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Are there useful life history indicators of stock recovery rate in gadoids?

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Age at maturity is one of the key variables determining the maximum rate of population growth and so may be a good indicator of stock recovery potential. Spawner age composition may also affect the probability of high recruitment and so could be relevant to stock recovery. This study examined the relation between early survival, age at maturity, and the demographic composition of spawners in many cod and haddock stocks. Reported measures of fecundity and maturity were used to estimate total egg production for comparison with numbers at age 1 and age at 50% maturity. The instantaneous rate of population growth (r) was estimated for cohorts from life history tables during periods when spawning biomass was depleted (e.g. $<B_{pa}$) using reproductive and mortality data for stocks. Age-specific survival was found to be far more important than reproductive rate in determining population growth rate. Stocks that experienced low and more variable survival matured early and had a high relative fecundity. Hence, while early maturing stocks have the potential for high population growth following favourable recruitment events, they would not be expected to recover any faster than late maturing stocks because of the generally low early survival rate that they experience. Measures of spawner age diversity and mean age were found to be positively correlated with offspring survivorship in a few cod stocks. However, in general, it appears difficult to infer recovery potential from life history characteristics, which may be expected, given that regional variation in reproductive success will ultimately be expected to shape local reproductive schedules.

Keywords: cod, haddock, population growth rate, recruitment, spawner age composition, stock recovery.

Introduction

Improving our understanding of how fish stocks recover has become a key requirement of fisheries science following agreement on international targets to rebuild depleted stocks (Ye *et al.*, 2013). Many gadoid stocks have collapsed and are now the subject of recovery plans involving a range of measures from fishing moratoria, area closures, and reductions in effort. However, the speed of recovery has been unexpectedly slow in many fish stocks, especially those that have been subjected to prolonged periods of high fishing pressure (Hutchings, 2000, 2001; Neubauer *et al.*, 2013). Theoretically, the rate of stock recovery of a depleted stock should be predictable from the intrinsic or maximum rate of population growth, r_{max}, which is expected to occur when a population has reached a stable age composition in the absence of fishing mortality. This measure of population growth integrates the effects of age-specific survival and factors influencing reproductive rate such as age at first maturity, fecundity, and the number of spawnings over the life time of a cohort and assumes no density-dependent limitation (Caswell,

2001). Life history traits such as early age at maturity, small body size, short lifespan, and rapid individual growth are all expected to be positively related to the rate of population growth and empirical comparisons among marine fish species using proxies of r_{max} tend to support these expectations (Jennings *et al.*, 1998; Reynolds *et al.*, 2001). A comparison among Atlantic cod (*Gadus morhua*) stocks has also supported the expected inverse relationship between r_{max} and age at maturity (Myers *et al.*, 1997). Given this relationship, age at maturity may be expected to be associated with the rate of recovery of depleted gadoid stocks.

Two approaches have been used to estimate the maximum rate of population increase in fish stocks: stock–recruitment and demographic models (Myers *et al.*, 1997, 1999; Gedamke *et al.*, 2007). Classic demographic models (e.g. life tables) provide a means of exploring the effects of life history parameters on expected lifetime reproductive output (often termed net reproductive rate) and when applied to depleted populations should provide estimates of population growth rate that approach r_{max} (Gedamke *et al.*, 2007).

However, the preconditions of a stable age composition and lack of density-dependence in demographic models are unlikely to be met in a harvested population (Jennings *et al.*, 1998). Spawning stock–recruitment models directly address reproductive success and density-dependence from the relationship between the offspring that survive and the parental stock. The slope at the origin of the stock–recruitment relationship (i.e. at the lowest stock sizes) provides an estimate of the number of spawners produced by each spawner per year, i.e. the maximum annual expected lifetime reproductive output and, together with estimates of generation time, have been used to derive estimates of r_{max} (Myers *et al.*, 1999). However, high variability in the number of recruits per spawner biomass can lead to considerable uncertainty in the stock–recruitment relationship and perhaps offspring survival rate may change over time invalidating the stationarity assumption of such relationships.

In many cod stocks, the substantial reduction in size has led to a comparatively clear relationship between recruitment and spawning-stock biomass and this allowed Myers *et al.* (1997; with corrected Table 1) to estimate r_{max} for 22 cod stocks. Based on these r_{max} estimates, they predicted that stock population growth rate should range from 24 to 115% per year in the absence of fishing. Unfortunately, these high population growth rates have never been realized in many depleted Northwest Atlantic stocks subject to fishing moratoria (Shelton *et al.*, 2006). Direct estimates of instantaneous population growth rate using a demographic model have provided an explanation for why one such stock, northern Gulf of St Lawrence cod, never achieved the 29% annual rate predicted by Myers *et al.* (1997). Lambert (2011, 2013) estimated that, even after accounting for fishing mortality, population growth rates achieved in the northern Gulf of St Lawrence cod stock were generally depressed due to environmentally related declines in individual growth, condition, and reproductive potential. Consequently, demographic models may have a use in disentangling the effects of fishing from environmental pressures on population growth rate.

In addition to demographic influences on population growth rate, the size and age composition of spawners may also affect stock recovery through maternal effects on offspring survival.

Alteration in spawner composition influences several aspects of reproductive potential. Fecundity per size can increase between first time and repeat spawners (Hislop, 1988) and experimental studies of Atlantic cod have shown that egg size and early survival of larvae are reduced in younger females (Chambers and Waiwood, 1996; Trippel, 1998). Removal of larger, older fish influences the temporal overlap between offspring production and favourable survival conditions. Older fish tend to spawn at more appropriate times for offspring survival than younger, inexperienced fish (e.g. Wright and Gibb, 2005). Consequently, spawning stocks composed of small individuals may have reduced reproductive potential due to lower quality of offspring produced and the increased potential for a mismatch with favourable environmental conditions for their offspring (Scott *et al.*, 2006; Wright and Trippel, 2009). Long reproductive lifespan, i.e. spawning over many seasons, has also been linked with higher maximum reproductive rate among fish stocks (Venturelli *et al.*, 2009). Consequently, size and age truncation due to fishing pressure may reduce the potential for recovery to a much greater extent than that expected from changes in spawning biomass alone.

In the present study, estimates of instantaneous cohort-specific population growth were made for a number of cod and haddock (*Melanogrammus aeglefinus*) stocks, with a focus on periods when stocks were in a depleted state, i.e. spawning-stock biomass was less than the precautionary or limit reference points. The causes of variation in inter- and intra-stock population growth rate achieved were explored in relation to early survival, fishing mortality, and maturation timing. Potential parental influences on reproductive success were considered by relating metrics of spawner age composition with reproductive value and survival of a year-class through to age 1. Differences in early survival rate among cod stocks have previously been reported based on the ratio of first recruits to spawning-stock biomass, including the recent study by Köster *et al.* (2013). However, as relative fecundity of cod varies by two to three times among stocks and is higher in southern latitudes (Witthames *et al.*, 2013) and many reported maturity–age keys for ICES assessed stocks do not reflect the annual variation (Wright *et al.*, 2011a, b), such a comparison may be inaccurate. Further, as

Table 1. Sources of information for the estimation of egg production, survival ratio, and *r*, together with the stock estimates of the mean eggs produced per gramme of the spawning-stock biomass.

Species	Stock	Numbers at age	Maturity	Fecundity	Mean eggs g^{-1} ssb (g^{-1})
Cod	3M	González-Troncoso *et al.* (2013)	González-Troncoso *et al.* (2013)	Wells and Baird (1989)	175
	3NO	Rideout *et al.* (2013)	Rideout *et al.* (2013)	Stares *et al.* (2007)	149
	3Ps	Shelton and Morgan (2013)	Shelton and Morgan (2013)	Stares *et al.* (2007)	218
	Baltic east	ICES (2012a)	ICES (2012a)	Kraus *et al.* (2000)	323
	Baltic west	ICES (2012a)	ICES (2012a)	Bleil and Oeberst (2001)	452
	Celtic	ICES (2012b)	ICES (2012b)	Witthames *et al.* (2013)—Irish Sea	333
	Icelandic	ICES (2012c)	ICES (2012c)	Marteinsdottir and Begg (2002)	236
	Irish	ICES (2012b)	Armstrong *et al.* (2004), Nash *et al.* (2010)	Witthames *et al.* (2013)	295
	Northeast Arctic	Table 3.16 ICES (2012d)	ICES (2012d)	Thorsen *et al.* (2006), Witthames *et al.* (2013)	257
	North Sea	ICES (2012e)	Wright *et al.* (2011)	Yoneda and Wright (2004)	372
	West of Scotland	ICES (2012b)	MSS West coast survey	Yoneda and Wright (2004)	302
Haddock	Northeast Arctic	ICES (2012d)	ICES (2012d)	Skjæraasen *et al.* (2013)	201
	North Sea	ICES (2012e)	Wright *et al.* (2011a)	Wright *et al.* (2011a)	193
	West of Scotland	ICES (2012b)	Scottish west coast survey	Wright (unpubl.)	214
	Rockall	ICES (2012b)	Filina *et al.* (2009)	Filina *et al.* (2009)	279

gadoids tend to recruit at older ages in high latitudes, they will have experienced a longer period of mortality. Consequently, in this study, estimates of total egg production were used in combination with recruitment estimates standardized across stocks to numbers at age 1. From these population growth rate and early survival estimates, the study examined the relative contribution of age-specific survival and reproductive rate to population growth rate, the importance of age at maturity on stock recovery, and the significance of spawner age composition to early survival rate in depleted stocks.

