturity concomitant with population decline for two of the most severely affected Northwest Atlantic cod stocks: Newfoundland and Labrador's northern cod and eastern Scotian Shelf cod. By examining prereproductive growth during periods of life history change, I am then able to evaluate the degree to which these changes can be explained solely as phenotypic responses to reductions in density. The influence of earlier maturity and smaller size at maturity on Atlantic cod population growth, and thus rate of recovery, is then assessed by a stochastic, age-structured life history model that allows survival costs of reproduction to increase with declining age at maturity (Beverton et al. 1994) and incorporates reduced hatching success among first-time spawners (Trippel 1998). This use of a stochastic model builds upon work pioneered by Lewontin and Cohen (1969), and extended by Roff (1974), who modelled the effects of random fluctuations in population growth rate on expectations of population size and probabilities of extinction.

Methods

Population growth rate

I used a stochastic, age-structured life history model previously developed by Hutchings (1999) to study the influence of changes to age and size at maturity on annual (r) and per-generation (R_0) rates of increase. Age-specific rates of survival and fecundity are used to estimate rates of population growth. These data are expressed as l_x, the probability of surviving from birth until the beginning of the breeding season at age x, and m_x, the number of eggs produced by a female breeding at age x. The intrinsic rate of population increase, r, can be calculated from the discrete-time version of the Euler–Lotka equation:

$$(1) \qquad 1 = \sum_{x=\alpha}^{x=\tau} l_x m_x \exp(-rx)$$

where α represents age at maturity and τ represents age at death ($\tau = 21$ years in the present analysis). Net reproductive rate, R_0, is given by

$$(2) \qquad R_0 = \sum_{x=\alpha}^{x=\tau} l_x m_x$$

Although probability distributions of the intrinsic rate of increase cannot be described by a stochastic model (because of the analytical constraint that r can only be calculated by iteration), r can be approximated by the natural logarithm of the net reproductive rate discounted by generation time (G) as $r = \ln(R_0)/G$, where $G = (\Sigma l_x m_x x)/(\Sigma l_x m_x)$. Probability distributions of R_0 were generated from 2000 randomizations per estimate using Microsoft® Excel. The highly positive skew of these distributions necessitated the calculation of r from median estimates of R_0. The population consequences of different life histories was summarized in terms of two model outputs: (*i*) an estimate of r (based on the median value of R_0, as determined from the simulations) and (*ii*) the expected probability of negative population growth (i.e., $\Pr(R_0 < 1)$).

The model contains both stochastic and deterministic elements, as described in more detail in the sections following. When estimating l_x, survival is partitioned into survival from birth to the beginning of age 3 (l_3), prereproductive survival ($l_{3-\alpha}$), and postreproductive survival ($l_{\alpha-\tau}$). Each of these is stochastic in the model. Age-specific fecundity (m_x) is a function of body weight, the proportional increase in body weight from one year to the next, and the relationship between body weight and fecundity. Weight at age and proportional increases in weight are stochastic; the relationship between body weight and fecundity was incorporated into the model without error. The only deterministic elements to the model are age at maturity, age at death, the parameter that specifies the survival cost of reproduction, and weights at maturity for individuals maturing at 4 and 6 years.

Age-specific survival, l_x, and survival costs of reproduction

The basic model incorporated observed or estimated variation in survival from birth to age 3, l_3 (the age at which most Northwest Atlantic cod are first recruited to commercial fishing gear), instantaneous rate of prereproductive mor-

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Table 1. Estimated changes in the abundance of mature individuals for Atlantic cod (*Gadus morhua*) stocks partially or entirely under Canadian management.

