ORIGINAL ARTICLE

Life-history evolution and elevated natural mortality in a population of Atlantic cod (*Gadus morhua*)

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Abstract

Fisheries-induced evolution has been hypothesized to delay the recovery of collapsed fish stocks through effects on their productivity. The cod stock in the southern Gulf of St. Lawrence (SGSL) collapsed in the early 1990s and has shown no recovery since then, due mainly to high natural mortality of adult cod. Age and size at maturation of SGSL cod decreased sharply over time in cohorts produced in the 1950s and 1960s, likely reflecting an evolutionary response to intensified fishing, and have remained low since then, despite severe reductions in fishing mortality over the past 15 years. A predicted consequence of early maturation is increased natural mortality due to higher costs to reproduction. Early maturation may be a cause of increases in natural mortality of SGSL cod in the 1970s but does not appear to be related to the much larger increases since then. Instead, the current high natural mortality of SGSL cod appears to be primarily a cause, rather than a consequence, of the continued early maturation in this population, now replacing fishing mortality as the agent of selection favouring early maturity. This striking example of the failure to reverse fisheries-induced evolution by relaxing fishing pressure emphasizes the need for management strategies that minimize the chances of harvest-induced genetic change.

Introduction

Evidence is accumulating that there can be rapid evolutionary responses in fish populations to the selection pressures imposed by fishing. Laboratory experiments have demonstrated rapid genetic changes in growth rate and a suite of correlated life-history traits in fish populations subjected to size-selective harvesting (Conover and Munch 2002; Walsh et al. 2006). Likewise, a growing number of studies on wild fish populations have revealed phenotypic changes consistent with an evolutionary response to fishing (e.g. Handford et al. 1977; Ricker 1981; Haugen and Vøllestad 2001; Grift et al. 2003; Olsen et al. 2004, 2005; Edeline et al. 2007; Swain et al. 2007; Biro and Post 2008; Nusslé et al. 2009). The phenotypic changes attributed to fisheries-induced evolution are most commonly in life-history traits such as growth rate and age and size at maturation. These traits are closely linked to population productivity and fishery yield. The phenotypic changes observed in response to exploitation result

in reduced population productivity in the unfished state (e.g. Hutchings 2005; Walsh et al. 2006) and may contribute to the slow recovery observed for many collapsed fish stocks (Hutchings and Reynolds 2004; Walsh et al. 2006).

Many of the populations of Atlantic cod (*Gadus morhua*) occurring in the Northwest Atlantic collapsed in the early 1990s due to overfishing. These populations have failed to recover despite severe restrictions on fishery removals over the past 15 years. The main factor delaying the recovery of these populations has been a decline in their productivity, in particular an increase in the natural mortality of adult cod (Shelton et al. 2006). This decline in productivity has been particularly dire for the cod population in the southern Gulf of St. Lawrence (SGSL). Natural mortality has risen to such a high level in this population that it no longer appears to be viable (Swain and Chouinard 2008). Causes of the increases in natural mortality in these populations are uncertain. Survival costs to reproduction are expected to increase as age and size at maturity decline. This led Hutchings (2005) to

suggest that the recent increases in natural mortality in these cod stocks may be partly due to fisheries-induced declines in age and size at maturation.

Fisheries scientists have traditionally described variation in maturation using maturity ogives, which specify the proportion of individuals that are mature at a given age and/or size. Maturity ogives are affected by rates of survival and growth before and after maturation. In an attempt to disentangle effects of changes in survival and growth from evolutionary changes in maturation, a second approach to describing maturation schedules, probabilistic maturation reaction norms (PMRNs), has recently been developed (Heino et al. 2002a,b; Barot et al. 2004). PMRNs describe the probability that an immature individual will become mature, conditional on having reached a certain age and size. Because PMRNs are intended to exclude the effects of phenotypic plasticity associated with variation in the average somatic growth rate, a change in PMRN provides much stronger support for the hypothesis of an evolutionary change in the maturation process than does a change in maturity ogives. However, the possibility that unaccounted plastic effects contribute to changes in PMRNs cannot be excluded (e.g. Morita and Fukuwaka 2006; Marshall and McAdam 2007).