Methods

Data sources

Stocks examined in this study were from the North Atlantic (Figure 1) and the data on numbers at age, weight at age, and natural and fishing mortality were obtained from stock assessments by ICES for the Northeast Atlantic stocks, NAFO for Flemish Cap (3M), and 3NO cod stocks and DFO Canada for the 3Ps cod stock (Table 1). Recruitment age in cod is reported for ages 1, 2, and 3 and for haddock at ages 1 or 3. For Northeast Arctic (NEA) cod where recruitment is reported for age 3, a run which included predation mortality estimates for ages 1 and 2 was used from the working group report. For other stocks, numbers at age 1 were extrapolated using estimates of natural mortality provided in assessments.

The annual record of age-specific proportion of mature fish was obtained from assessment reports for Northwest Atlantic and high latitude Northeast Atlantic stocks. For North Sea and west of the UK stocks, data on sex, maturity stage, age, and length were extracted from the first-quarter International Council for the Exploration of the Sea International Bottom Trawl SMALK database (DATRAS) and maturity ogives were calculated. These bottom trawl surveys were undertaken between January and March, which is usually within 1 month of the usual commencement of spawning in cod and haddock (Wright and Gibb, 2005; Morgan *et al.*, 2013). Published estimates of potential fecundity were used to derive age-specific relative fecundity (eggs g^{-1} soma) relationships either based on given relationships with age or derived from relationships with size and mean weight-at-age values from assessments (Table 1).

Annual total egg production (*TEP*) was calculated according to:

$$TEP_y = \sum_{x=1}^{\omega} M_{x,y}F_{x,y}W_{x,y}N_{x,y}, \tag{1}$$

where *M*, *F*, *W*, and *N* refers to the proportion mature, relative fecundity, mean weight, and numbers of females for a given age, *x*, and year, *y*, up to a maximum reproductive age *ω*. Female numbers at age were taken from the assessment, assuming a 1:1 sex ratio. *F* was taken directly from published studies or estimated for the mean size at age from published fecundity–length or weight relationships. Differences in age-specific fecundity among cod stocks coupled to the age composition of spawning stocks
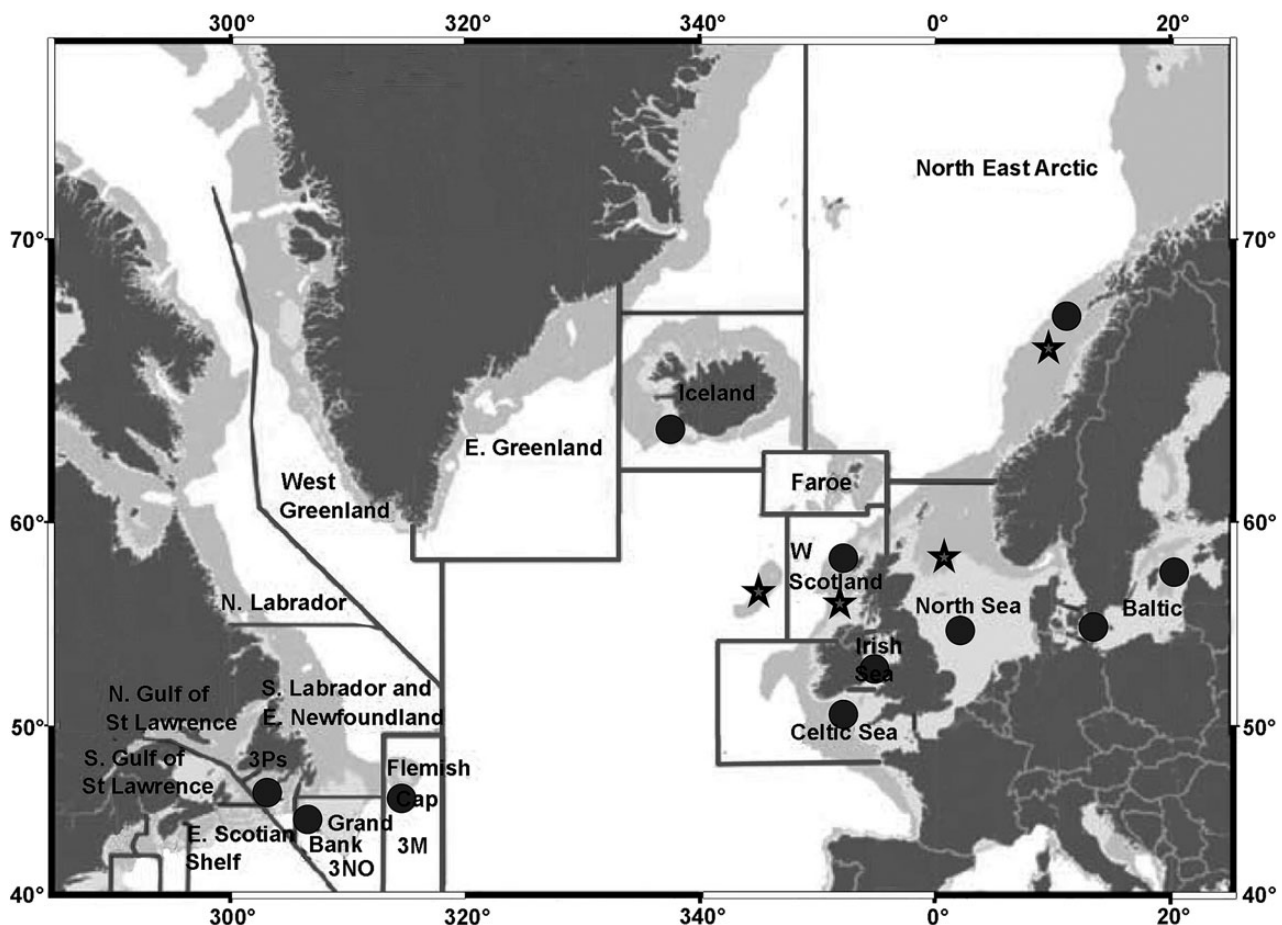

Figure 1. Location of cod (solid circle) and haddock (grey star) stocks examined in the study in the North Atlantic. ICES and NAFO stock boundaries are shown together with shelf waters <200 m (grey shading).

resulted in a range of 150–452 eggs g^{-1} ssb (g^{-1}), being higher in early maturing stocks.

Survival ratio from egg to age 1 (S_1) and age at 50% maturity (S_m) were calculated according to:

$$S_{1_y} = \frac{N_{1,y+1}}{TEP_y}, \tag{2}$$

$$S_{m_y} = \frac{N_{A_{50}}}{TEP_y}, \tag{3}$$

where $N_{1,y+1}$ is numbers at age 1 lagged by a year to correspond to the year-class produced by a *TEP* and $N_{A_{50}}$ is the number at the age of 50% maturity, which was interpolated from the numbers at the whole ages pre- and proceeding that age using year-class estimates of total mortality. This second measure of survival rate is more relevant to considering reproductive success because it considers survival up to the reproductive phase of the offspring.