Stock	NAFO division(s)	Data source	Population decline (%)	Years
Northern cod	2J3KL	VPA–survey	99	1968–2001
Southern Grand Bank	3NO	VPA	98	1968–2001
Cabot Strait	4Vn	VPA	95	1981–2000
Northern Gulf	3Pn4RS	VPA	93	1975–2002
Eastern Scotian Shelf	4VsW	Survey	92	1975–2002
Western Scotian Shelf	4X	VPA	78	1979–2002
Georges Bank	5Zj,m	VPA	70	1979–2002
St. Pierre Bank	3Ps	VPA	46	1968–2001
Southern Gulf	4T	VPA	23	1973–2002

Note: Stocks are delineated by Northwest Atlantic Fisheries Organization (NAFO) divisional boundaries. Decline estimates are those reported for the three-generation periods corresponding to each stock by COSEWIC (2003). Abundance estimates were based on either fisheries-independent surveys or virtual population analysis (VPA).

tality, M_{imm}, and mortality of mature, postreproductive individuals, M_{mat}. Distinguishing mortality prior to and following maturity acknowledges, and allows for the inclusion of, a survival cost of reproduction (Beverton et al. 1994; Roff 2002). Survival from birth to age 3 was quantified from abundance estimates of northern cod (Lilly et al. 2001) and from age-specific fecundities, as described below, such that survival from birth to age 3 in year t, $l_{3(t)}$, was assumed to be a function of the number, n, of 7- to 11-year-olds in year $t – 3$ multiplied by the average fecundity of those individuals such that

$$(3) \qquad l_{3(t)} = n_{3(t)} / \sum_{x=7}^{x=11} n_{x(t-3)} m_{x(t-3)}$$

Survival from birth to age 3 estimated in this manner for the 1962 through the 1988 year-classes of northern cod was weakly density dependent (see Myers et al. 1995) and averaged $1.13 \times 10^{-6} \pm 1.11 \times 10^{-6}$ (±SD). I assumed that variation in annual mortality attributable to factors unrelated to reproduction (e.g., predation) was best reflected by a beta distribution given as

$$(4) \qquad f(x) = \frac{(x/s)^{(\theta-1)}[1 - (x/s)]^{(\beta-1)}}{\Gamma(\theta)\Gamma(\beta)/\Gamma(\theta + \beta)}$$

where $\Gamma(\beta)$ is the gamma function. The scale parameter, s, establishes the upper bound of the distribution at 1.0, and the mean of the distribution ($\theta/(\theta + \beta)$) is set to annual survival probabilities (e.g., $\exp(-M_{imm})$ of 0.91), which correspond to $M_{imm} = 0.10$. As a consequence, survival was approximated by a negatively skewed distribution. The rationale for selecting a beta distribution to model survival data is based on its simplicity, smoothness, and flexibility, making it an ideal choice for distributions that have restricted support (i.e., whose range is limited), in this case between 0 and 1 (Johnson et al. 1994).

Postreproductive mortality, M_{mat}, was assumed to differ with age at maturity. There is considerable evidence to suggest that earlier maturing individuals suffer higher survival costs of reproduction than later maturing individuals (e.g., Beverton et al. 1994; Hutchings 1994; Schultz and Conover 1999). This seems to be particularly true when early matu-

rity is accompanied by smaller body size (e.g., Festa-Bianchet et al. 1998). Disproportionately higher survival costs experienced by smaller individuals can be attributed to energetic constraints imposed by metabolic allometry. Smaller individuals utilize proportionately more energy to maintain basal metabolic rate than larger individuals (Schmidt-Nielsen 1984). In addition, for a given expenditure of energy, larger individuals can be expected to bear lower costs because of their higher lipid reserves (e.g., Brett et al. 1969; Elliott 1976; Schultz and Conover 1999).

Among fishes, evidence that M_{mat} declines as age at maturity increases has been documented for several species, including brook trout (*Salvelinus fontinalis*) (Hutchings 1994), Atlantic silverside (*Menidia menidia*) (Schultz and Conover 1999), sand goby (*Pomatoschistus minutus*) (Lindström 1998), and threespine stickleback (*Gasterosteus aculeatus*) (Dufresne et al. 1990). There are also empirical data to suggest that M_{mat} is negatively related to age at maturity in Atlantic cod. Based on their exhaustive examination of Northeast Arctic cod otoliths collected from the 1930s, 1940s, and 1950s, Beverton et al. (1994) concluded that M declines as age at maturity increases. Specifically, they reported that M was equal to 0.25, 0.17, and 0.15 for individuals maturing at ages 6, 7, and 8 years, respectively.

