

Influence of growth and survival costs of reproduction on Atlantic cod, *Gadus morhua*, population growth rate

Jeffrey A. Hutchings

Abstract: A stochastic, age-structured life history model was used to examine how age at maturity (θ), pre- (Z_{imm}) and postreproductive (Z_{mat}) mortality, and postreproductive growth rate can affect maximum reproductive rates of fish at low population size. Simulations suggest that annual (r) and per-generation (R_0) metrics of population growth for Newfoundland's northern Grand Bank Atlantic cod, *Gadus morhua*, are primarily influenced by changes to mortality prior to and following reproduction. At observed weights at age and $Z_{mat} = 0.2$, r ranged between 0.135 and 0.164 for cod maturing at between 4 and 7 years. Incremental increases in either Z_{imm} or Z_{mat} of 0.1 were associated with 0.03–0.05 reductions in r . To effect similar reductions, individual growth rate would have to decline by approximately one half. At observed weights at age, increases in Z_{mat} from 0.20 to 0.45 increased the probability of negative per-generation growth from 3 to 26% for cod maturing at 4 years and from 6 to 46% for cod maturing at 7 years. Thus, even in the absence of fishing mortality, little or no population growth by Atlantic cod may not be unexpected in the presence of environmental stochasticity, particularly when accompanied by increases in mortality and declining individual growth.

Résumé : Un modèle stochastique du cycle vital selon l'âge a été utilisé pour étudier de quelle manière l'âge à la maturité (θ), la mortalité avant la reproduction (Z_{imm}) et après la reproduction (Z_{mat}), et le taux de croissance après la reproduction peuvent influencer sur le taux maximal de reproduction des poissons d'une population peu abondante. Selon les simulations, les mesures annuelles (r) et les mesures par génération (R_0) de la croissance de la population de la morue (*Gadus morhua*) de la partie nord du Grand Banc de Terre-Neuve sont surtout influencées par des modifications de la mortalité avant et après la reproduction. Pour les poids selon l'âge observés et une valeur de $Z_{mat} = 0,2$, r était compris entre 0,135 et 0,164 dans le cas de la morue qui atteint la maturité entre 4 et 7 ans. Les augmentations par échelon de 0,1 de Z_{imm} ou de Z_{mat} étaient associées à des baisses du facteur r comprises entre 0,03 et 0,05. Pour obtenir des baisses similaires, le taux de croissance individuel devrait chuter d'environ la moitié. Pour des valeurs observées de poids selon l'âge, des hausses de Z_{mat} variant de 0,20 à 0,45 augmentaient la probabilité d'une croissance par génération négative de 3 à 26 % chez la morue qui atteint la maturité à l'âge de 4 ans, et de 6 à 46 %, chez celle qui atteint la maturité à l'âge de 7 ans. En conséquence, même en l'absence de mortalité due à la pêche, une croissance faible, voire nulle, de la population de morue en présence de la stochasticité environnementale n'est pas à exclure, en particulier lorsqu'elle est accompagnée d'une augmentation de la mortalité et d'une baisse de la croissance individuelle.

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Introduction

The parameter of greatest import in population dynamics, evolutionary ecology, and evolutionary biology is rate of increase. The fitness of a genotype, for example, is defined as the rate at which it transmits its genes to future generations relative to that of other genotypes in the same population (Stearns 1992). From an evolutionary perspective, Bell (1997) has argued that rate of self-replication is the only attribute that can be selected directly. And the ability of a population to persist in the face of demographic and environmental stochasticity in survival and fecundity appears to

be best reflected by that population's rate of increase (Lande 1993). This point is of particular importance to commercially harvested populations for which spatial and temporal variation in natural mortality is compounded by spatial and temporal variation in mortality due to harvesting.

From a conservation perspective, quantifying rate of increase is perhaps most important when a population has been reduced to a small fraction of the size at which it was presumed stable. For commercially harvested fish populations, the ability of a stock to "recover," i.e., return to some usually arbitrary level of abundance after population collapse, and the time required for such recovery to occur are both functions of that stock's rate of increase at low abundance.

The most widely accepted metrics of maximum population growth rate are the instantaneous, or intrinsic, rate of natural increase, given as r ; and the net reproductive rate, R_0 (Roff 1992; Stearns 1992; Charlesworth 1994). The

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J.A. Hutchings. Department of Biology, Dalhousie University, Halifax, NS B3H 4J1, Canada.
e-mail: jhutch@mscs.dal.ca

units of the former parameter are “individuals per individual per unit time” (usually per year), while those of the latter are “individuals per individual per generation.” Thus, r is an annual rate of increase, expressed as a percentage by $(\exp(r) - 1)100$, while R_0 is a per-generation rate of increase.

Since their collapse in the early 1990s, most of Canada’s Atlantic cod, *Gadus morhua*, fisheries remain closed to commercial exploitation because of low realized rates of population increase. Among the stocks, northern cod, extending from southern Labrador to the northern half of the Grand Bank (i.e., Northwest Atlantic Fishery Organization (NAFO) Divisions 2J, 3K, and 3L), once supported Canada’s largest cod fishery. Based on their analysis of the relationship between spawner biomass and recruitment of the 1962–1989 cohorts, Myers et al. (1997a) estimated r to be 0.26 (correction made by R.A. Myers to the 0.17 estimate provided by Myers et al. 1997a), corresponding to a maximum annual rate of increase for northern cod of 30%. The observation that this stock in the late 1990s appears not to have grown significantly since a commercial fishing moratorium was imposed in 1992 may reflect a lack of sensitivity of research surveys to detect low rates of increase for a widely distributed stock at low abundance. A second possibility is that Myers et al.’s (1997a) maximum growth estimate rate of $r = 0.26$ may have been overestimated or may no longer be representative of a population whose age structure has been severely truncated. A third possibility, and one that I wish to explore further here, is that the observed rate of change in abundance of northern cod, and potentially other Northwest Atlantic cod stocks, since 1992 may not be unexpected given natural, stochastic variation in the life history variables that directly influence the stock’s rate of increase.

I use an age-structured life history model to estimate rates of population increase and their associated frequency distributions for a population of Atlantic cod in the Northwest Atlantic. The stochastic version of this model incorporates observed or estimated variation in the following: (i) age-specific increases in weight, (ii) survival from birth to age 3 years, (iii) annual prereproductive survival probabilities, (iv) annual survival costs of reproduction, and (v) annual growth costs of reproduction. The costs of reproduction represented by the fourth and fifth parameters reflect the observation that, for indeterminately growing organisms, reproduction at age x usually results in reduced survival to, and slower rates of growth at, subsequent ages (Roff 1992; Stearns 1992; Hutchings 1993).

Based on fecundity and growth data available for cod inhabiting the northern half of Newfoundland’s Grand Bank, the region containing most of the research survey biomass for northern cod in the 1990s (Lilly et al. 1998), my objectives were to (i) use a stochastic, age-structured life history model to estimate maximum population growth rates (r and R_0) for Atlantic cod, (ii) quantify the effects of age at maturity, pre- and post-reproductive mortality, and growth costs of reproduction on population growth rate, and (iii) evaluate how per-generation probabilities of population doubling, i.e., $\Pr(R_0 > 2)$, and of population decline, i.e., $\Pr(R_0 < 1)$, vary with reproductive costs. 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.