Population growth rate

The instantaneous rate of population growth was obtained by solving the Euler–Lotka equation:

$$\sum_{x=\alpha}^{\omega} e^{-rx} l_x m_x = 1, \tag{4}$$

where l_x is the probability of survival to age x, m_x the number of female offspring produced at age x, α the age at first maturity, and the maximum reproductive age (ω) was set as 20 years for species in these calculations. In the present study, r was defined as the instantaneous rate of population growth that would be achieved, given the observed sets of life history parameters for the different year-classes. Year-class estimates of reproductive rate and instantaneous rate of population growth were limited to years with reliable maturity data, starting with year-classes in 1978–1981 and ending with 2001–2003, dependent on stock. The expected lifetime reproductive output, R_0, is given by

$$R_0 = \sum_{x=\alpha}^{\omega} l_x m_x. \tag{5}$$

The instantaneous rate of population growth r can be approximated by the natural logarithm of the expected lifetime reproductive output divided by generation time, G

$$G = \frac{\sum l_x m_x x}{\sum l_x m_x}, \tag{6}$$

$$r = \frac{\ln(R_0)}{G}. \tag{7}$$

l_x for a cohort was calculated from age- and year-specific fishing and natural mortality values given in assessments and m_x was calculated from the fecundity and proportion maturity-at-age data. As r assumes no density-dependent effects, cohorts (year-classes) were distinguished into those formed when the spawner biomass was below the biomass reference point used for that stock B_{pa} (Northeast Atlantic stocks) or B_{lim} (3M, 3N, 3Ps) and those above it. Cohort estimates of r were derived considering the total age-specific mortality rates, the instantaneous population growth rate

(r_z), and reported natural mortality only to give the maximum instantaneous population growth rate (r).

The sensitivity of population growth rate to survival and reproductive parameters was examined using age-specific elasticity, which gives the proportional change of $\exp(r)$ for a proportional change in a demographic parameter assuming a stable age distribution (Caswell, 2001). Because elasticities sum to 1, they can be compared among parameters to identify which parameters contribute the most to changes in population growth rate. Following Mollet and Cailliet (2002), elasticities were summed for reproductive rate (E_1), juvenile survival (age 1 up to A_{50}; E_2), and adult survival (E_3). The ratios of these elasticities were used to consider the relative impact of changes in E_1, E_2, and E_3 on population growth rate. The contribution of S_1 was considered by comparing temporal variation in r and r_z with just this component of population growth.

Reproductive value at age, V_x, which represents the present and future egg production of offspring by an individual breeding at age x and living through to its maximum population lifespan (i.e. $x = \omega$), discounted by the probability of that individual surviving to its maximum age, was measured according to:

$$V_x = \sum_{t=x}^{\omega} \frac{l_t m_t}{l_x}, \tag{8}$$

where l_t and m_t represent the age-specific schedules of survival and fecundity, respectively. Reproductive value increases until the age that the increased fecundity is offset by a very low probability that a female will reach that age. Estimates of reproductive value were derived from life tables of total mortality for years where a published fecundity–size relationship was available.

Life tables analysis, including reproductive value, was made using PopTools 3.2 (Hood, 2010), an add-in tool for Microsoft Excel (available for download from http://www.poptools.org).

Spawner age composition

The possible influence of three different metrics of spawner age composition on S_1 was examined for each stock. The Shannon diversity index, as first used by Marteinsdottir and Thorarinsson (1998) to describe spawner composition, is:

$$H_y = \frac{1}{n} \left(n \ln(n) - \sum_{x=1}^{k} f_x \ln(f_x) \right), \tag{9}$$

where n is the total number of mature females in all age groups, f_x the number of mature females aged x, and k the number of age groups. A modified version, H_{TEP}, in which the annual numbers of eggs by age were substituted for numbers of females was also used to account for the varying contribution of egg production by age-class. Greater values of H indicate a more even distribution of spawners across age classes and is predicted to enhance recruitment.

The second measure of age diversity was the weighted age of the annual egg production (MA), where the mean age in each year, y, was calculated weighting by the annual egg production at each age, x up to a maximum, ω:

$$MA_y = \frac{1}{TEP_y} \sum_{x=1}^{\omega} x TEP_{x,y}. \tag{10}$$

Higher *MA* indicates that a larger proportion of eggs are produced by older females.

The proportion of egg production by first-time spawners (P_{first}) in each year was calculated according to:

$$P_{\text{first}_y} = \frac{\sum TEP_{y,\ \alpha - A_{50}}}{TEP}, \qquad (11)$$

where α is age at first maturity and A_{50} the age at 50% maturity.

A stock dominated by a large number of first-time spawners will have a higher P_{first}. This can arise from both age truncation and when there is a large year-class entering the spawning stock.

The correlation between metrics of spawner composition (H, H_{TEP}, MA, P_{first}) and TEP was explored for each stock to test whether the indices were independent of egg production. The correlation between spawner composition metrics and survival to age 1 was explored for low spawner biomass (i.e. $<B_{\text{pa}}$ or B_{lim}) periods, as survival rates should not be limited by parent density at these times.

Statistical analysis

All variables were tested for normality and homogeneity of variance. Where possible, general linear models were used in which S_1, r, r_z, or elasticity was the dependent variable, year, TEP, and A_{50} as covariates, and stock as a factor. Non-parametric tests were used as an alternative to parametric tests when assumptions of normality and homogeneity of variance were not met. Analyses comparing stocks were restricted to overlapping periods of available data for each of the two species.

Spearman's rank correlation was used to avoid any assumption about the form of relationships in correlative analyses. To avoid over inflation of significance values due to autocorrelation within time-series, the number of degrees of freedom used was corrected using the modified Chelton method (Pyper and Peterman, 1998):

$$\frac{1}{N_2} = \frac{1}{N} + \frac{2}{N} \rho_1(1)\rho_2(1), \qquad (12)$$

where N and N_2 are the initial and corrected numbers of degrees of freedom, respectively, and $\rho_1(1)\rho_2(1)$ the 1-year lag autocorrelations in the two variables considered.

Results
Survival rates

Interannual variation in survival to age 1 (S_1) differed significantly among stocks (Figure 2a) across the same range of years for cod (1984–2008; Kruskal–Wallis $H_{11} = 145.7$; $p < 0.001$) and haddock (1990–2008; Kruskal–Wallis $H_3 = 19.5$; $p < 0.001$), and these differences were also evident when only low spawner biomass ($<B_{\text{pa}}$ or B_{lim}) years were considered ($p < 0.001$). For the same periods, there was a significant increase in survival to age 1 in the eastern Baltic cod stock (Spearman's rank $r_s = 0.72$; $p < 0.01$) and a negative time-trend in survival rates for North Sea and 3Ps cod as well as North Sea and West of Scotland haddock (r_s; $p < 0.01$). The lowest survival to age 1 occurred in the southernmost cod stocks; to the west of the UK, while those in northern latitudes varied from moderate (e.g. Icelandic cod) to often comparatively high levels (e.g. NEA). Given the very low natural mortality rate (0.2 year^{-1}) used to estimate age 1 numbers, the Icelandic cod S_1 estimates were probably an underestimate. Survival to age 1 in North Sea and Baltic cod stocks was intermediate between those of NEA cod and Northwest Atlantic stocks. In haddock, survival to age 1 in the NEA stock was on average lower than that of North Sea haddock but higher than stocks

further west. In general, interannual variation in S_1 was greater in haddock than cod stocks, except the 3M and 3NO cod stocks that underwent very large changes during the period of stock collapse.

The mean S_1 for cod stocks ranged from 3.8×10^{-7} to 1.8×10^{-5}, i.e. a 47-fold difference, while that for survival to age at 50% maturity, S_m, ranged from 1.80×10^{-7} to 1.95×10^{-6}, i.e. an 11-fold difference (Table 2). Hence the magnitude of mortality difference among stocks was less when considering survival up to A_{50}. This was due to the generally greater mortality rate up to age 1 in many early maturing stocks coupled to the lower mortality rate of age 2+ fish in most late maturing stocks. Rockall had the lowest mean S_1 of the four haddock stocks, while, the latest maturing stock, NEA haddock had the lowest mean S_m. As with S_1, interannual variation in S_m was greater in haddock than cod stocks, except the 3M and 3NO cod stocks (Figure 2b). There was also a significant positive trend in S_m with time in the Icelandic cod stock ($r^2 = 0.42$; $p = 0.0004$).

There was no consistent relation between S_1 and standardized annual egg production as the slopes differed among stocks (GLM $F_{11,498} = 2.747$; $p = 0.002$). Early survival in Eastern Baltic and Icelandic cod (r_s; $p < 0.001$) as well as North Sea and west of Scotland haddock (r_s; $p < 0.05$) was negatively correlated with annual egg production consistent with a density-dependent effect. In contrast, 3M cod exhibited a weak but significant positive relationship ($r_s = 0.34$; $p = 0.05$) and there was no significant trend for all other stocks ($p > 0.1$).