In this study, I describe long-term variation in age and size at maturation in the SGSL cod population. Both the age and size at which 50% of individuals were mature declined sharply in this population in the 1960s and early 1970s (Beacham 1983a). I show here that these changes reflect equally rapid and dramatic changes in PMRNs. I also extend the maturation time series to 2008, revealing that there has been no recovery in age and size at maturation in this stock in the 30 years since their decline, despite very low fishing mortality over the past 15 years. Finally, I compare the time trends in age and size at maturity with the estimated trend in natural mortality. I conclude that the decline in age and size at maturation may be a cause of increases in natural mortality in the 1970s, but that early maturation does not appear to be the cause of the much greater increases in natural mortality since then. I instead suggest that age at maturation has failed to recover in this population despite very low fishing mortality because high natural mortality has now replaced fishing mortality as an agent of selection favouring early maturation.

Materials and methods

Study population
The SGSL cod population has been commercially exploited since at least the 16th century, but landings increased substantially following the introduction of otter trawling in the late 1940s. The exploitation rate on the

stock increased steadily from the early 1950s to the mid-1970s (Fig. 1A). For the younger age classes exploited by the fishery, exploitation rate in the mid-1970s had reached a level nearly seven times that experienced in the early 1950s. Population biomass declined during this period in response to this increase in fishing intensity, but then recovered quickly to historical highs in the 1980s (Fig. 1B). The population collapsed a second time in the late 1980s and early 1990s, and has not yet shown any sign of recovery despite 15 years with little fishing (Swain et al. 2009).

Southern Gulf of St. Lawrence cod overwinter in warm deep waters along the southern slope of the Laurentian Channel in the Cabot Strait area (Fig. S1). In spring (late April to early May), the population migrates onto the Magdallen Shallows, where spawning and feeding occur prior to the migration back to the overwintering grounds in late fall. Gonad maturation begins in late November during the migration back to the overwintering grounds (Schwalme and Chouinard 1999). Gonad growth is largely complete by January for males, but maximum gonad development is not attained by females until late April or early May (Schwalme and Chouinard 1999). Powles (1958) reported that the spawning period of cod in the
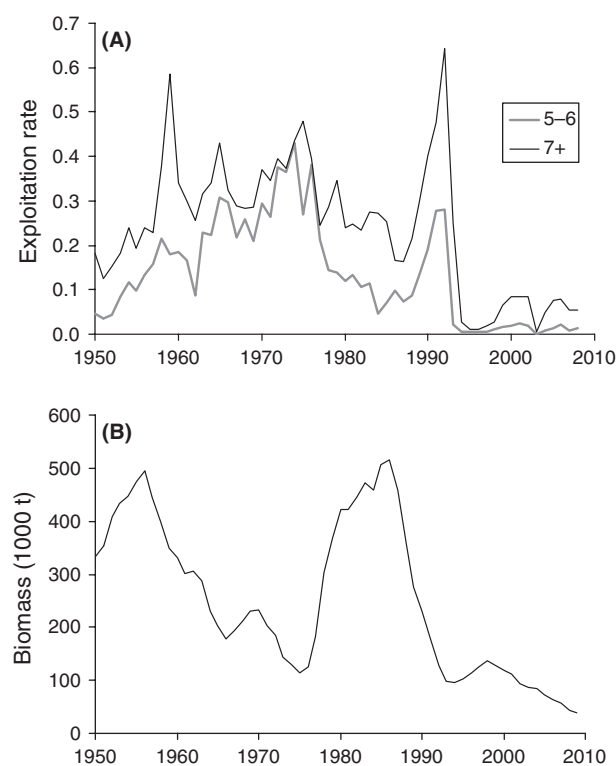

Figure 1 Exploitation rate on southern Gulf of St. Lawrence cod aged 5–6 or 7+ years (A) and stock biomass (B, ages 3 years and older). Data from Swain et al. (2009).

southern Gulf lasted from May to September, with peak spawning in late June. Other studies suggest that peak spawning occurs somewhat earlier, in late May (Jean 1963; Lett 1980). Schwalme and Chouinard (1999) reported that reductions in gonadosomatic indices associated with spawning occurred in June and July.

Data

A stratified-random bottom trawl survey of the southern Gulf has been conducted each September since 1971. During this survey, subsamples of cod catches are obtained for age determination and maturity measurements [see Hurlbut and Clay (1990) for details]. Additional fixed-station surveys were conducted in fall (mainly September) from 1959 to 1970 (though data could not be retrieved for the surveys in 1960, 1963 and 1964). Data were also available from spring and early summer surveys (mainly April–July) in 1960–1962, 1968 and 1990–1995, January surveys in 1960, 1961, 1964 and 1994–1996, and from a fish condition monitoring programme (April–July) in 1998–2001 and 2005–2007. These data sets are summarized in Table S2.