Materials and methods

Age-specific rates of survival and fecundity can be used to estimate rates of population increase in an age-structured population. 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 is calculated from the discrete-time version of the Euler–Lotka equation:

$$(1) \quad l = \sum_{x=\theta}^{x=\tau} l_x m_x e^{-rx}$$

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

$$(2) \quad R_0 = \sum_{x=\theta}^{x=\tau} l_x m_x.$$

Probability distributions of the intrinsic rate of increase cannot be described by a stochastic model of population growth because of the analytical constraint that r can only be calculated by iteration. However, the intrinsic rate of natural increase can be approximated by the natural logarithm of the net reproductive rate discounted by generation time, G , as

$$(3) \quad r = \ln(R_0)/G$$

where

$$(4) \quad G = \left(\sum l_x m_x x \right) / \left(\sum l_x m_x \right)$$

Probability distributions for all estimates of R_0 presented here were generated from 2000 randomizations. The highly positive skew of these distributions necessitated the calculation of r from median estimates of R_0 .

Age-specific fecundity

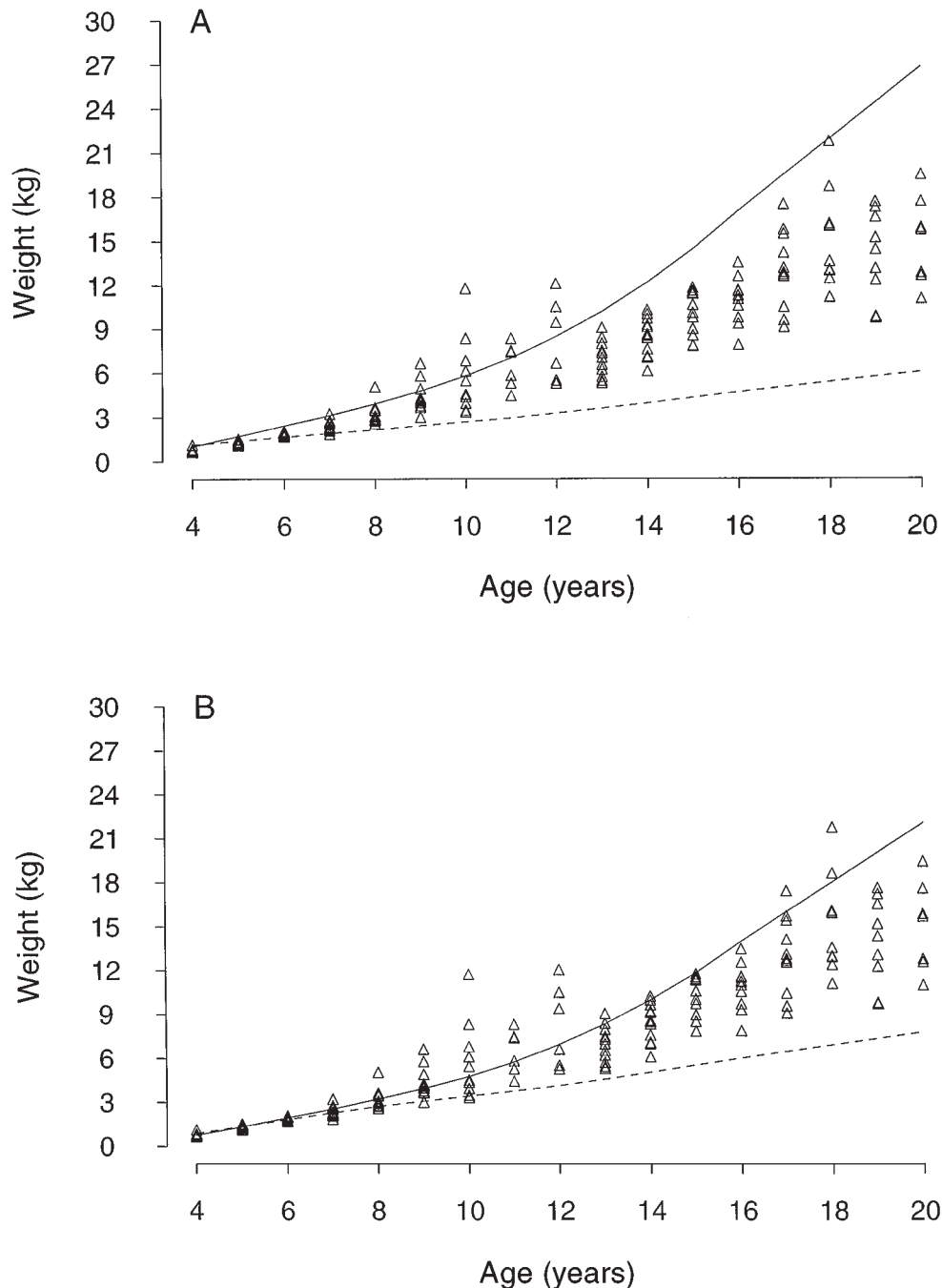
Fecundity was calculated from the relationship between gilled-and-gutted weight and number of eggs per female reported by May (1967) for Atlantic cod collected from several locations off northeastern Newfoundland, including the Grand Bank. Gilled-and-gutted weight, w_{gg} , was estimated from round weight, w , using a relationship derived from samples of prespawning female cod captured between March and May in NAFO Division 3L between 1978 and 1989, i.e., $w = 1.45w_{gg} - 0.37$ (G.R. Lilly, Department of Fisheries and Oceans, P.O. Box 5667, St. John’s, NF A1C 5X1, Canada, personal communication). Substituting this equation into May’s (1967) relationship, age-specific fecundities, m_x , were calculated as

$$(5) \quad m_x = (0.48((w_x + 0.37)/1.45) + 0.12) \times 10^6.$$

Age-specific growth rate

Individual growth rates were approximated by expected changes to size at age throughout an individual’s lifetime. The resultant weights at each age x were calculated by initially multiplying the average weight at age 4 years by the expected age-specific increase in body size between ages 4 and 5 years, i.e., w_5/w_4 , to obtain an estimate of weight at age 5 years, then multiplying this estimate of weight at age 5 years by w_6/w_5 to obtain an estimate of weight at age 6 years, and so on until the age of 20 years. Empirical esti-

Fig. 1. Observed and modelled weights at age for Atlantic cod maturing at (A) 4 years and (B) 7 years. Triangles represent weights measured for 4- to 12-year-old cod captured on northern Grand Bank (NAFO Division 3L) by research surveys between 1981 and 1996 and for 13- to 20-year-old northern cod (NAFO Divisions 2J, 3K, and 3L) captured by commercial vessels between 1981 and 1992. The solid lines represent modelled relationships based on observed mean annual changes in weight at age x , i.e., w_{x+1}/w_x . The broken lines describe changes in weight at age at 50% of the observed growth rates. See text for more details.