Variation in population growth rate r_z and r

Depleted spawning-stock biomass was not associated with a consistently high instantaneous population growth rate in any cod stock. While there were significant differences in r among stocks, these differences could not be explained by age at maturity (GLM; stock $F_{11,142} = 5.858$; $p < 0.001$; A_{50}: $F_{1,142} = 0.363$; $p = 0.55$). Pairwise comparisons of r indicated that North Sea and NEA cod stock would have had a significantly higher population growth in the absence of fishing than Icelandic, 3M, and 3NO cod stocks (Bonferroni adjusted pairwise probability $p < 0.01$). For many cod stocks, fishing mortality was persistently too high to enable cohorts to replace themselves leading to a negative r_z (Figure 3). However, even when the effect of fishing mortality was removed, estimated r in cod stocks in the north of the species range, i.e. 3M, 3Ps, 3NO, Icelandic, and NEA cod, was negative in some years. The maximum instantaneous population growth, r, rarely approached the maximum intrinsic population growth rate estimated by Myers et al. (1997). However, in many stocks, the maximum instantaneous population growth rate observed was consistent with these stock estimates of $r_{\max}$. Some estimates of population growth rate for NEA cod were higher than that reported by Myers et al. (1997). Estimates of r were also generally lower than the surplus production-derived estimates of intrinsic rate of population growth reported by Neubauer et al. (2013).

Annual estimates of r differed among the four haddock stocks ($H_3 = 7.9$; $p = 0.05$) with North Sea and Rockall haddock having a greater population growth rate than NEA haddock. For some year-classes in the NEA and West of Scotland, there were negative estimates of r in years of low spawning biomass, indicating that factors other than fishing also affected population growth. However, in general, expected lifetime reproductive output exceeded 1 in the absence of fishing mortality, so that cohorts would have replaced the number of eggs that generated them.
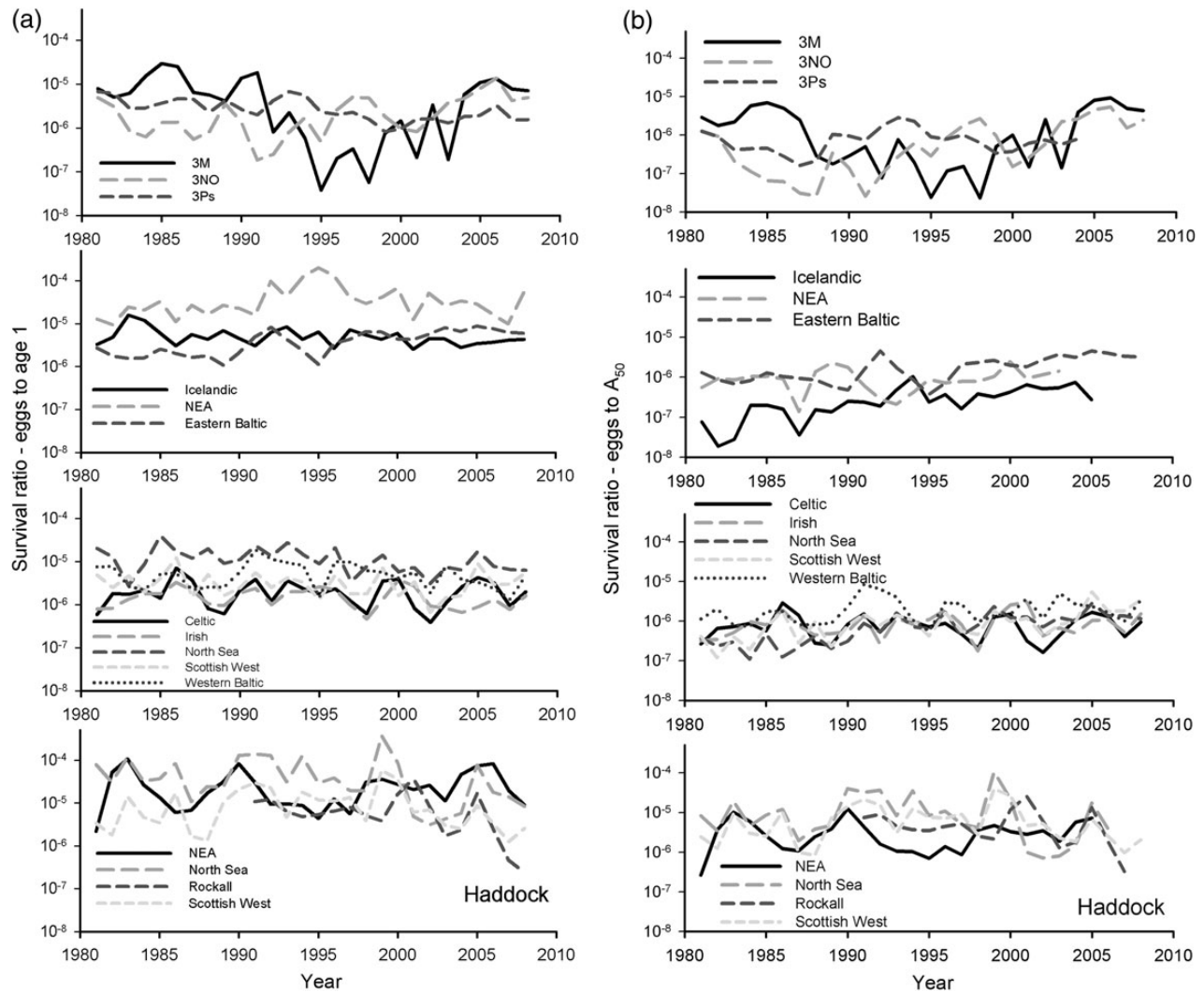
Figure 2. Interannual variation in $\log_{10}$ survival ratio from egg to (a) age 1 and (b) age at 50% maturity for a range of cod and haddock stocks. (Top panel) Northwest Atlantic cod stocks, (middle top panel) Northeast Atlantic cod stocks where recruitment is reported for ages 2+, (middle lower panel) Northeast Atlantic cod stocks where recruitment is reported for age 1, and (bottom panel) haddock stocks.

Elasticity of r_z to age-specific survival and reproductive rate for two early and late maturing cod and haddock stocks is shown in Figure 4. These examples illustrate that age-specific survival rate had a much larger influence on r_z than age-specific reproductive rate, although this influence declined substantially with age. Elasticity of r_z to reproductive rate increased to a maximum shortly after the A_{50}. Stock estimates of elasticity for reproductive rate, juvenile, and adult survival for r are given in Figure 5. The position of each point on the plot gives the relative contribution to population growth. All stocks were close to the juvenile and adult survival axes indicating the important contribution of survival rate. Elasticity of juvenile survival rate ranged from 1.5 to 5.2 times that of reproductive rate indicating that for a 10% reduction in juvenile survival, reproductive output would have to increase by 15–52% to compensate for such a change. Elasticity of r to S_m was positively correlated with the age at maturity ($r_s = 0.59$; $p = 0.02$). Elasticity of adult survival rate ranged from 0.6 to 8.0 times that of reproductive rate, indicating that for a 10% reduction in adult survival, fecundity would have to increase by 6–80% to compensate for such a change. Reproductive rate only accounted

for 0.09–0.28 elasticity in r_z, and was inversely related to age at maturity (Spearman's rank $r_s = -0.62$; $p = 0.01$). Consequently, early maturing stocks appear more responsive to changes in reproductive rate than late maturing stocks, while late maturing stocks are most responsive to changes in juvenile survival.

Changes in instantaneous population growth rate were primarily sensitive to juvenile or adult survival, although there were significant trends in E_1 for 3M cod, which had a significant negative temporal correlation ($r_s = -0.79$; $p < 0.01$) and North Sea cod ($r_s = 0.75$; $p < 0.01$) which had a significant positive correlation with time. Temporal trends in r, r_z, and S_1 for a range of cod and haddock stocks are presented in Figure 6a and b, respectively. These illustrate that the relation between S_1 and r differed among stocks with much lower S_1 being necessary for positive r in early maturing stocks (see also Table 2). The West of Scotland cod example (Figure 6a top panel) is broadly representative of early maturing west UK stocks, where the pattern in r and r_z generally follows that of S_1 highlighting the close correspondence between early survival rate and population growth rate. The other two panels are from cod stocks where the contribution of S_1 to r appears less important. In 3M cod, there

Table 2. Median estimates of age at 50% maturity, survival ratio, S_1 and S_m, expected lifetime reproductive output, instantaneous population growth rate either excluding (R_0, r) or including fishing mortality (R_{0z}, r_z) for stocks of Atlantic cod (cohorts range from 1984 to 2008) and haddock (cohort range 1990–2005).