I used Beverton et al.'s (1994) estimates to incorporate a higher postreproductive mortality for early-maturing individuals, given the absence of such estimates for Northwest Atlantic cod. I first converted their estimates of instantaneous rates of mortality for individuals maturing at age x to mortality probabilities (i.e., $1 - \exp(-M_{mat(\alpha=x)})$ equalled 0.22, 0.16, and 0.14 for $\alpha = 6$, 7, and 8 years, respectively). Prior to their collapse in the early 1990s, the natural mortality rate, M, of Northwest Atlantic cod was assumed to be 0.20 (Pinhorn 1975). Based on this estimate, it seemed reasonable to let $M_{mat(\alpha=6)} = 0.20$ in the simulations, which corresponds to an annual mortality rate of 18%. I then estimated postreproductive mortality for individuals maturing at age 4 in two ways. Using the ratios of mortality rates estimated by Beverton et al. (1994) (i.e., 0.22/0.14 and 0.22/0.16) and multiplying these by 0.18, I let the instantaneous rates of natural mortality for cod maturing at age 4 ($M_{mat(\alpha=4)}$) be 0.34 and 0.30, respectively. To be consistent with Beverton et al.'s (1994) results, individuals maturing at age 4 experi-

enced these elevated rates of natural mortality each year until death.

Age-specific fecundity, m_x

Age-specific fecundity is a function of growth rate, reflected by changes to body weight with age, and to a first approximation by the number of eggs produced per unit body weight. Weights at age subsequent to maturity were calculated by multiplying the average weight at maturity, w_α, by the expected age-specific increase in body size between ages α and $\alpha + 1$ year (i.e., $w_{\alpha+1}/w_\alpha$) to obtain an estimate of weight at age $\alpha + 1$ year and then multiplying this estimate of weight at age $\alpha + 1$ year by $w_{\alpha+2}/w_{\alpha+1}$ to obtain an estimate of weight at age $\alpha + 2$ years and so on until the simulated age at death, 21 years. Estimates of $w_{\alpha+1}/w_\alpha$ were calculated from data provided by Lilly (1997) and Murphy et al. (1997). As described by Hutchings (1999), empirical estimates of annual changes in body size among fish older than 6 years are assumed to include the reductions in growth concomitant with maturation. To account for these growth costs of maturation prior to age 6, I assumed the percent reduction in annual growth rate to be equal to the proportional allocation of body tissue to gonads, as determined from estimates provided by McIntyre and Hutchings (2003). Based on these data, weights at maturity for cod maturing at ages 4 and 6 were 1.12 and 2.06 kg, respectively. The natural variability associated with individual increases in weight, ε_w, was assumed to be normally distributed with the standard deviation of each age-specific error distribution set equal to the standard deviation of the observed annual mean increases in weight at age (w_{x+1}/w_x).

Within some populations of Atlantic cod, reductions in size at maturity have been substantive. As discussed in more detail below, length at maturity among eastern Scotian Shelf cod has declined from approximately 42 cm in the late 1970s to 32 cm in the early 2000s (Fanning et al. 2003). These length reductions correspond roughly to a decline in weight from 700 to 500 g (Fanning et al. 2003). To examine how a reduction in size at maturity, independent of a decline in age at maturity, might affect population growth, I reduced weight at maturity (w_α) in the simulations by 200 g relative to those observed. Given the small lengths of the cod (32–42 cm) used to derive this empirically based reduction, such a decline in size at maturity can be considered conservative, given that the reduction in weight corresponding to a similar absolute decline in length for larger fish would be proportionately greater.

Numbers of eggs per female in Atlantic cod, as with most fishes, depend primarily on body weight (e.g., McIntyre and Hutchings 2003). Fecundity estimates were based on May's (1967) fecundity–weight relationship for cod collected from several locations off northeastern Newfoundland and modified, as described by Hutchings (1999), to yield the following association between age-specific fecundity, m_x, and age-specific weight:

(5) $\qquad m_x = \{0.48[(w_x + 0.37)/1.45] + 0.12\} \times 10^6$

Age and size at maturity

The simulations presented here are used to evaluate the consequences to population growth rate of reductions in age at maturity from 6 to 4 years and reductions in weight at ma-

turity of 200 g. To assess the degree to which these changes reflect those observed in the wild, I present data for two cod stocks in the Northwest Atlantic: northern cod, whose geographical range extends from Labrador southeast to the northern half of Grand Bank, and eastern Scotian Shelf cod, which inhabit the waters from Halifax north to Cape Breton. Age at 50% maturity for northern cod has been estimated by Canadian Department of Fisheries and Oceans scientists (Lilly et al. 2001, 2003). The most reliable of these data are those for the years extending back to the late 1970s – early 1980s; these data were obtained from random samples collected by fisheries-independent surveys. Age at maturity estimates for previous years were calculated from various combinations of surveys (G.R. Lilly, Department of Fisheries and Oceans, P.O. Box 5667, St. John's, NL A1C 5X1, Canada, personal communication). As a consequence, these earlier data should be treated with some caution because it is not known whether they represent truly random samples. Having said that, the similarity in age at maturity estimates immediately prior to and following the initiation of the fisheries-independent surveys throughout the range of northern cod in 1981 (Fig. 1a) suggests that the earlier estimates may not be unduly misleading (with the possible exception of data based on the 1973 samples). Age and length at maturity for eastern Scotian Shelf cod were estimated by Fanning et al. (2003). Estimates of prereproductive growth rate presented here for each of the stocks were calculated from length at age data compiled by Lilly et al. (2001) and Fanning et al. (2003) for northern cod and eastern Scotian Shelf cod, respectively.
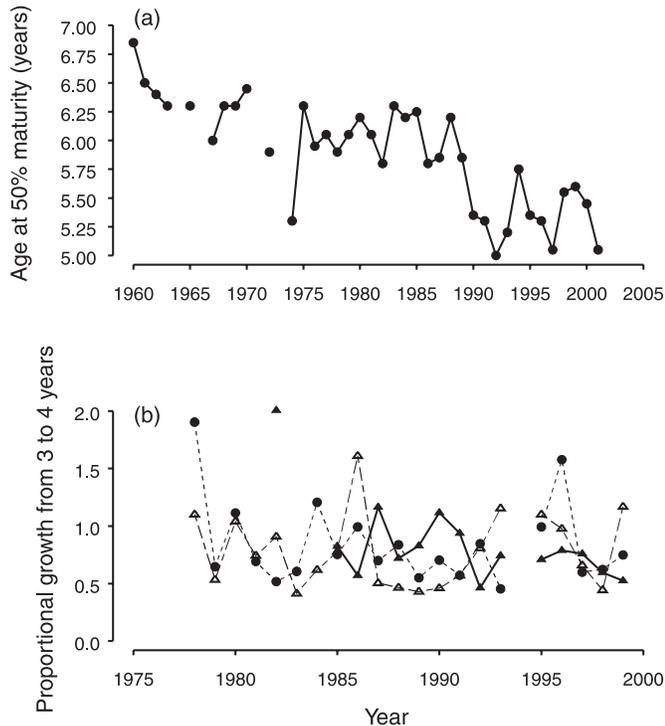
Parity-dependent fertilization success

There is experimental evidence to suggest that spawning success in Atlantic cod depends on parity (i.e., the number of times an individual has produced offspring), such that individuals reproducing for the first time produce considerably fewer offspring per reproductive bout than individuals that have spawned at least once in their lives. Based on a comparison of hatching success in the laboratory, Trippel (1998) reported that hatching rates of first-time spawners were 20% of those of females that had previously spawned. To account for the possibility that spawning success is lower at maturity than at later ages, I varied egg survival$_{\text{first-time spawners}}$/egg survival$_{\text{others}}$ from 0.2 to 1.0.

Results

Changes to life history traits in Atlantic cod

Reductions in abundance of 99% and 92% have been associated with significant changes in life history among northern cod and eastern Scotian Shelf cod, respectively (Figs. 1 and 2). Within the former stock, age at 50% maturity among females has declined approximately 1 year since the late 1970s and early 1980s (Fig. 1a). Comparing maturity estimates on northern cod sampled in the early 1960s with those in recent years, age at maturity may have declined by as much as 2 years. Growth rate during prereproductive ages for northern cod is represented by the proportional increase in length between 3 and 4 years of age. From 1978 to 1999, the observed reduction in age at maturity was not accompa-

Fig. 1. Temporal changes in (*a*) age at maturity and (*b*) pre-reproductive growth for northern cod (*Gadus morhua*). The former represent data on age at 50% maturity for females presented by Lilly et al. (2003); the latter represent changes in the proportional increase in length between ages 3 and 4 years, as calculated from data provided by Lilly et al. (2001). Prereproductive growth rate data are presented separately for North Atlantic Fisheries Organization (NAFO) divisions 2J (△), 3K (●), and 3L (▲).