mates of w_{x+1}/w_x were calculated in part from weights at age for cod aged 4–12 years measured during research surveys between 1981 and 1996 in NAFO Division 3L (Lilly 1997; and excluding weights at age based on sample sizes of less than 5). The comparatively few fish older than age 12 years sampled by the surveys necessitated the use of commercial catch statistics, combined for NAFO Divisions 2J, 3K, and 3L (1981–1992), to estimate growth rates for cod aged 13–20 years (Murphy et al. 1997). Although the latter data included weights of the slower-growing cod inhabiting

the more northerly Divisions 2J and 3K, these do not seem to unduly affect the estimated growth rates for cod older than 12 years used in the present model (Fig. 1). Any bias in estimated individual growth rates for 3L cod introduced by the inclusion of cod from 2J and 3K is unlikely to be large, given the comparatively small influence of individual growth rate on population growth rate, documented later in this paper, and given the wide range in growth costs of reproduction considered in the present model (i.e., from observed to 50% reductions in annual changes to weight at

Table 1. Age(x)-specific rates of weight (w) increase, i.e., w_{x+1}/w_x , for Atlantic cod aged 4–20 years.

Age-class (years)	Mean growth rate (w_{x+1}/w_x)	SD
4–5	1.62	0.20
5–6	1.43	0.17
6–7	1.30	0.16
7–8	1.28	0.23
8–9	1.26	0.19
9–10	1.21	0.50
10–11	1.10	0.51
11–12	1.26	0.44
12–13	1.21	0.11
13–14	1.21	0.14
14–15	1.25	0.16
15–16	1.11	0.13
16–17	1.30	0.35
17–18	1.24	0.39
18–19	0.94	0.13
19–20	1.08	0.28

Note: Data are means \pm SD based on weights at age for cod aged 4–12 years measured during research surveys between 1981 and 1996 in NAFO Division 3L (minimum of five fish per sample; Lilly 1997) and based on weights at age for cod aged 13–20 years measured from the commercial catches of cod captured from NAFO Divisions 2J, 3K, and 3L (Murphy et al. 1997).

age). In addition, the range in individual growth rates considered here (the solid and broken lines in Fig. 1) encompass most of the observed weights at age measured from the survey and commercial catch data (Fig. 1). The error 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) (Table 1).

Given the negative association between individual growth rate and age at maturity, θ , that has been repeatedly demonstrated in fish (Roff 1992; Hutchings 1993, 1996, and references therein), weights at age can be expected to differ among cod whose age at maturity ranges between 4 and 7 years (Murphy et al. 1997; Trippel et al. 1997). However, random samples of weights at age for cod maturing at ages 4, 5, 6, and 7 years are not available for northern cod (G.R. Lilly, Department of Fisheries and Oceans, P.O. Box 5667, St. John's, NF A1C 5X1, Canada, personal communication). To account for the high probability that cod maturing at ages 4–6 years will be the largest individuals at those ages (a supposition with empirical support for Georges Bank cod; Trippel et al. 1995), I calculated weight at maturity, w_θ , by incorporating both the observed age-specific incidence of maturity for northern cod (these data are unavailable for northern Grand Bank cod alone) and the normal distribution of weights at age, as determined from the research surveys (Murphy et al. 1997). Thus, for the present analysis, weights at maturity for ages $\theta = 4, 5,$ and 6 years (there is a greater than 90% probability that cod aged 7 years are mature; Murphy et al. 1997) were randomly sampled from the upper $p\%$ of the normal distribution of weights for each age, where $p\%$ equals the observed incidence of maturity by age. The 1981–1996 average incidences of maturity were 1.5, 21.7, and 56.7% for $\theta = 4, 5,$ and 6 years, respectively. Based on this formulation, the median weights at maturity of cod reproducing initially at ages 4, 5, and 6 years were 1.12, 1.55, and 2.06 kg, respectively. The weight of cod maturing at age 7 years was set equal to the observed average

weight of 7-year-old cod measured during the research surveys between 1981 and 1996, i.e., 2.44 kg.

Growth cost of reproduction

The diversion of energy from somatic tissue production to the production of gonadal tissue effects a reduction in growth rate of reproductive individuals when compared with that of non-reproductive individuals (Bell 1980; Wootton 1990). The magnitude of this cost can range quite widely among populations of the same species. For example, in two populations of brook trout, *Salvelinus fontinalis*, on Cape Race, Newfoundland, the percentage reduction in annual growth rate experienced by maturing females was approximately equal to their gonadosomatic index (GSI) (gonad weight/total body weight) of roughly 10–15% (Hutchings 1993). At the other extreme, within another trout population on Cape Race (Freshwater River), for which individually marked fish were monitored for 4 years, annual increases in growth rate of reproductive individuals were 85% less than those of nonreproductive individuals of the same age (J.A. Hutchings, unpublished data).

There are comparatively few data on GSI for Atlantic cod. Estimates of average GSI for spawning female cod in the Northwest Atlantic in the early 1990s range from 0.08 in the southern Gulf of St. Lawrence (Schwalme and Chouinard 1999) to 0.19 in the northern Gulf (Lambert and Dutil 1997), giving a midrange GSI of 0.14. If the reduction in growth rate concomitant with maturation in cod can be approximated by the percentage of body tissue allocated to gonads, as it can for some populations of brook trout (Hutchings 1993), then the annual growth rates of reproductive cod would be about 14% less than those of nonreproductive cod at the same age. For cod maturing at age 7 years, I assumed that the observed weights at age from the survey and commercial catch data incorporated the reduction in growth rate effected by reproduction. For cod maturing at ages 4, 5, and 6 years, I multiplied their observed annual growth rates (w_{x+1}/w_x) by 0.86 until they reached age 7 years to simulate a 14% reduction in individual growth. Although the observed data include weights at age for both mature and immature fish, the incidence of maturity is comparatively low among 4- and 5-year-olds (1.5 and 21.7%, respectively, between 1981 and 1996), albeit increasing to 56.7% among 6-year-olds (Murphy et al. 1997). Thus, the incorporation of a growth cost of reproduction as applied here may underestimate the growth rate of cod maturing at age 6 years between ages 6 and 7 years. To examine how changes to this growth cost of reproduction influence population growth rate, I reduced observed growth rates (Table 1) by 10, 20, 30, 40, and 50%.

Prereproductive mortality and survival costs of reproduction

I partitioned the survival of cod into three categories: survival from birth to age 3 years (the age at which northern cod are first recruited to commercial fishing gear), instantaneous rate of mortality of immature individuals, Z_{imm} , and instantaneous rate of mortality of mature individuals, Z_{mat} .

Survival from birth to age 3 years was quantified from virtual population analysis estimates of age-specific abundance reported by Murphy et al. (1997) and from age-specific fecundities as defined above. Survival from birth to age 3 years 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

$$(6) \quad l_{3(t)} = n_{3(t)} \prod_{x=7}^{x=11} n_{x(t-3)} m_{x(t-3)}$$

Survival from birth to age 3 years estimated in this manner for the 1962–1988 year-classes of northern cod was weakly density de-

Table 2. Survival parameter values used in the age-structured model of Atlantic cod life history.