| Region	Stock	A_{50} (age)	Age 1 survivors per egg (S_1) $\times 10^{-6}$	A_{50} survivors per egg (S_m) $\times 10^{-6}$	R_0 (per generation)	r (per year)	R_{0z} (per generation)	r_z (per year)
Cod Eastern North Atlantic	Irish Sea	2.2	1.79	0.81	5.5	0.29	0.4	−0.32
	Celtic Sea	2.2	1.92	0.78	6.0	0.37	1.0	−0.01
	West of Scotland	2.5	2.52	0.77	3.8	0.26	0.3	−0.28
	West Baltic	2.7	5.66	1.5	26.7	0.43	0.5	−0.17
	East Baltic	3.2	3.88	1.55	9.5	0.31	1.4	0.08
	North Sea	3.3	12.78	0.51	20.8	0.50	0.9	−0.04
	Northeast Arctic	6.9	26.59	0.86	12.7	0.35	1.4	0.05
	Icelandic	6.4	4.59	0.2	1.7	0.07	0.7	−0.05
Cod Western North Atlantic	3M	4.5	3.33	0.51	8.3	0.25	0.8	−0.02
	3NO	5.8	1.54	0.32	2.5	0.08	0.6	−0.05
	3Ps	5.9	2.74	0.79	4.6	0.14	1.0	0.00
Haddock	Rockall	2	6.48	4.55	5	0.29	1.1	0.03
	West of Scotland	1.7	10.11	7.15	7.4	0.36	1.4	0.08
	North Sea	2	36.43	8.29	7.5	0.27	0.5	−0.11
	Northeast Arctic	5.6	13.47	2.46	5.6	0.18	0.6	−0.06
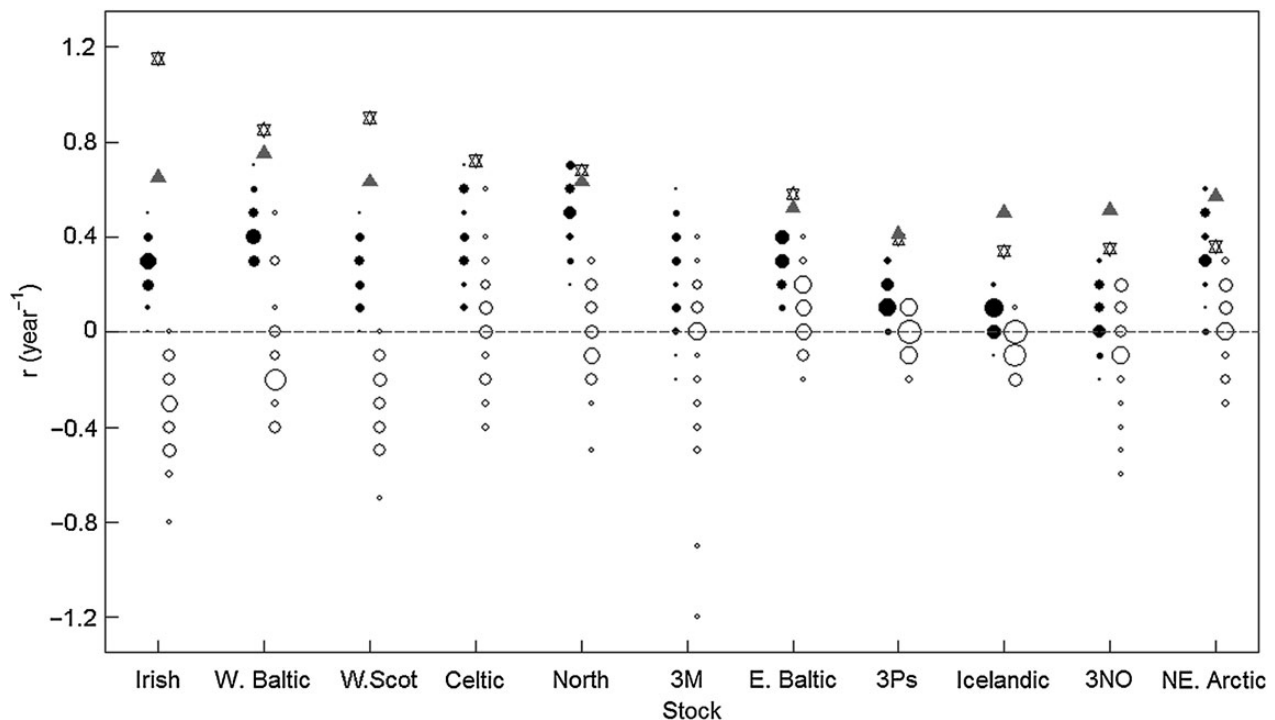
Figure 3. Annual estimates of the instantaneous rate of population increase in cod stocks. Estimates for both natural, r (closed circles), and total mortality, r_z (open circles), are presented grouped into bins of 0.1. Diameter of circle reflects range of between 1 and 13 cohorts per bin. Stock-based estimates of r_{max} from Myers *et al.* (1997; stars) and Neubauer *et al.* (2013; triangles) included for comparison.

were two periods when successive cohorts had positive or close to positive growth, the 1981–1987 year-classes and the 1999–2004 year-classes. In the first of these periods, fishing mortality was high and above average estimates of r_z mostly corresponded to above average estimates of S_1. However, positive r_z was also seen when early survival was comparatively low in the 1999–2004 year-classes. Cohort estimates of adult survivorship indicated that this had a much greater influence on population growth in this latter period than in the first period (mean E_3: 1981–1987 = 0.33; 1999–2004 = 0.70) and E_3 was negatively correlated with fishing

mortality on ages 3–5 ($r_s = -0.84$; $p < 0.001$). In NEA cod, there were years in the 1980s where r varied despite little variation in S_1. Above average S_1 from 1992 to 1996 was not associated with above average r_z, indicating that fishing mortality initially reduced the benefit of more favourable conditions for early survival. Like early maturing cod stocks, trends in r, r_z, and S_1 for both late (NEA) and early maturing haddock stocks exhibited a close correspondence (Figure 6b). Hence, although fishing mortality has a marked effect on the population growth rate, it appears to rarely alter the initial impact that a large or small year-class makes.
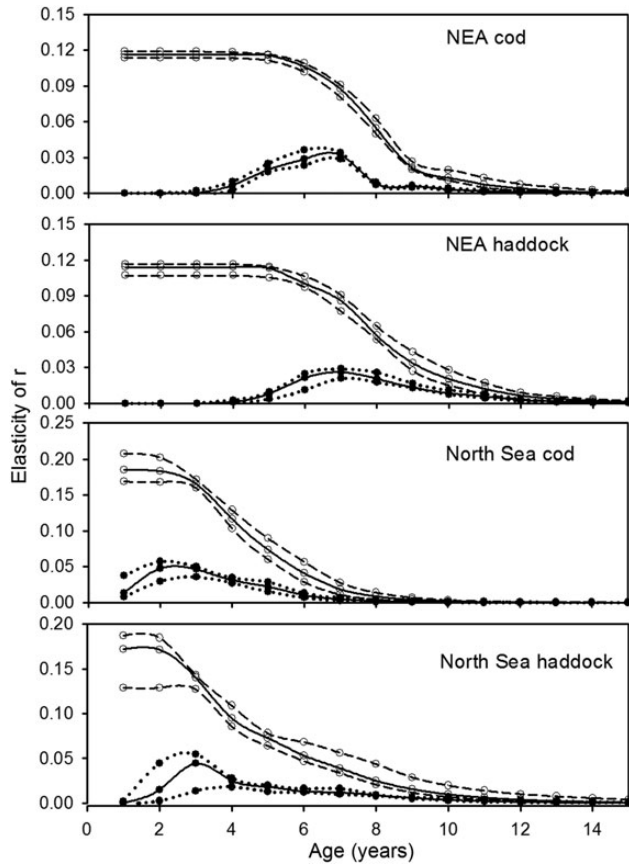
Figure 4. Elasticity of the instantaneous rate of increase to age-specific survival (open circles) and reproduction (closed circles). Median (solid lines), 25 and 75% values are presented to indicate the range in variation in elasticity over the range cohorts from low spawner biomass years for each stock.
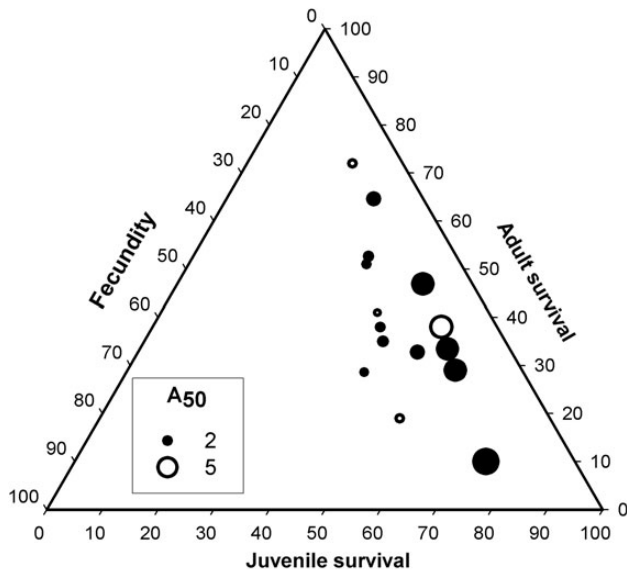