The original work by Beacham (1983a,b) was criticized because it included samples from outside the spawning season when it may be difficult to distinguish between immature fish and resting mature fish (Halliday 1987; but see Beacham 1987). I evaluated this potential problem by comparing maturity ogives based on data collected during the spawning season (spring and early summer) with ogives based on September data. After adjusting for growth between spring and fall, no bias was evident between results from the two seasons in the 1960s data but a consistent bias was evident in the 1990s data (Data S3). In the 1990s data, lengths and ages at 50% maturity were estimated to be lower using the September data than using data from spring and early summer, suggesting a tendency to misclassify immature fish as resting or recovering mature fish in the September data. Time-series analyses were conducted to identify when a change in the quality of the September data occurred (Data S4). These analyses indicated a change in the data in 1983. This coincided with a change in the group conducting the September surveys and a change in the description of maturity stages for cod (Hurlbut and Clay 1990). I concluded that the September maturity data were unreliable after 1982, and excluded these data from the analyses presented here. Inclusion of these data would result in even stronger time trends in age and size at maturation than those reported here (see Data S3 for time trends in the 1983–2008 September data).

Because data were limiting in some time periods, I combined data collected in all seasons for this analysis. Length was adjusted to length in the fall (September–October) for surveys conducted in other seasons, as follows:

$$L'_{i,a} = L_{i,a} + \bar{L}_{F,a} - \bar{L}_{S,a}, \qquad (1)$$

where $L'_{i,a}$ and $L_{i,a}$ are the adjusted and observed lengths for fish i of age a collected in season S, respectively, and $\bar{L}_{F,a}$ and $\bar{L}_{S,a}$ are the mean lengths at age a in fall and season S, respectively. Fall was chosen as the reference season because data were available from this season in all years except 1960, 1963 and 1964. Means were calculated over blocks of years over which length-at-age varied little to obtain substantial sample sizes at each age. For example, spring data were compared to fall data for the following groups of years: 1959–1962, 1968, 1990–1995, 1998–2001 and 2005–2007. Sexes were combined for these adjustments because differences between the sexes in length-at-age were small compared to seasonal differences. Analyses were restricted to ages 2–12 years.

Because gonad growth was completed (males) or well underway (females) in January (Schwalme and Chouinard 1999), maturity status in January was considered representative of the status at spawning in the following spring and early summer rather than at spawning in the previous year. Thus, a January 1 'birthday' was used here; i.e. age was incremented by 1 year in the January data.

Maturity ogives

Ogives for age or length at maturity were fit separately for males and females using the following logistic regression model:

$$\text{logit}(o) = \beta_0 + \beta_{1,C} + \beta_2 X + \beta_{3,C} X, \qquad (2)$$

where o is the probability of being mature, X is age or length, and C indexes cohort group starting at 2 (cohort group 1 was the reference cohort). Neighbouring cohorts were grouped together where necessary to obtain sufficient sample sizes (a minimum of about 50 individuals for most age groups). Maturity schedules were summarized by the predicted age or length where 50% of individuals were mature (A_{50} or L_{50}), given by $-\beta_0/\beta_2$ for cohort group 1 or $-(\beta_0 + \beta_{1,C})/(\beta_2 + \beta_{3,C})$ for other cohort groups. Confidence intervals around A_{50} and L_{50} were obtained by bootstrapping with 1000 replicates. Bootstrap replicates were obtained by randomly sampling with replacement within age/cohort group cells. For each replicate, the model specified by equation (2) was fit and the parameter estimates were used to calculate A_{50} or L_{50} for each cohort group. Confidence intervals were given by the 2.5th and 97.5th percentiles of the resulting estimates of A_{50} or L_{50} for each cohort group. Time trends in A_{50} and L_{50} were summarized using generalized additive models (GAMs), based on smoothing splines with 4 degrees of freedom.