Fig. 2. Temporal changes in (*a*) age at maturity, (*b*) length at maturity, and (*c*) prereproductive growth for Atlantic cod (*Gadus morhua*) on the eastern Scotian Shelf (data are from Fanning et al. 2003). Data on age and size at maturity are presented separately for cod found in North Atlantic Fisheries Organization (NAFO) divisions 4Vs (●) and 4W (▲). Prereproductive growth represents the proportional increase in length between ages 2 and 3 years.
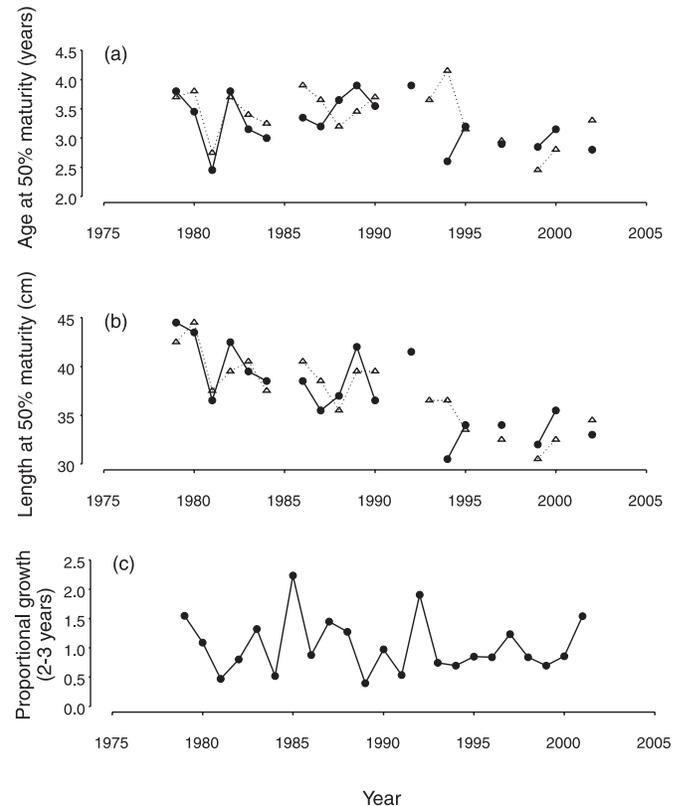

nied by a discernable trend in prereproductive growth (Fig. 1*b*).

Eastern Scotian Shelf cod also experienced a decline in age at maturity of approximately 1 year from the late 1970s to the late 1990s – early 2000s (Fig. 2*a*). However, given the younger reproductive ages among these cod, this 1-year reduction represents a greater proportional decline than that experienced by northern cod. Eastern Scotian Shelf cod have also experienced considerable reductions in length at maturity (Fig. 2*b*). In the eastern portion of the stock's range (Northwest Atlantic Fisheries Organization division 4Vs), length at maturity has declined from 42 to 36 cm since 1979. In the western portion of the stock's range (division 4W), the reduction from 40 to 32 cm is even greater. As with northern cod, these changes in life history were not associated with an obvious temporal trend in prereproductive growth, represented for eastern Scotian Shelf cod as the proportional increase in length between ages 2 and 3 years (Fig. 2*c*).

Influence of reduced age and size at maturity on population growth

Population growth rate declines with age at maturity. At best, when relative hatching rate is independent of parity, the reduction in *r* associated with earlier maturity is comparatively small (Fig. 3*a*). Among cod maturing at 6 years, $r = 0.155$ (16.8% per annum) as compared with the estimates of 0.146 (15.7%) and 0.136 (14.6%) for cod maturing at age

4 years and experiencing postreproductive mortality rates, M_{mat}, of 0.30 and 0.34, respectively. However, as the hatching rate of first-time spawners declines relative to that of later spawners, the reduction in *r* associated with earlier maturity progressively increases. For example, at the relative hatching rate of 0.2 reported by Trippel (1998), *r* declines from 0.143 (15.4% per annum) at $\alpha = 6$ years to 0.130 (13.9%) and 0.111 (11.7%) at $\alpha = 4$ years.