Figure 5. Ternary plot of reproductive (E_1), juvenile (E_2), and adult (E_3) components of elasticity (expressed as a percentage) for stocks based on natural mortality, r. Numbers refer to the mean age at maturity in stock and open circles refer to haddock stocks.
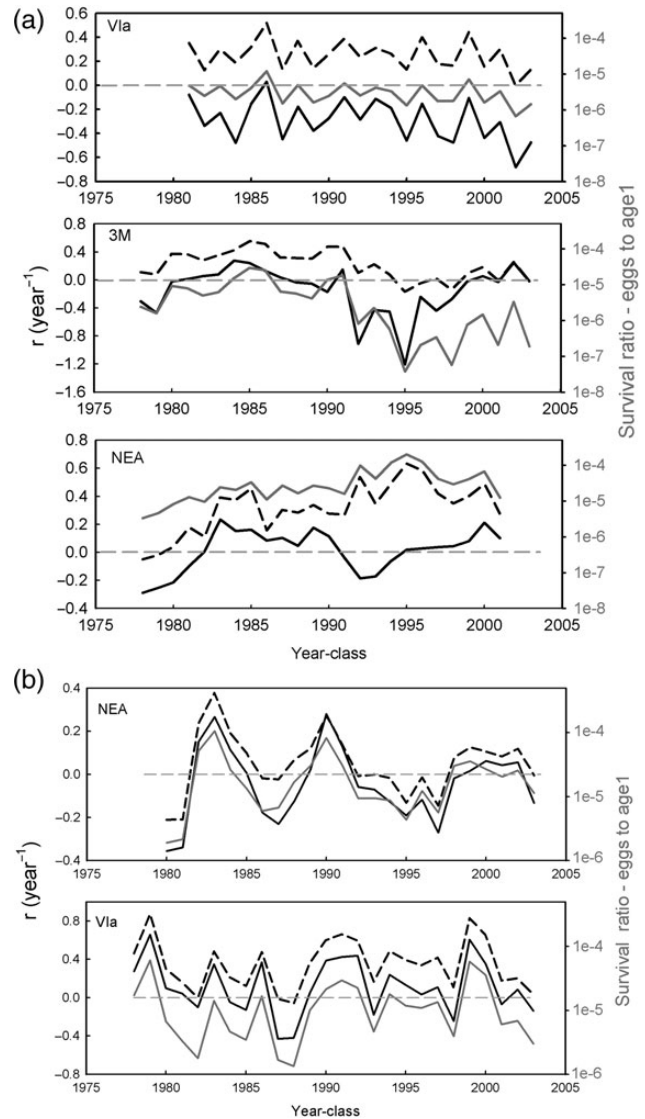

Figure 6. Interannual variation in instantaneous rate of population increase in (a) three cod and (b) two haddock stocks. Estimates for both natural, r (black dashed), and total mortality, r_z (black solid), are presented along with $\log_{10}$ survival ratio from egg to age 1 (solid grey). Stipled grey line indicates $r = 0$.

Spawner influences on lifetime fecundity and offspring survival

Reproductive value for selected cohorts from a range of cod and haddock stock, standardized to the age when fish first matured, is shown in Figure 7. The height of the reproductive value curve reflects both the age-specific mortality pattern and the increase in size-dependent fecundity. Standardized reproductive value generally increased until well after all females had matured before falling back at the very oldest ages. The two cod stocks that showed little or no increase in reproductive value with age were both from stocks where age-specific mortality during the adult phase exceeded juvenile mortality, although even in West of Scotland cod, the effect of a high fecundity–size exponent can be seen by ages 7–18. In Rockall haddock, the negative trend in reproductive value with age arises due to the substantially greater mortality of ages 3+ than younger ages.
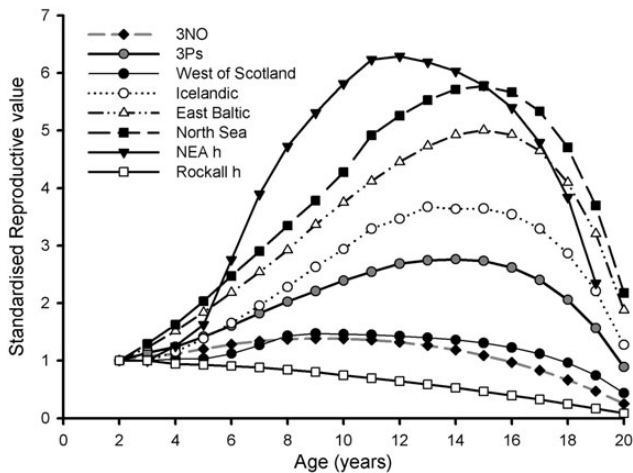
Figure 7. Age-specific reproductive value in a range of cod and haddock stocks based on life tables that included total mortality. All values are standardized to the minimum age at maturity for each stock.

The stock-based metric of age diversity, H, was found to be positively correlated with *TEP* ($p < 0.05$). However, the modified version H_{TEP} was not correlated with *TEP*, and so to avoid the possible confounding effect of *TEP* and age diversity, all subsequent analyses used this metric. Age diversity (H_{TEP}) was positively related to A_{50} across ($F_{1,652} = 7.482$; $p = 0.006$) and within ($F_{15, 652} = 6.988$; $p < 0.001$) stocks. This reflects the potential for a broader age structure in late maturing stocks. The mean age of egg producers was not related to A_{50} ($p > 0.1$). Significant long-term negative trends in H_{TEP} occurred in the Irish Sea, North Sea, Scottish west coast, and Icelandic cod stocks (r_s; $p < 0.01$), although in the latter, there was a recovery in H_{TEP} after the mid-1990s. Positive trends in H_{TEP} were seen for North Sea and Scottish west coast haddock, following a reduction in F in the recent decade (ICES 2012b, e). S_1 was positively related with H_{TEP} at low SSB in the Icelandic ($r^2 = 0.49$; $p = 0.001$; Figure 8a), Irish Sea, and North Sea cod stocks (Table 3). Similarly, S_1 in these three cod stocks was significantly related with the mean age of egg producers (*MA*; e.g. North Sea cod $r^2 = 0.30$; $p = 0.003$; Figure 8b). A significant correlation between S_1 and H_{TEP} was also found in 3M cod, although contrary to expectation, a positive effect of proportion of egg production by first-time spawners (P_{first}) was also found. In addition, 3Ps also had a significant positive correlation between S_1 and P_{first}. NEA haddock had a marginally significant negative relationship with P_{first} when SSB was low, suggesting that a large proportion of first-time spawners may negatively affect recruitment and this relationship was improved if all years with maturity data were considered ($r^2 = 0.35$; $p < 0.001$; Figure 8c).