Maturation reaction norms

Because first-time and repeat spawners could not be distinguished, PMRNs were estimated using the method developed by Barot et al. (2004). The probability of maturing at age a and length l, $m(a,l)$, was estimated based on the maturity ogive with respect to age and length, $o(a,l)$, and the mean growth increment from age $a-1$ to a, $\Delta l(a)$:

$$m(a,l) = [o(a,l) - o(a-1, l-\Delta l(a))]/ \atop [1 - o(a-1, l-\Delta l(a))] \tag{3}$$

Equation (3) estimates the frequency of fish maturing for the first time at age a and length l relative to the frequency of fish of this age and length that were not mature the previous year. This equation assumes that immature and mature fish of a given age and length class have the same growth and survival rates, but Barot et al. (2004) demonstrated that their method is relatively robust to violations of this assumption. Likewise, Pérez-Rodríguez et al. (2009) found that this method and a direct method not requiring these assumptions (because first-time spawners could be identified) produced comparable results for Flemish Cap cod.

Separate analyses were conducted for males and females. A coarser grouping of cohorts was used to obtain a minimum sample size of 100 for most cohort/age cells. Barot et al. (2004) showed that this sample size was required to obtain robust estimates with the model used here. Maturity ogives were fit using the following model:

$$\text{logit}(o) = \beta_0 + \beta_{1,C} + \beta_2 a + \beta_{3,C} a + \beta_4 l + \beta_{5,C} l \atop + \beta_6 al + \beta_{7,C} al, \tag{4}$$

where a is age and l is length. This model was the best model for both males and females based on AIC. Following Barot et al. (2004), $\Delta l(a)$ was estimated as the difference in mean length between ages a and $a-1$ within cohort groups. Mean growth increments calculated in this way will be biased if there is size-selective mortality between ages $a-1$ and a. Size-selective mortality has been demonstrated in SGSL cod (Sinclair et al. 2002a). However, biases in growth increments due to size-selective mortality had a negligible effect on estimates of PMRN midpoints (Data S5). PMRN midpoints were estimated by fitting the following logistic regression model to the values of m obtained using equations (3) and (4):

$$\text{logit}(m) = \beta_0 + \beta_{1,C} + \beta_2 a + \beta_{3,C} a + \beta_4 l + \beta_{5,C} l \atop + \beta_6 al + \beta_{7,C} al. \tag{5}$$

Probabilistic maturation reaction norm midpoints were calculated using the parameters estimated for equation (5). For the reference cohort group, the length at 50% maturation probability at age a is given by $-(\beta_0 + \beta_2 a)/(\beta_4 + \beta_6 a)$. For other cohort groups the PMRN midpoints are given by $-[\beta_0 + \beta_{1,C} + (\beta_2 + \beta_{3,C})a]/[\beta_4 + \beta_{5,C} + (\beta_6 + \beta_{7,C})a]$. Confidence intervals around the PMRN midpoints were based on bootstrapping. Bootstrap replicates were obtained by sampling with replacement within age/cohort group cells. The steps described above [i.e. estimating $\Delta l(a)$, fitting $o(a,l)$ using equation 4, estimating $m(a,l)$ using equation 3, and fitting the resulting estimates of m using equation 5] were repeated for each of 1000 bootstrap replicates.

Rates of change

Rates of phenotypic change were expressed in darwins, the proportional change per million years, calculated as:

$$d = \frac{\ln(Z_1/Z_0)}{\Delta t \times 10^{-6}}, \tag{6}$$

where Z_0 and Z_1 are the phenotypic values at the beginning and end, respectively, of a period Δt years in duration. Rates were calculated for the whole study period, and separately for each half of the period. Following Sharpe and Hendry (2009), I used the predicted values from the GAMs fit to the time series of A_{50} and L_{50} as estimates of Z_0 and Z_1 to account for year-to-year fluctuations in these time series.

Natural mortality

The status of the SGSL cod stock is assessed using sequential population analysis (SPA) calibrated using abundance indices from the annual research vessel survey and a number of fishing-industry surveys (e.g. Swain et al. 2009). Calibration involves finding the parameter estimates that produce the best match between the abundance indices and the SPA estimates of population size. Parameters typically include terminal abundance (i.e. abundance at age in the most recent year) and catchability coefficients for the surveys. Using a simulation study, Chouinard et al. (2005) demonstrated that SPA can also be used to estimate trends in the instantaneous rate of natural mortality (M). Following this work, and an earlier study by Sinclair (2001) who demonstrated that M was at a high level in the SGSL cod stock during the fishing moratorium in the mid-1990s, recent assessments of this stock have estimated M for various blocks of years. These estimates are for all ages (2 years and older) aggregated together.

While SPA can correctly identify the trends in M in simulated populations, it sometimes has difficulty identifying the correct level for these trends (Chouinard et al.