Not surprisingly, reductions in size at maturity exacerbate the reductions in population growth affected by earlier maturity (compare the estimates of *r* in Figs. 3*a* and 3*b*). When size at maturity is reduced by 200 g for cod maturing at age 4 and 6 years, *r* declines from 0.145 (15.6% per annum) at $\alpha = 6$ years to 0.131 (14.0%) and 0.127 (13.5%) at $\alpha = 4$ years when hatching rate is independent of parity. However, at the relative hatching rate of 0.2, earlier maturity has an even greater impact on population growth, with *r* declining from 0.134 (14.3% per annum) at $\alpha = 6$ years to 0.114 (12.1%) and 0.097 (10.2%) at $\alpha = 4$ years.

The reduction in population growth generated by earlier age and smaller size at maturity is perhaps more dramatically reflected by changes to the probability of experiencing negative growth on a per-generation basis, which would result in declining abundance. Under the most favourable sce-

Fig. 3. Atlantic cod (*Gadus morhua*) (*a* and *b*) population growth rate, *r*, and (*c* and *d*) the probability of negative per-generation population growth (Pr($R_0 < 1$)) as functions of age at maturity, size at maturity, and parity effects on hatching rate represented by egg survival$_{\text{first-time spawners}}$/egg survival$_{\text{others}}$. For cod maturing at age 4 years, the solid lines in each panel are those for which postreproductive mortality, M_{mat}, was 0.30; the broken lines are those for which $M_{\text{mat}} = 0.34$. The effects of smaller size at maturity on *r* and Pr($R_0 < 1$) are presented in Figs. 3*b* and 3*d*.

Relative hatching rate of first-time spawners
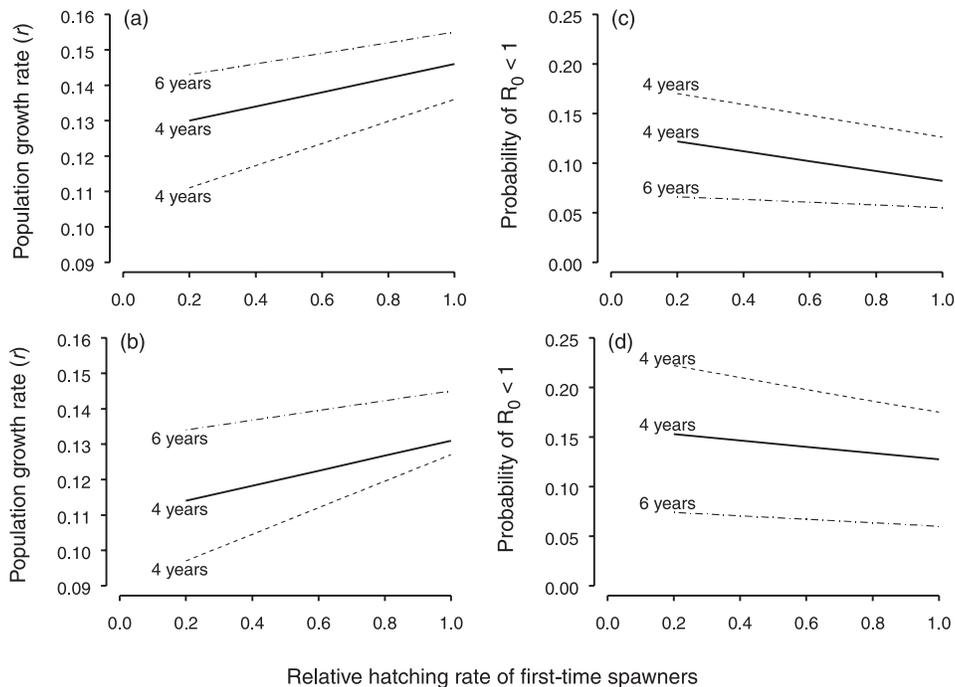
nario, when hatching rate was independent of parity, Pr($R_0 < 1$) increased from 5.5% at α = 6 years to 8.2% and 14.5% at α = 4 years (Fig. 3*c*). At a relative hatching rate of 0.2 (Trippel 1998), the probability of negative growth ranged from 6.6% among cod maturing at 6 years to 17.5% for cod maturing at 4 years and for which $M_{\text{mat}} = 0.34$.