Discussion

Early survival rate was the most important influence on population growth rate in all stocks, as evident from the high elasticity of early age-specific survival rate and the general concordance between survival to age 1 and maximum instantaneous population growth rate, r. A similar dependence on early survival rate was also reported for northern Gulf of St Lawrence cod (Lambert, 2011, 2013) and in a simulation of population growth rate in northern cod using a stochastic age-structured population model (Hutchings, 1999). The estimates of population growth achieved in a range of cod and
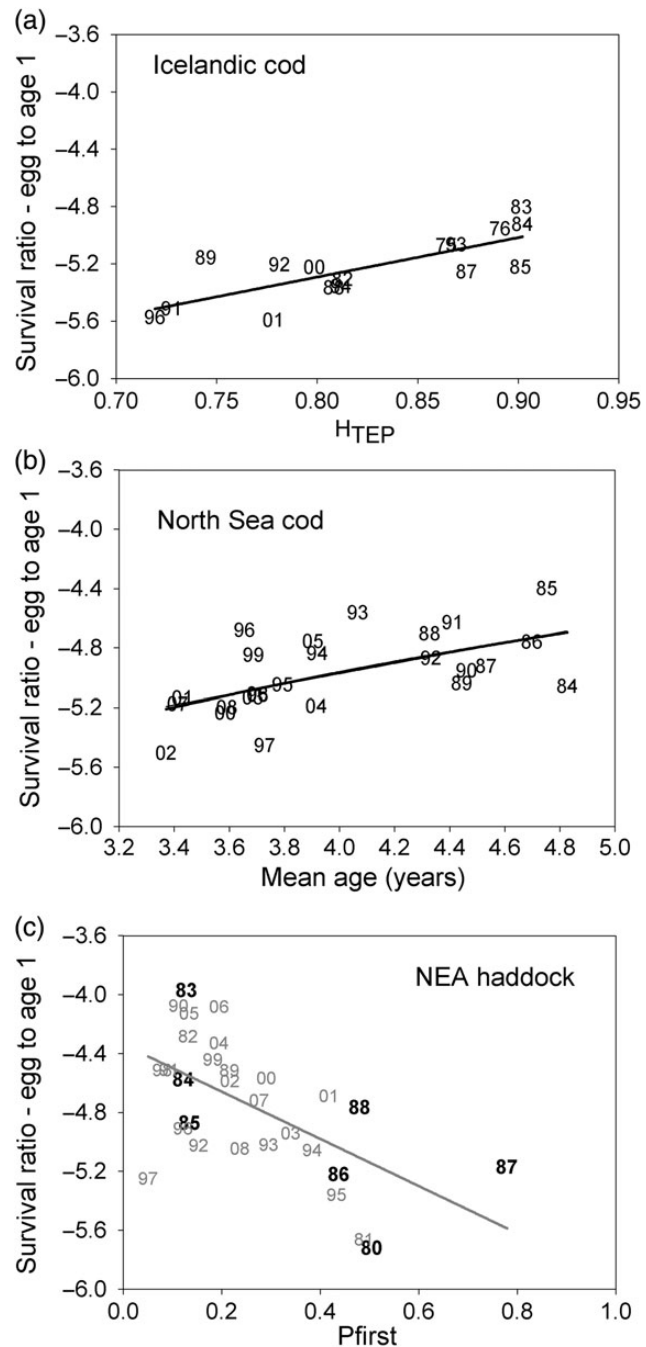

Figure 8. Relationship between $\log_{10}$ survival ratio from egg to age 1 (S_1) and (a) spawner age diversity, H_{TEP}, in Icelandic cod at low spawner biomass, (b) mean spawner age in North Sea cod, and (c) proportion of first-time spawners in NEA haddock. Numbers refer to the year of the parents associated with S_1 estimates. Fitted linear regressions are shown although for NEA haddock, years where SSB was both $<B_{pa}$ (black numbers) and $>B_{pa}$ (grey numbers) were used in the relationship.

haddock stocks suggest that, in the absence of fishing mortality, population growth should be positive in the early maturing stocks, but that population decline is possible even without the additional mortality from a fishery in many northerly late maturing stocks. Importantly, the estimates of maximum instantaneous population growth rate in the absence of fishing, r, from the present study were generally substantially lower than the r_{max}

Table 3. Spearman's rank correlations between S_1 and metrics of spawner age at low spawner biomass; age diversity (H_{TEP}), mean age (*MA*), and proportion of first-time spawners (P_{first}).

Species	Stock	H_{TEP}		*MA*		P_{first}	
		r_s	*p*-value	r_s	*p*-value	r_s	*p*-value
Cod	3M	0.40	<0.05	−0.08	>0.1	0.42	<0.05
	3NO	0.11	>0.1	−0.37	0.08	0.08	>0.1
	3Ps	−0.2	>0.1	−0.22	>0.1	0.67	0.01
	Baltic east	0.06	>0.1	0.36	>0.1	0.19	>0.1
	Baltic west	−0.41	>0.1	−0.16	>0.1	0.19	>0.1
	Celtic	0.34	>0.1	0.09	>0.1	0.08	>0.1
	Icelandic	0.72	0.01	0.45	0.05	−0.08	>0.1
	Irish	0.36	<0.05	0.41	<0.05	−0.25	>0.1
	Northeast Arctic	0.1	>0.1	−0.32	0.05	0.19	>0.1
	North Sea	0.51	<0.01	0.60	<0.01	−0.53	<0.01
	West of Scotland	−0.06	>0.1	0.08	>0.1	−0.13	>0.1
Haddock	Northeast Arctic	−0.464	>0.1	−0.036	>0.1	−0.71	0.05
	North Sea	0.24	>0.1	0.48	>0.1	0.00	>0.1
	West of Scotland	−0.17	>0.1	−0.08	>0.1	−0.05	>0.1
	Rockall	0.3	>0.1	−0.39	>0.1	0.287	>0.1

values that Myers *et al.* (1997) estimated from stock–recruitment relationships. Theoretically, r_{max} can only occur at the lowest population size when density-dependent compensation is at a maximum (Gedamke *et al.*, 2007). However, although more than just the lowest spawner biomass was considered for each stock, there was a general lack of compensation and large variation in early survival. Mangel *et al.* (2010) illustrate why single values of steepness of the slope of stock–recruitment relationship are never biologically realistic or precautionary due to the variation in reproductive rates and environmentally driven recruitment. Consideration of cohort variability and the general lack of a compensatory survival response to low egg production may help explain why cohort estimates of *r* in the present study rarely achieved the values of r_{max} estimated by Myers *et al.* (1997). The disparity between the range in *r* achieved at low spawning stock size in the present study and r_{max} reported by Myers *et al.* (1997) highlights that such single stock estimates give an overly optimistic prediction of stock recovery potential. Minto *et al.* (2013) also found significant annual variability in expected lifetime reproductive output in cod stocks using a multivariate state-space development of the stock–recruitment slope approach used by Myers *et al.* (1997). However, stock-specific life table estimates of expected lifetime reproductive output from Lambert (2013) and the present study indicate greater interannual variation than the model estimates of Minto *et al.* (2013), suggesting that the methodology also affects the perception of population growth rate variability.

The comparatively high survival to age 1 of cod stocks from northern latitudes in the present study contradicts the decreasing latitudinal trend of early survival based on recruitment–spawner biomass ratios previously reported (Köster *et al.*, 2013). Similarly, in haddock, early survival was higher in the NEA stock than the two stocks to the west of the UK. Age standardization explains a substantial component of this difference and clearly, there is much greater uncertainty in estimates of age 1 numbers derived from reported numbers at age 2 or 3 than for those where recruitment is reported for age 1. Nevertheless, even conservative estimates of age 1 numbers derived from a natural mortality rate of 0.2 year^{-1} indicated that Icelandic cod survival rate would rarely fall to the mean survival rate of the early maturing stocks. The threefold difference in relative fecundity further magnified the differences in survival rate among stocks, with fecundity being lowest in northern latitude stocks and

highest in the Baltic Sea. No account of skip spawning could be made in this study which may have led to a positive bias in some *TEP* estimates. However, reports of skip spawning are largely confined to northern stocks (Rideout *et al.*, 2005) and so any such bias would tend to lead to an overestimate of *TEP* and an even greater underestimate of survival to age 1. The use of a single fecundity–length relationship for most stocks will have also ignored potentially significant variation in the fecundity–size relationship (Kraus *et al.*, 2000; Lambert, 2011). However, as Lambert (2013) demonstrated most variation in *TEP* will be generated by changes in age composition and maturity at age in the spawning stock. The previous use of fixed and outdated maturity age keys for North Sea and west UK stocks in stock assessments (ICES 2012b, e) meant that spawner biomass and egg production was often underestimated in recent years due to the increasing trend towards smaller and earlier age at maturation (Wright *et al.*, 2011a, b). The only exception to this was for the West of Scotland cod where a fixed maturity age key derived from recent data had been used to hindcast SSB. Overall then, the use of recruitment–spawner biomass ratios to infer survival rate will clearly bias survival estimates and while there is uncertainty about the presented values due to assumptions made, they are still likely to provide a more realistic among stock comparison than past estimates.

Differences in the range of early survival rates may offer an explanation for the variability in maturation schedules among stocks. Population growth was negative in cohorts of late maturing stocks subject to the average egg-age 1 survival rate of the early maturing warm water stocks. Indeed, survival rates through to the age at maturity for late maturing stocks fell within the range of that of early maturing stocks, despite a difference in A_{50} of up to 5 years. Therefore, the high early mortality rates of warm water stocks are likely to be an important selection pressure against delayed maturity and conversely late maturity only appears possible in northern stocks due to the more favourable conditions for early life stages. This apparent trade-off between reproductive investment and pre-recruit mortality contradicts previous suggestions that differences in maturation schedules among stocks are predominantly linked to phenotypic plasticity (Köster *et al.*, 2013). Certainly, early maturing stocks do occur in warmer regions and both experimental and field studies have demonstrated that such warmer temperatures

promote early maturation in gadoids indirectly through effects on somatic growth (Godø and Moksness, 1987) and directly via gametogenesis (Tobin and Wright, 2011). Nevertheless, there have been significant changes in maturation schedules in both North Sea cod and haddock that cannot be explained by warming alone (Wright *et al.*, 2011a, b). Indeed, a comparison among cod and haddock stocks found that differences in the rate at which maturity at size had declined were positively related to total mortality, although the effects were more severe in slower growing stocks (Devine *et al.*, 2012). The present study highlights that delayed maturation, similar to that found in northern stocks, would lead to population declines in warm water stocks due to the high level of prerecruit mortality. Consequently, the early onset of maturation may be facilitated by warmer temperatures but also appears constrained by the more hostile environment experienced by early life stages.