2005). Thus, the level of M should be fixed or 'anchored' in some period using ancillary information. In recent assessments of this stock, M has been fixed at 0.2 in 1971–1979 and at 0.4 in 1994–1997 and estimated for the remainder of the time series in several blocks of years (e.g. Swain et al. 2009). The value for 1971–1979 was based on independent analyses using data from the 1970s and earlier. These studies estimated that M was near 0.1–0.2 (see references in Sinclair 2001). The value for 1994–1997, when there was a moratorium on directed fishing for cod, was based on estimates of total mortality which indicated that M was 0.4 or higher (0.4–0.6; Sinclair 2001; Swain et al. 2009).

For this study, I adopted the SPA model used to provide the most recent management advice for this stock (Model 1, Swain et al. 2009). I modified this model slightly, fixing M at either 0.1 or 0.2 in 1971–1975, and estimating M in the following blocks of years: 1976–1980, 1981–1986, 1987–1993, 1994–2000 and 2001–2008. This modification allowed finer resolution in estimating the onset of increases in M, and allowed an estimate of M that was >0.4 in 1994–1997 (as suggested by the estimate of total mortality for this period). Calculations were conducted using the ADAPT software package (Gavaris 1988). To compare the time trend in M with the temporal changes in maturation, annual L_{50}s (Fig. S2, omitting the 1983–2008 September data) were summarized using GAMs as described above.

I also summarized trends in total mortality by estimating survival from age 3 to 8 years, as follows:

$$S_j = \prod_{i=3}^{7} \exp(-F_{i,j+i} - M_{j+i}), \qquad (7)$$

where i and j index age and cohort, respectively, $j + i$ indexes year, and F is the instantaneous rate of fishing mortality. Estimates of F and M for 1971–2008 are from the SPA model described above (with M for 1971–1975 set at 0.2). The time series is extended to earlier years (1950–1970) using the model described by Maguire et al. (1983), which assumed that M was 0.2 in this earlier period.

Results

Maturation

For both males and females, age and length at 50% maturity steadily declined over time in cohorts produced in the 1950s and 1960s (Fig. 2). A_{50} was substantially greater in females than in males in the mid-1950s cohorts but had declined to similar levels in both sexes in cohorts produced in the early 1970s (Fig. 2A,B). A_{50} declined by about 40% in females, from 6.7 years in the mid-1950s to 4.0 years in the early 1970s, and by about 30% in males, from 5.6 to 3.8 years. A_{50} differed little between cohorts produced in the early to mid-1970s and those produced after the
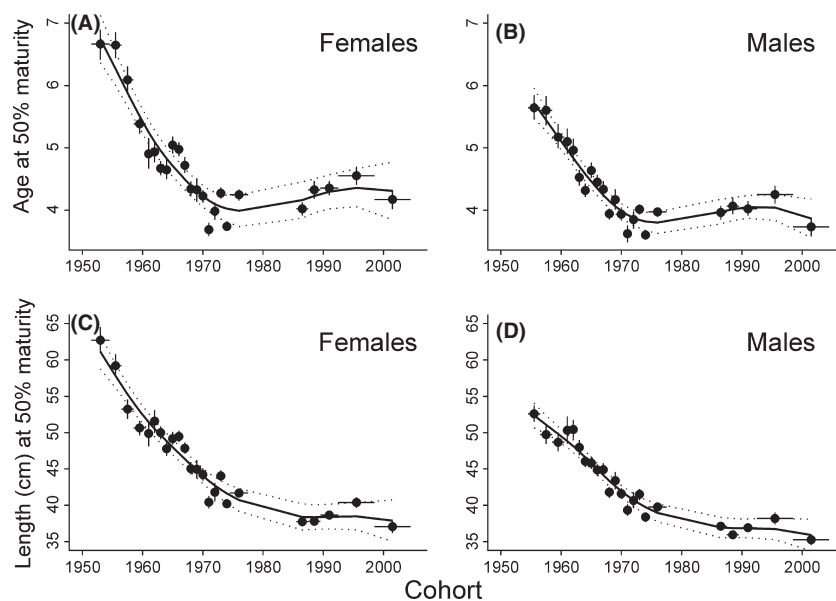

Figure 2 Age and length at 50% maturity for female and male cod in the southern Gulf of St. Lawrence. Vertical lines are 95% confidence intervals. Horizontal lines indicate the range of cohorts grouped together for an estimate. Time trends are summarized by a smoothing spline (heavy line) ± 2 SE (dotted lines). Lengths have been adjusted to September values.

mid-1980s, with values in the latter period averaging only marginally (about 5%) higher than those in the earlier period.