Instantaneous mortality of immature females (Z_{imm})	Annual survival of immature females ($\exp(-Z_{imm})$)	Survival cost of reproduction ($1 - \gamma$)	Annual survival of mature females ($\exp(-Z_{imm})\gamma$)	Instantaneous mortality of mature females (Z_{mat})
0.10	0.91	0.10	0.82	0.20
		0.20	0.73	0.32
		0.30	0.64	0.45
0.20	0.82	0.10	0.74	0.30
		0.20	0.66	0.42
		0.30	0.57	0.55
0.30	0.74	0.10	0.67	0.40
		0.20	0.59	0.52
		0.30	0.52	0.65

pendent (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

$$(7) \quad f(x) = \frac{(x/s)^{\alpha-1}(1-(x/s))^{\beta-1}}{\Gamma(\alpha)\Gamma(\beta)/\Gamma(\alpha+\beta)}$$

where $\Gamma(\beta)$ is the Gamma function. With the scale parameter, s , establishing the upper bound of the distribution at 1.0 and the mean of the distribution ($\alpha/(\alpha + \beta)$) set to annual survival probabilities, i.e., $\exp(-Z_{imm})$ of 0.91, 0.82, and 0.74 (corresponding to Z_{imm} of 0.1, 0.2, and 0.3, respectively), 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).

Survival from birth to age x , i.e., l_x , will differ between reproductive and nonreproductive individuals. The survival costs of reproduction experienced by reproductive cod may be attributable to factors such as the energetic consequences of producing gonadal tissue (Lambert and Dutil 1997), the repertoire of behaviours involved in mate competition and possibly mate choice (Brawn 1961; Hutchings et al. 1999), and a cessation of feeding often concomitant with breeding (Fordham and Trippel 1999). I assume here a cost ($1 - \gamma$) of 0.10, such that survival from age x to age $x + 1$ for an individual reproducing at age x is

$$(8) \quad l_{x+1} = l_x \exp(-Z_{imm}) \gamma.$$

The influence of higher survival costs on population growth rate was examined by reducing γ from 0.9 to 0.8 and to 0.7. The full range of parameter values for survival used here is given in Table 2.

Results

Influence of age-specific survival and weight on maximum population growth rate (r)

For the same survival probabilities and growth costs of reproduction, rates of increase of early-maturing Atlantic cod ($\theta = 4$ years) were consistently greater than those of late-maturing cod ($\theta = 7$ years) (compare Figs. 2A–2C with Figs. 2D–2F). At low prereproductive mortality ($Z_{imm} = 0.10$), the annual rate of increase of cod maturing at age 4 years was about 2–4% higher than that of cod maturing at 7 years. This difference in r between early- and late-maturing cod increased with increases in prereproductive

mortality, Z_{imm} (Fig. 2). The highest estimates of r for cod maturing at ages 4 and 7 years were 0.164 and 0.135, respectively, corresponding to maximum rates of increase of 18 and 14% per annum.

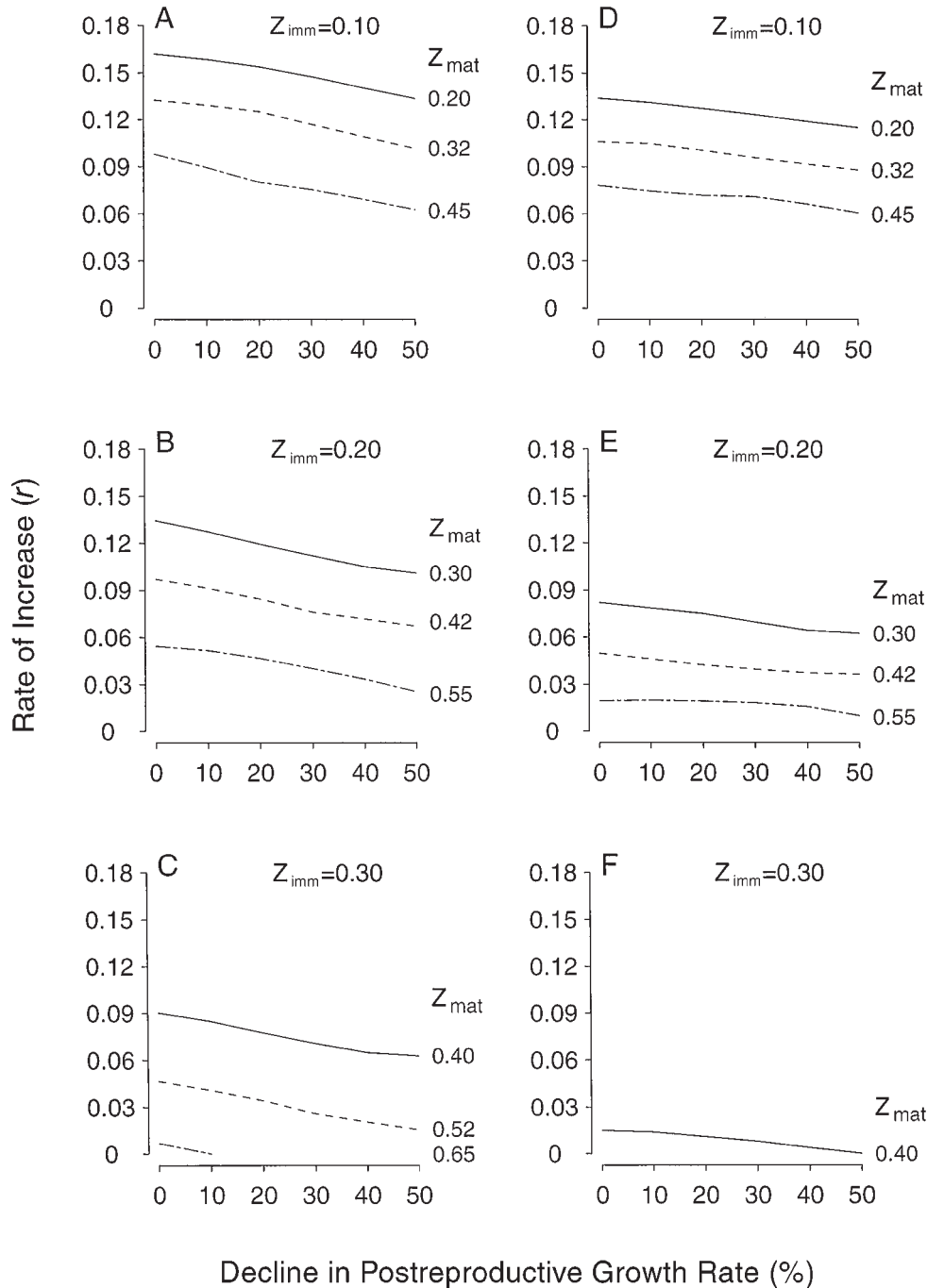
Population rates of increase were particularly sensitive to changes in survival prior to and after maturity (Fig. 2). All else being equal, an increase in Z_{imm} of 0.1 was associated with a reduction in r of about 0.03–0.05. Similarly, 10% increases in survival costs of reproduction (reflected by the incremental increases in Z_{mat} on Fig. 2) were associated with declines in r of about 0.03 to 0.04, independent of age at maturity. Particularly large increases in prereproductive mortality from $Z_{imm} = 0.1$ to 0.3, especially when coupled with increases in survival costs of reproduction, often resulted in negligible or negative population growth (e.g., Figs. 2C, 2E, and 2F).