Reductions in size at maturity increased the probability of negative growth even further. At the relative hatching rates for first-time spawners documented by Trippel (1998), and when $M_{\text{mat}(\alpha=4)} = 0.34$, earlier maturity more than trebles the probability of per-generation declines in abundance (compare the left-most point of the line corresponding to α = 6 with the left-most point of the broken line corresponding to α = 4 in Fig. 3*d*).

Discussion

Historical declines in the abundance of two Northwest Atlantic populations of Atlantic cod have been associated with changes in two life history traits of fundamental importance to population growth. These declines cannot be parsimoniously explained as phenotypic responses to reductions in population density. Rather the data are consistent with the hypothesis that earlier age and smaller size at maturity are best explained as genetic responses to fishing-induced selection against late-maturing, and large-maturing, genotypes (Hutchings 1999; Olsen et al. 2004, 2005). The primary objective of the present study was then to explore the degree to which these life history changes, irrespective of the reasons for them, might affect population growth and, thus, rate of recovery.

Overexploitation of Northwest Atlantic cod has been associated with significant reductions in age and size at maturity in most stocks (Trippel et al. 1997). Among these, northern cod have experienced a reduction in age at maturity of at least 16% (comparing the early 1980s with the early 2000s) and possibly as much as 22% since the early 1960s. Among eastern Scotian Shelf cod, age at maturity declined almost 30% between the late 1970s and the early 2000s. Concomitant with the change in age at maturity in this stock was a 20% reduction in length at maturity. Given that these stocks have sustained fishing mortality for a considerably longer period of time than that for which life history data are available, the patterns evident in the past 20–40 years may well represent declines initiated several decades earlier.

The question of whether these changes are primarily genetic or phenotypic in origin is a fundamentally important one. Phenotypically plastic responses in life history to changes in density are readily reversible, comparatively speaking. For example, if earlier maturity is a response to increased pre-reproductive individual growth brought about by reduced competition, then the higher densities associated with population recovery will effect a slowing of individual growth and an older age at first reproduction. By comparison, genetic responses to exploitation are relatively slow to change, particularly in the absence of strong selective pressures akin to those produced by fishing (Law 2000).

There is good reason to believe that the reductions in age and size at maturity documented for some Northwest Atlantic cod stocks can be partly explained as genetic responses to fishing-induced selection against late-maturing, and larger-maturing, genotypes (Hutchings 1999; Olsen et al. 2004). Phenotypic changes to age at maturity are almost always ac-

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companied by changes to individual growth and (or) condition, such that faster growth and increased condition lead to earlier reproduction (Policansky 1993; Roff 2002). There is no evidence that condition has improved among northern or eastern Scotian Shelf cod in the past few decades; if anything, the opposite may be true (e.g., Drinkwater 2002). As the data presented here indicate, there is no evidence that reductions in either age or size at maturity have been associated with increased growth during prereproductive ages. Thus, the most parsimonious explanation for the observed changes in traits whose heritability has been documented repeatedly in fishes (Hutchings 2002; Roff 2002) is that the changes are primarily genetic in nature.

The simulations presented here, based on a stochastic, age-structured life history model, suggest that earlier age and smaller size at maturity can have negative consequences for population growth, and rate of recovery, in Atlantic cod. These reductions in r increase with the magnitude of the survival cost of reproduction associated with earlier maturity and with reductions in the relative hatching rate of virgin spawners. At the higher of the two survival costs considered here for $\alpha = 4$ years, and at the relative hatching rates documented by Trippel (1998), a reduction in age at maturity from 6 to 4 years is associated with a 24% reduction in annual population growth; the reduction in population growth increases to 29% when size at maturity declines as well. The negative effects on recovery of lower age and size at maturity are further reflected by the increased probability of negative per-generation growth, reductions in age at maturity from 6 to 4 years more than doubling the likelihood of population decline.