While there is a general inverse relationship between population growth rate and age at maturity among taxa (Jennings *et al.*, 1998; Hutchings *et al.*, 2012), the present study demonstrates that components of reproductive rate only have a minor influence on this variation. Importantly, the comparatively low survival to age 1 in early maturing cod and haddock stocks appears to counteract the benefit of a short generation time. At moderate to high fishing mortality, positive population growth rate in these stocks appears dependent on the generation of unusually large year-classes. So while an exceptionally high early survival event in 2009 led to a rapid increase in Celtic Sea cod spawning stock to above the precautionary biomass level (ICES, 2012b), in general, stock recovery has not been more frequently observed in the early maturing than in late maturing stocks. Hence, consistent with ICES and NAFO advice, the present study indicates that fishing mortality is still the main reason many stocks have not recovered. In addition to fishing mortality, the high sensitivity of late maturing stocks to juvenile survival rate may be linked to a combination of factors like the poor environmental conditions that led to reduced growth, condition, and reproductive rate in northern Gulf of St Lawrence cod (Lambert, 2011). For example, NEA cod have undergone substantial changes in growth and condition (Marshall *et al.*, 1998) that may explain the low population growth rates in some years of moderate survival rate during the 1980s. Changes in maturity schedules may also have affected the sensitivity of growth to juvenile and adult mortality, as for 3M cod, where population growth rate became very sensitive to adult survival rate during a significant decline in age at maturity in that stock (González-Troncoso *et al.*, 2013).

Spawner age composition may be relevant to population growth both in terms of the expected lifetime reproductive output and in promoting high reproductive success. With respect to expected lifetime reproductive output, peak reproductive value for exploited stocks generally occurred after all individuals within a year-class had matured. Indeed, the general temporal pattern of reproductive value of the various cod stocks examined in the present study was similar to that reported by Hutchings and Rangeley (2011) for northern cod. The exceptions to this pattern were linked to a higher total mortality in the adult ages than for juveniles. This is an unusual pattern but can arise where area closures substantially reduce mortality on juveniles, as for Rockall haddock (Newton *et al.*, 2008). Hence, older females generally have a greater relative contribution to expected lifetime reproductive output than younger females. This is consistent with the meta-analysis by Venturelli *et al.* (2009) that found that maximum reproductive rate in fish stocks increased with reproductive lifespan. Consequently, fisheries management that promotes recovery of spawner age structure, rather than just

spawner biomass, may be expected to increase the expected lifetime reproductive output of depleted stocks. However, high expected lifetime reproductive outputs do not necessarily equate to high reproductive success since environmental conditions and predation are more important influences to offspring survival up to age 1 than the number of eggs produced by the parental stock. Spawner age composition may affect the foraging success and predator exposure of progeny through effects on spawning time and larval viability (Trippel, 1998; Wright and Trippel, 2009), but whether such influences are a first- or second-order effect on the reproductive success of cohorts is unknown as progeny survival can only be considered annually (Wright, 2013).

Spawner age effects on annual recruitment have been widely studied, but in the present study, the focus was on depleted stocks, where such effects could be relevant to recovery. Measures of spawning stock age were found to be positively correlated with early survivorship in just a few stocks. For two of the cod stocks, Icelandic and Irish Sea, the present results confirm past evidence for a positive relation with the mean spawner age (Brunel, 2010). Similarly, Morgan *et al.* (2007) did not find a significant effect of spawner age diversity metrics on recruitment in 3NO cod. In both these studies, survival rate was based on a residual analysis of stock–recruitment relationships that would produce estimates of survival rate on the ascending part of the S–R relationship comparable with that used in the present study. The present study also found that spawner age diversity had a positive influence on survival rate in North Sea cod and 3M cod, although in the latter, a positive effect of first-time spawners was also found. The proportion of first-time spawners also appears to have negatively influenced recruitment in NEA haddock.

In contrast to Morgan *et al.* (2007), the estimate of the mean spawner age was not found to be significantly correlated with survival rate in 3Ps cod and there was a positive relationship with the proportion of eggs produced by first-time spawners. The lack of a spawner age effect in some of the stocks examined also appears contrary to previous studies but may be related to the different methods of considering a possible age effect (Cardinale and Arrhenius, 2000a, b), the past use of a fixed maturity age key (Brunel, 2010), or just differences in the year ranges considered. Some earlier studies have focused on the eggs produced by first and repeat spawners. For example, Marshall *et al.* (1998) and Cardinale and Arrhenius (2000a) found that a significant relationship between recruitment and annual egg production in NEA cod could only be obtained if the number of eggs produced by repeat spawners was considered. Similarly, Wigley (1999) obtained a better stock–recruitment fit for haddock by ignoring the contribution of first-time spawners. Ignoring the contribution of first-time spawners may be reasonable if it can be shown that the eggs of these spawners produce far less viable eggs as suggested in some laboratory studies (e.g. Chambers and Waiwood, 1996). However, as spawner age effects may be more subtle than just the number and viability of eggs produced (Wright and Trippel, 2009), the metrics used in the present study provide a more direct means of considering possible spawner age effects.

The lack of a significant correlation between spawner age metrics and early survivorship in many stocks is not sufficient evidence to dismiss potential maternal effects. Notably, no significant relationship was found for North Sea haddock, despite clear empirical evidence for strong selection for the progeny of older spawners in this stock based on an otolith survivorship study (Wright and Gibb, 2005). Any contribution of spawner age to the interannual variability in recruitment is likely to be through an interaction

with environmental influences. For example, in Baltic cod, the influence of spawner age on recruitment depended on the volume of water suitable for cod development (Cardinale and Arrhenius, 2000b), while in NEA cod, the correlation between sea temperature and recruitment increased with age truncation (Ottersen *et al.*, 2006). The need to account for these interacting influences on population growth rate has recently been addressed by generalized additive modelling, using elasticity of early survivorship as the response variable. From such an approach, Durant *et al.* (2013) demonstrated that population growth rate in NEA cod was sensitive to the mean spawner age (expressed as generation time) after accounting for the effects of fishing mortality and temperature on recruitment. The increasing sensitivity of population growth to environmentally driven variation in recruitment in age-truncated stocks indicated by Durant *et al.* (2013) and similar studies of other gadoids (e.g. Hidalgo *et al.*, 2011) suggest that high age diversity acts to dampen the effect of environmental stochasticity on year-class strength. While a similar integrated analysis of environmental and age diversity influences is beyond the scope of the present study, cod and haddock stocks that did mature early and hence had short generation times did exhibit a greater elasticity in survival to age 1 than those that matured late (Figure 4). As one of the few potential sources of recruitment variation that fisheries management can influence, the contribution of spawner age composition to recruitment variability and population stability deserves further investigation and as the study by Durant *et al.* (2013) illustrates, future analyses need to account for the possible interaction between spawner age composition and environmental drivers of recruitment.

The present study has demonstrated that reproductive characteristics of a stock have a comparatively minor role in gadoid stock recovery. Early survival rate plays a far greater role in population growth than age at maturity or other components of reproductive rate. Gadoid stocks that are very productive in terms of growth and reproductive output generally occur in environments that are comparatively hostile for offspring, based on the early survival estimates of the present study. Indeed, measures of survival up to the average spawning age suggest that reproductive success could be similar across a range of environments that cod and haddock inhabit. This is not too surprising given that regional variation in reproductive success will ultimately be expected to shape local reproductive schedules (Pianka, 1976). As older individuals generally have a higher value to expected lifetime reproductive output and do seem to promote high recruitment at least in some stocks, recovery plans for at least some gadoid stocks should consider spawner age composition as a potential management target. This would, for example, be consistent with the European Union's Marine Strategy Framework Directive descriptor 3.3 requirement for a healthy age and size structure. Reductions in fishing mortality consistent with F_{msy} may generate sufficiently age diverse spawning stocks. However, as is apparent from the importance of early survival rate to population growth rate found in many gadoid stocks, year-class strength can be more important in driving stock demography.

Acknowledgements

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