By contrast, changes to individual growth rate, as reflected by increased growth costs of reproduction, had comparatively little effect on population rates of increase (Fig. 2). Linear regressions relating r to reductions in individual growth rate (Table 3) for the values of pre- and post-reproductive mortality used here revealed a similarity in slopes, specific to age at maturity, such that a 10% reduction in postreproductive individual growth rate was predicted to reduce r by only 0.006 and 0.003 (the averages of the regression slopes) for individuals maturing at 4 and 7 years, respectively. At most, all else being equal, declines in post-reproductive growth rate of up to 50% of observed values were associated with reductions in r of only about 0.03 (Fig. 2).

Probabilities of negative population growth

The frequency distributions of R_0 produced by the stochastic population growth model (e.g., Fig. 3) can be used to estimate the probabilities with which various rates of population growth rate can be achieved under specific combinations of age at maturity, survival and growth costs of reproduction, and individual postreproductive growth rate. These distributions were used to estimate the probabilities of northern Grand Bank cod experiencing growth rates that would allow the population to more than double (i.e., $R_0 > 2$) or to decline during a single generation (i.e., $R_0 < 1$). Generation times, which vary with age-specific survival and fecundity (see eq. 4), ranged between 5.4 and 11.4 years for cod maturing at age 4 years and between 8.3 and 12.9 years for cod maturing at age 7 years (Table 4).

Fig. 2. Changes in maximum Atlantic cod population growth rate, r , with changes in age at maturity of (A–C) 4 years and (D–F) 7 years, prereproductive mortality (Z_{imm}), postreproductive mortality (Z_{mat}) effected by incremental declines in survival probabilities, and individual postreproductive growth rate.



Although the probability of a per-generation doubling in population size declined with decreases in postreproductive growth rate and with increases in age at maturity, their influence on $\Pr(R_0 > 2)$ was comparatively small when compared with that of changes in survival (Fig. 4). At observed weights at age (i.e., 0% decline in observed postreproductive growth rate) and at the survival probabilities assumed to be typical for this stock (i.e., $Z_{imm} = 0.1$; $Z_{mat} = 0.2$, e.g., Pinhorn 1975), the probability of northern Grand Bank cod doubling every generation, at population sizes comparatively uninfluenced by density, was about 0.84 (the average of the

probabilities for $\theta = 4$ and 7 years; Figs. 4A and 4D). Incremental increases in prereproductive mortality, Z_{imm} , from 0.1 to 0.2 and to 0.3 were associated with incremental declines in $\Pr(R_0 > 2)$ of 10–20%. Similar incremental reductions in $\Pr(R_0 > 2)$ were associated with incremental 10% declines in postreproductive mortality.

The probability of negative population growth between generations, i.e., $\Pr(R_0 < 1)$, was also comparatively uninfluenced either by individual growth rate or by age at maturity (Fig. 5). At observed weights at age and at presumed typical mortalities of Z_{imm} and Z_{mat} of 0.1 and 0.2, respectively, the

Table 3. Linear regressions between Atlantic cod population growth rate (r) and proportional reduction (G) in annual individual growth rate (w_{x+1}/w_x) between ages x and $x + 1$ for ages at maturity (θ) of 4 and 7 years and for different instantaneous rates of mortality prior to (Z_{imm}) and following (Z_{mat}) maturity.

θ	Z_{imm}	Z_{mat}		R^2	p
4	0.10	0.20	$r = -0.058G + 0.164$	0.97	<0.001
		0.32	$r = -0.066G + 0.136$	0.95	<0.001
		0.45	$r = -0.065G + 0.094$	0.96	<0.001
	0.20	0.30	$r = -0.071G + 0.134$	0.96	<0.001
		0.42	$r = -0.066G + 0.097$	0.97	<0.001
		0.55	$r = -0.060G + 0.057$	0.90	0.004
7	0.30	0.40	$r = -0.061G + 0.091$	0.89	0.004
		0.52	$r = -0.068G + 0.048$	0.96	<0.001
		0.20	$r = -0.039G + 0.135$	0.98	<0.001
	0.10	0.32	$r = -0.039G + 0.108$	0.95	<0.001
		0.45	$r = -0.027G + 0.078$	0.66	0.049
		0.42	$r = -0.043G + 0.082$	0.94	0.002
0.20	0.42	$r = -0.028G + 0.049$	0.94	0.001	
	0.55	$r = -0.017G + 0.022$	0.43	0.157	
	0.30	0.40	$r = -0.032G + 0.017$	0.94	0.002

Fig. 3. Frequency distributions of net reproductive rate, R_0 , as determined from 2000 iterations of a stochastic, age-structured model of population growth for Atlantic cod maturing at ages 4 and 7 years at two instantaneous rates of postreproductive mortality (Z_{mat}). The black vertical lines correspond to the net reproductive rate at which individuals are replacing themselves between generations, i.e., $R_0 = 1$. The proportion of the frequency distributions to the right of the black lines (grey lines) represents the probability that the population will grow between generations. Prereproductive mortality is held constant at $Z_{imm} = 0.1$.