The reduction in r associated with earlier age and smaller size at maturity raises the question of whether the increased natural mortality observed among some Northwest Atlantic cod stocks in recent years (Smedbol et al. 2002) can be partly attributable to changes in life history. The ubiquity of reproductive costs (Roff 2002), coupled with the likelihood that these costs increase as age and size at maturity decline, suggests that recent increases in M, often attributable to ecosystem-level changes in the strength of interspecific interactions (such as predation and competition), might be partly a function of fishing-induced changes to life history.

The present study differs from previous life history analyses of this species (e.g., Myers and Doyle 1983; Trippel et al. 1995; Hutchings 1999) in that it allows the survival cost of reproduction to increase with reductions in age at maturity. The theoretical basis for such a reciprocal relationship, based on constraints imposed by metabolic allometry, appears sound (Schmidt-Nielsen 1984). However, notwithstanding the taxonomic breadth of its empirical basis (Hutchings 2002), Beverton et al.'s (1994) study of Atlantic cod is the only one available for this species and, to my knowledge, the only study of survival costs for a commercially exploited marine fish. The paucity of such work needs to be remedied, given the intimate association between survival costs and population growth rate.

In the context of the present study, the survival costs incorporated here may well have been underestimated, having been based on estimates of M for Northeast Arctic cod, which mature at considerably larger sizes (68–80 cm; Beverton et al. 1994) than northern cod (Lilly et al. 2001)

and eastern Scotian Shelf cod (Fanning et al. 2003). Similarly, the reduction in size at maturity used here (200 g) is not particularly large, based as it is on the reduction in weight observed among eastern Scotian Shelf cod, a stock with a comparatively small size at maturity. As a consequence, the reductions in r documented here for earlier maturity and smaller size at maturity may well have been underestimated. Further compounding any negative effects of smaller body size on r is the potential for reduced offspring survival owing to the production of smaller eggs (Murawski et al. 2001) and increased variability in recruitment (Hutchings and Myers 1993).

The weaknesses of any modelling approach ultimately lie in the empirical bases, or lack thereof, of the model parameters. The parameter values used here were estimated from data collected from the field. With the exception of the beta distributions used to model the error in survival, the same was true for the error distributions applied to each parameter. One limitation inherent in a previous application of this modelling approach (Hutchings 1999) has been remedied here. By allowing for a reduction in age-specific fecundity of virgin spawners relative to previous spawners, the model incorporates the finding that hatching rate among first-time spawners may be as low as one fifth that of second-time spawners (Trippel 1998). As the simulations presented here suggest, such an effect, if manifested in the field as well as the laboratory, can have a dramatic influence on population growth (also see Murawski et al. 2001). Of importance to the recovery of depleted stocks for which age and size at maturity have declined is the observation that the reduction in r associated with reduced hatching rate among virgin spawners increases as α declines and as M_{mat} increases.

One additional simplification of note is the fact that the model used here did not incorporate any effects of density on age-specific survival or fecundity. Potentially the most important density-dependent effect would be on the probability of survival from birth to age 3 years, l_3. However, inclusion of such a density-dependent influence would not alter the main conclusions drawn here that reductions in age and size at maturity can negatively influence population growth, although absolute estimates of r would be adjusted upward. On the other hand, given that demographic stochasticity and environmental stochasticity on life history parameters almost certainly increase as population size declines (Lande et al. 2003), stochastically based estimates of r might, in fact, result in lower rates of population growth than those estimated here, even if weak density-dependent effects on offspring survival are included in the model.

Random variation in population growth rate can have seriously destabilizing effects on population dynamics, even though the expected population size may increase with time (Lewontin and Cohen 1969; Roff 1974). These destabilizing effects can be expected to be greater in small populations than in large ones (Lande et al. 2003). To some degree, the use of a stochastic, age-structured life history model captures these effects, perhaps most evidently when estimating the likelihood that a population will achieve particular rates of growth (e.g., $\Pr(R_0 < 1)$).

The present study draws attention to a factor rarely considered to have a major influence on recovery in severely depleted marine fishes (Hutchings and Reynolds 2004). It would

be instructive to quantify life history changes at the population level concomitant with overexploitation for a broad range of fishes (Hutchings and Baum 2005), to assess the degree to which these changes represent phenotypic or genetic responses to fishing, and to evaluate the influence that these changes may have on population growth rate, independent of changes to fishing pressure, species interactions, and other correlates of recovery.

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