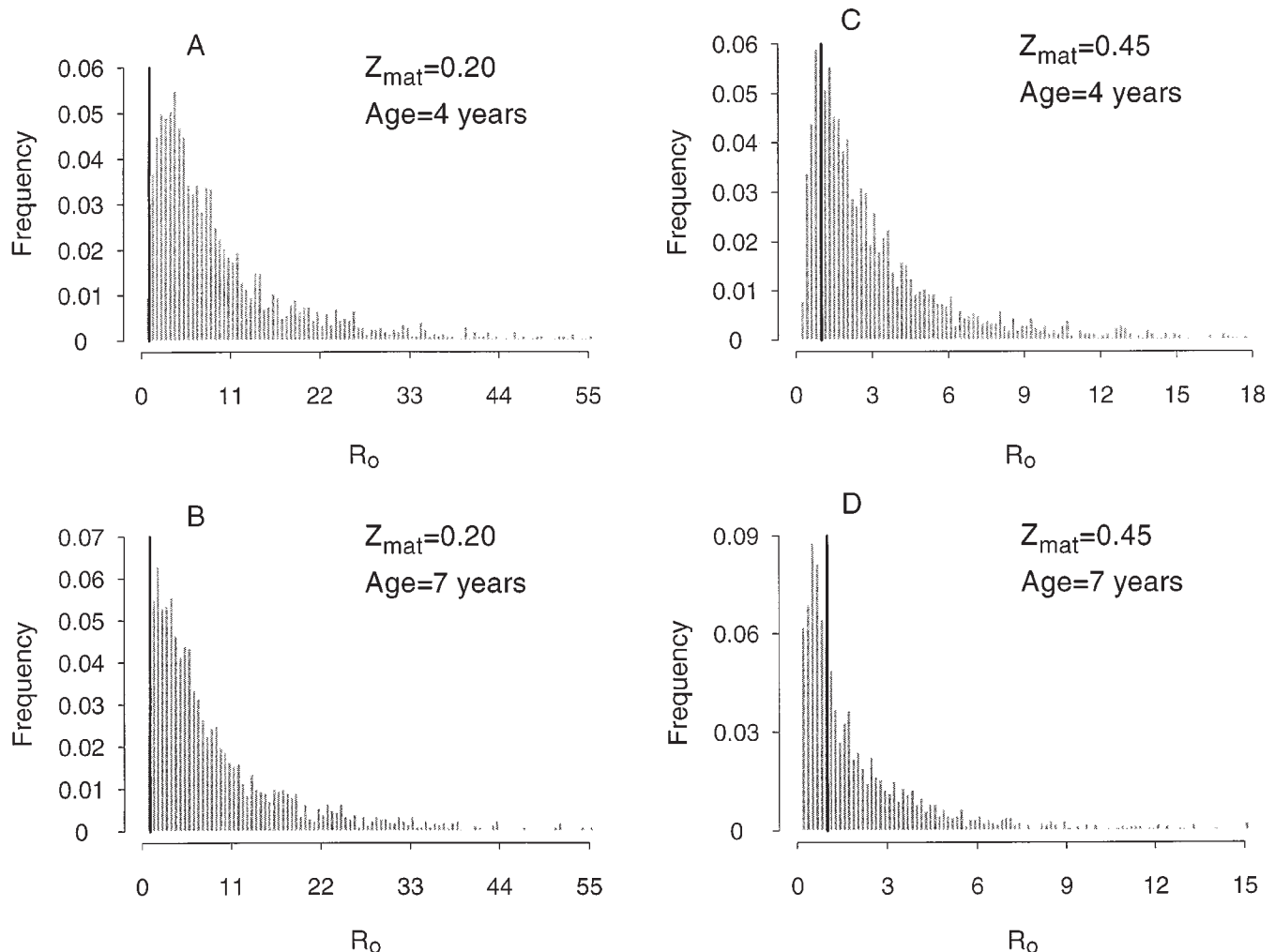


Table 4. Deterministic estimates of maximum population growth rate (r , R_0) and generation time (G) for Atlantic cod maturing at ages 4 and 7 years at observed and 50% of observed postreproductive growth rates and at different levels of prereproductive mortality (Z_{imm}) and postreproductive mortality (Z_{mat}).

Z_{imm}	Z_{mat}	Postreproductive growth rate	Age at maturity = 4 years			Age at maturity = 7 years		
			r	R_0	G (years)	r	R_0	G (years)
0.10	0.20	Observed	0.204	10.14	11.36	0.174	9.36	12.89
		50% decline	0.178	5.34	9.40	0.154	6.01	11.66
	0.32	Observed	0.178	4.94	8.95	0.147	5.19	11.19
		50% decline	0.154	3.18	7.53	0.130	3.79	10.24
	0.45	Observed	0.150	2.91	7.12	0.122	3.28	9.77
		50% decline	0.123	2.17	6.29	0.107	2.66	9.17
0.20	0.30	Observed	0.171	4.88	9.27	0.116	3.74	11.41
		50% decline	0.144	3.06	7.76	0.095	2.69	10.42
	0.42	Observed	0.144	2.94	7.48	0.088	2.42	10.07
		50% decline	0.116	2.31	6.53	0.069	1.92	9.39
	0.55	Observed	0.111	2.01	6.29	0.060	1.73	9.07
		50% decline	0.083	1.61	5.74	0.044	1.47	8.66
0.30	0.40	Observed	0.135	2.82	7.69	0.052	1.70	10.23
		50% decline	0.105	2.01	6.67	0.030	1.33	9.51
	0.52	Observed	0.104	1.97	6.52	0.023	1.24	9.27
		50% decline	0.073	1.54	5.89	0.004	1.04	8.81
	0.65	Observed	0.069	1.49	5.75	-0.005	0.96	8.59
		50% decline	0.042	1.25	5.37	-0.020	0.85	8.3

probability of northern Grand Bank cod declining during a single generation was less than 5% (Figs. 5A and 5D). However, $\Pr(R_0 < 1)$ increased by about 10–20% for every 0.1 incremental increase in Z_{imm} and for every 0.1 reduction in postreproductive survival probability.

The stochastic estimates of population growth (e.g., Fig. 3) were consistently less than those estimated by the deterministic model, in which rates of survival and fecundity were assumed invariant within age (Table 4). Varying with pre- and post-reproductive mortality and with growth costs of reproduction, deterministic estimates of r generally exceeded their corresponding stochastic estimates by 0.04–0.06. At assumed typical pre- and post-reproductive mortalities of $Z_{imm} = 0.1$ and $Z_{mat} = 0.2$, differences between deterministic (0.204 and 0.174 at $\theta = 4$ and 7 years, respectively) and stochastic (0.164 and 0.135 at $\theta = 4$ and 7 years, respectively) estimates of r corresponded to a 5% difference in annual rate of increase.

Discussion

Maximum rates of population increase for northern Atlantic cod

The present study describes how age at maturity, individual growth rate, and pre- and post-reproductive survival can influence metrics of population increase for Atlantic cod. It differs from previous efforts to incorporate reproductive costs in life history analyses of this species (e.g., Myers and Doyle 1983; Trippel et al. 1995) by attempting to disentangle the effects of individual age, growth, and mortality on maximum population growth rate. Based on an age-structured life history model, and incorporating stochastic variation in survival and fecundity (the latter through changes in weight at age), annual (r) and per-generation (R_0) rates of population increase appeared to be most sensitive to changes in pre- and post-reproductive survival probabilities

and less sensitive to changes in age at maturity and post-reproductive growth rate.

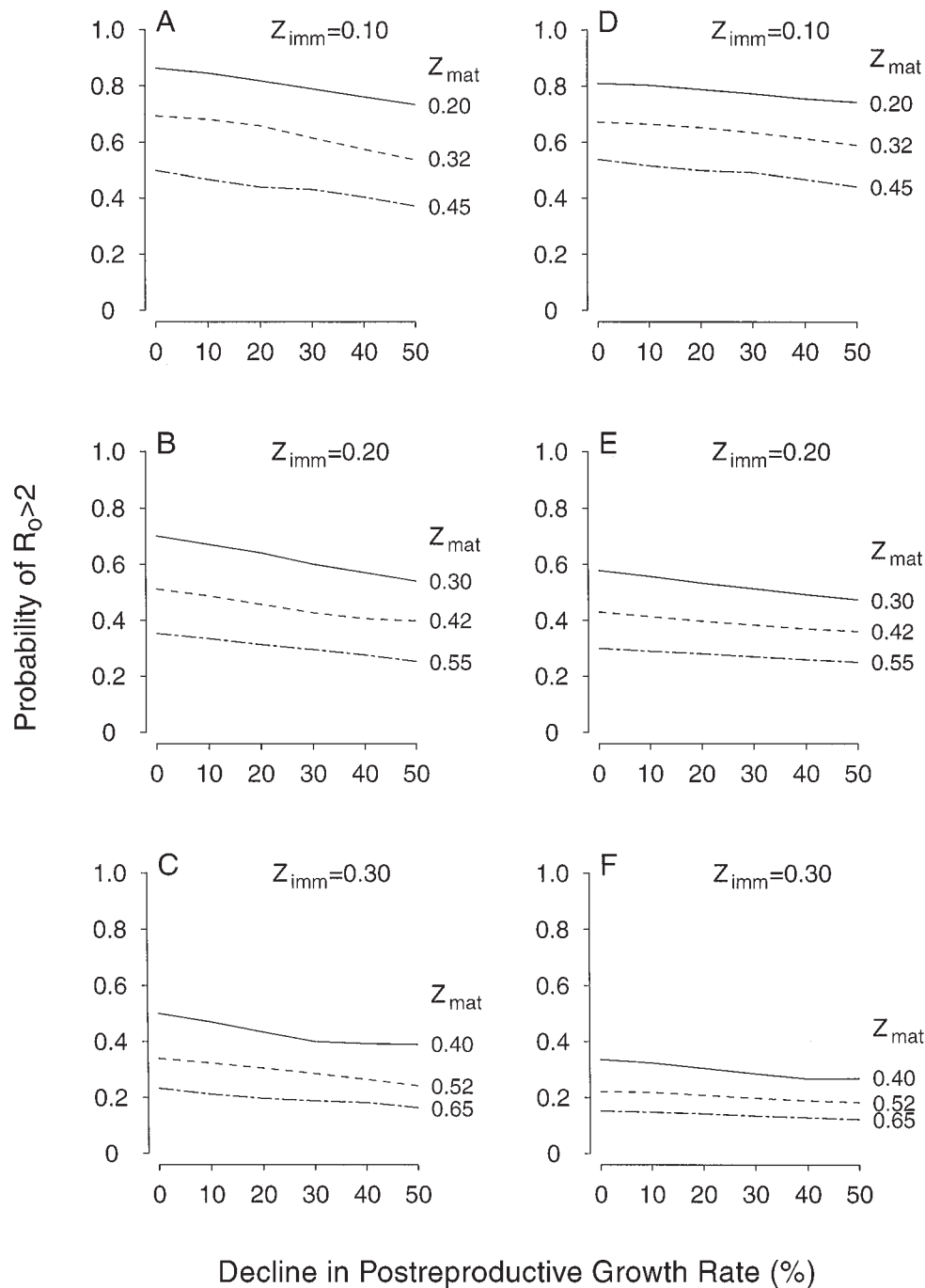
At observed weights at age and at the instantaneous rate of natural mortality generally assumed typical for northwest Atlantic cod, i.e., $M = 0.2$, or $Z = 0.2$ in the absence of fishing, median estimates of r for ages at maturity of 4–7 years were estimated here to range between 0.135 and 0.164. These estimates, coupled with that of 0.26 previously estimated for northern cod (Myers et al. 1997a), correspond to a range of maximum annual rates of increase of 14–29% and may provide a reasonable approximation of the typical range in r for Atlantic cod inhabiting the waters off northern and eastern Newfoundland.

Influence of increased mortality on population growth rate

The present study suggests that changes in mortality may have a larger effect on population rate of increase than changes to individual growth rate or age at maturity. Significant reductions in r were associated with increases in either pre- or post-reproductive mortality, although the effect on r generated by changes to Z_{imm} was greater for cod maturing at 7 rather than at 4 years of age (Fig. 2). This can be attributed to the greater number of years experienced by late-maturing cod prior to initial reproduction. At observed weights at age and at a prereproductive mortality of $Z_{imm} = 0.1$, increases in Z_{mat} from 0.20 to 0.45 are predicted to reduce r from 0.162 to 0.098 for cod maturing at age 4 years and from 0.134 to 0.079 for cod maturing at 7 years.

If the M of some Atlantic cod stocks has increased since the commercial fishery closures in the early 1990s (DFO 1998a, 1998b), and if an increase in M (effectively Z in the absence of fishing) from 0.2 to 0.4 is a reasonable approximation of the magnitude of this change (Sinclair 1999), the negative consequences to population growth rate may be substantial. The present study suggests that an increase in

Fig. 4. Probability of Atlantic cod more than doubling in population size within a single generation, $\Pr(R_0 > 2)$ as a function of age at maturity of (A–C) 4 years and (D–F) 7 years, prereproductive mortality (Z_{imm}), postreproductive mortality (Z_{mat}), and individual growth rate. Generation times are given in Table 4.



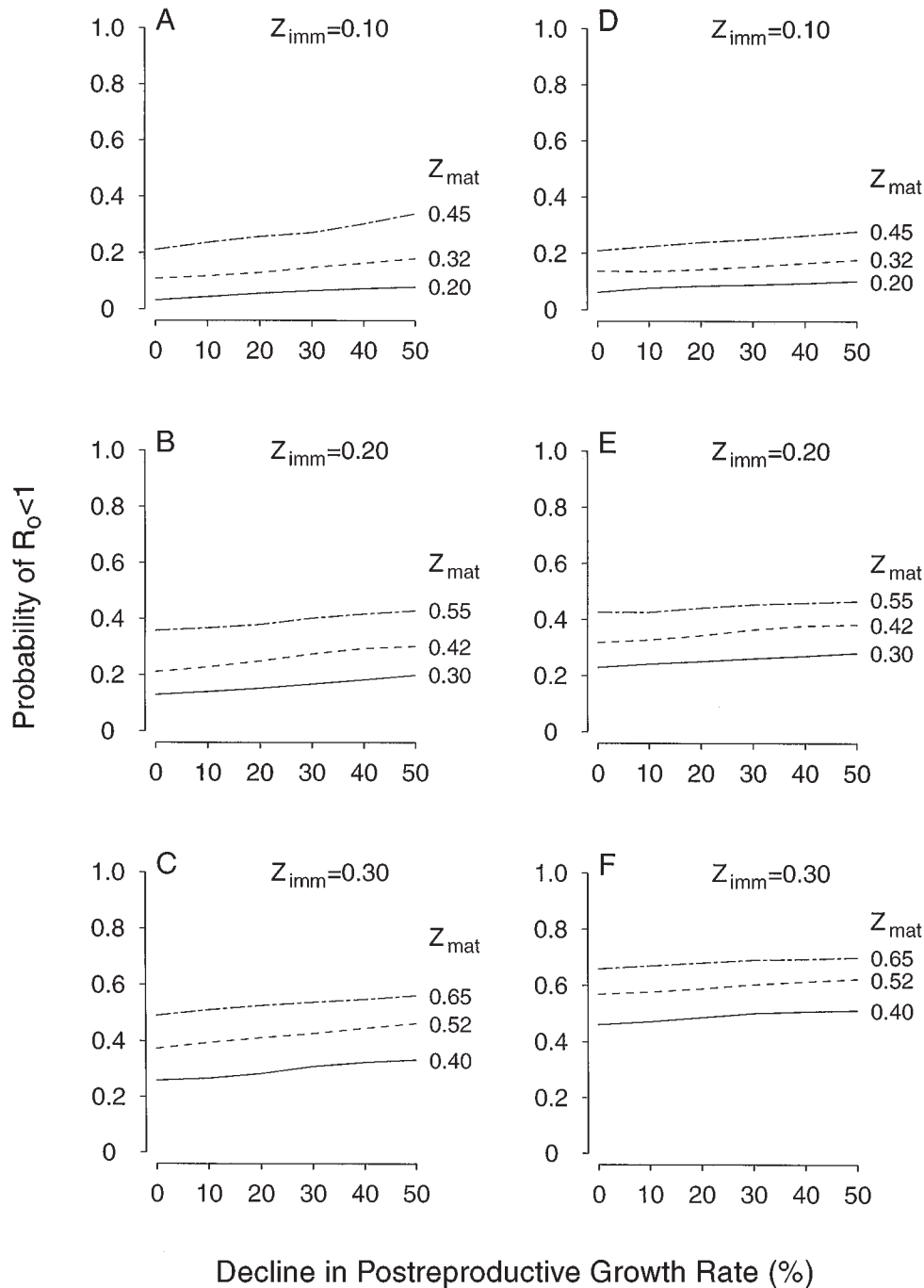
Z_{mat} from 0.20 to 0.45, in the absence of changes to weights at age and to prereproductive mortality, will reduce the annual growth rate of northern Grand Bank cod from between 14 and 18% to between 8 and 10% per annum. In terms of doubling time, i.e., $\ln(2)/r$, such an increase in mortality would effect increases in doubling time from 4.3 to 7.1 years for cod maturing at 4 years and from 5.2 to 8.8 years for cod maturing at 7 years.

Age at maturity and population growth

There is evidence to suggest that age at maturity for some

Atlantic cod stocks may have decreased during the past decade (Murphy et al. 1997; Trippel et al. 1997). Rapid declines in age at maturity in fishes are usually associated with increasing growth rates prior to first reproduction (Roff 1992; Stearns 1992; Hutchings 1993, 1996). Such a negative association between growth rate and age at maturity has, for example, been documented for Atlantic cod on Georges Bank (Trippel et al. 1995). However, evidence of such an increase in individual growth rate is not apparent from recent research survey estimates of weights at age for Northwest Atlantic cod (e.g., Trippel et al. 1997). Increases in body

Fig. 5. Probability of negative population growth within a single generation, $\Pr(R_0 < 1)$, as a function of age at maturity of (A–C) 4 years and (D–F) 7 years, prereproductive mortality (Z_{imm}), postreproductive mortality (Z_{mat}), and individual growth rate. Generation times are given in Table 4.



condition can also effect reduced ages at maturity (Stearns 1992). But, again, the apparent declines in age at maturity have not been associated with appreciable increases in body condition (e.g., Lilly 1997).

A third explanation for declining age at maturity is differential loss of genotypes from the population. Assuming that age at maturity is heritable in Atlantic cod, as it is in most organisms (Roff 1997), a decline in age at maturity may have been caused by an increase in the proportional representation of early-maturing genotypes predicated by the higher fishing mortality experienced by the comparatively

large, late-maturing genotypes in the late 1980s and early 1990s (Hutchings and Myers 1994; Myers et al. 1997b; Lilly et al. 1998).

Nonetheless, irrespective of what may have caused a decline in θ , a decline in age at maturity would appear, all else being equal, to have a positive, although comparatively small, effect on population growth rate (Fig. 2). This result may, however, be misleading. The estimates of r in the present analyses, incorporating the well-documented effect of individual growth rate on age at maturity, were based on the assumption that cod maturing relatively early in life were

the fastest growers in the population. This resulted in comparatively larger weights at age and correspondingly higher age-specific fecundities for early-maturing individuals. If, however, early-maturing genotypes share the same age-specific schedule of weight as late-maturing genotypes, the analyses of r presented here will overestimate the intrinsic rate of increase of early-maturing genotypes. Additional factors that may reduce the fitness of comparatively small, early-maturing individuals may include reduced hatching success (Trippel 1998), reduced mating success (Hutchings et al. 1999), and increased recruitment variability (Hutchings and Myers 1993).

Weaknesses and strengths of the present model

The weaknesses of the present model ultimately lie in the empirical bases, or lack thereof, of the model parameters. The variances used in the error distributions are, with the exception of those assumed for the mortality experienced by cod older than 3 years, empirically based on virtual population analysis estimates of abundance (to quantify survival from birth to age 3 years), research survey and commercial catch estimates of weights at age, and a very broadly based fecundity–weight relationship. Clearly, these estimates can be improved upon. For example, there is a need to construct detailed fecundity – body size regressions for Atlantic cod throughout its range (e.g., see Pinhorn 1984), given that population differences in fecundity per unit weight will generate population differences in rate of increase.

Additional limitations of the present analysis lie in the assumptions that fecundity is independent of parity and that the probability of surviving from birth to age 3 years is independent of parental age or body size. Trippel (1998), for example, documented hatching rates of virgin cod that were 25% those of previously spawned females. Presumably, such a decline in hatching success would be evident irrespective of age at maturity, although such an experiment has yet to be undertaken. An effect of age and body size on cod reproductive success was suggested by Hutchings and Myers (1993) who posited that the shorter spawning period expected of younger, smaller females may increase recruitment variability because of a reduced probability of temporal overlap between periods of phytoplankton blooms and larval cod feeding. The present model also includes the assumption that cod spawn annually. If they do not, population growth rates will be negatively affected.

Perhaps the primary advantage of using a stochastic life history model to estimate rates of population increase lies in its potential to account for empirically reasonable variation in the parameters and variables on which rates of increase are based. For example, depending on the magnitude of survival and growth reproductive costs, the present study suggests that the probability of very slow or even negative growth can be significant for Atlantic cod. This is consistent with the findings of Lewontin and Cohen (1969) and Roff (1974) that random variation in population growth rate can have seriously destabilizing effects on population dynamics, even though the expected population size may increase with time. Also, the effect of age-specific changes to survival and individual growth on population growth rate cannot be readily quantified by other means of estimating r , e.g., stock–recruitment relationships (Myers et al. 1997a). In ad-

dition, stochastic models provide probabilities with which specific population rates of increase might be realized. As examples, I selected the probabilities with which a population will decline and double every generation. Such probabilities may prove useful in risk analyses.

The use of stochastic, age-structured life history models in fish stock assessment and fish conservation biology appears to have merit. The strengths and weaknesses of such an approach warrant further examination.

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