Patterns in L_{50} were similar to those observed in A_{50} (Fig. 2C,D). Declines in L_{50} between cohorts produced in the mid-1950s and those produced in the early to mid-1970s were substantial, 31% (19 cm) for females and 21% (11 cm) for males. L_{50} continued to decline between cohorts produced in the early to mid-1970s and those produced after the mid-1980s, but these declines were small compared to those in the 1950s and 1960s, about 3.5 cm for both sexes.

Maturation reaction norms changed rapidly in the 1950s and 1960s, with cohorts produced late in this period maturing at a much smaller length than those produced early in this period (Fig. 3). For females aged 4 and 5 years, the probability of maturing reached 50% by a length of 41–45 cm for cohorts produced in the late 1960s and early 1970s but not until a length over 70 cm for those produced in the mid-1950s. A similar pattern was evident for males, though males matured at slightly shorter lengths than females in early cohorts. In contrast to the 1950s and 1960s, differences in maturation reaction norms between cohorts produced in the early to mid-1970s and those produced since the mid-1980s were relatively minor; PMRN midpoints were on average <4 cm lower in recent cohorts than in those from the early to mid-1970s.

Maturation reaction norms are shown for three cohort groups (the early 1950s, the mid-1970s and the early 1990s) in Fig. 4. Slopes of these reaction norms are generally very shallow, indicating that maturation depends mostly on attaining a particular size rather than a particular age, at least up to 5 years of age. A dramatic difference in reaction norms is evident between cohorts produced in the early 1950s and those produced in the mid-1970s. In contrast, the difference in reaction norms between cohorts produced in the mid-1970s and those produced in the early 1990s is minor.

Rates of change in these life-history traits were very rapid between the mid-1950s and the mid-1970s, ranging from −14 410 to −23 770 darwins (average −19 778 darwins; Table 1). Rates of change averaged about an order of magnitude slower in the second half of the study period.

Mortality

Both revised SPA models fit the data slightly better than the assessment model (MSE 0.242–0.243 vs 0.257) and were better models based on AIC_C (Burnham and Anderson 2002). Estimated M increased steadily from the late 1970s to the present (Fig. 5). The large decline in length and age at maturity in the 1960s and early 1970s was associated with an increase of 0.05–0.1 in estimated M, depending on whether the value chosen for the period prior to 1976 was high or low in the range of estimates for this period by earlier studies. Estimated M increased by 0.4 from the late 1970s to the present, a period over which size at maturity changed little.
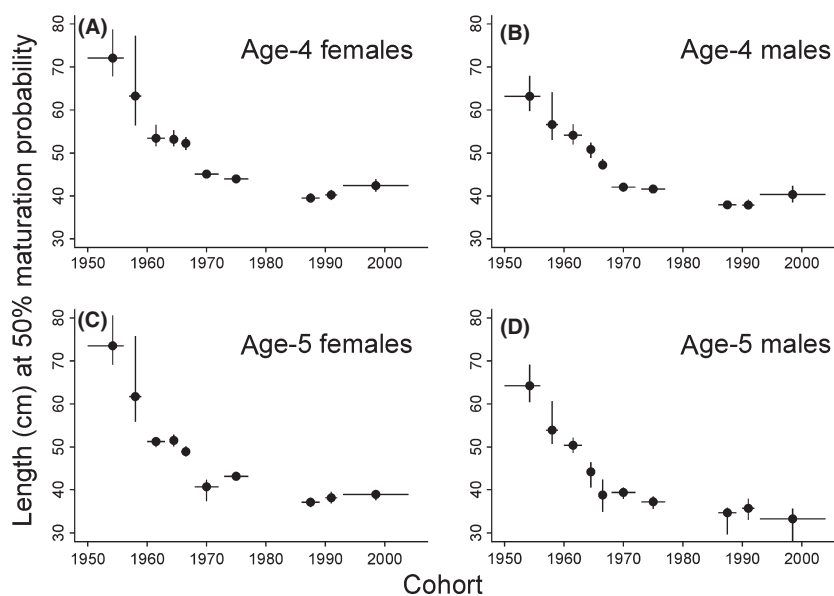

Figure 3 Temporal trends in maturation reaction norm midpoints for southern Gulf of St. Lawrence cod at ages 4 and 5 years. Vertical lines are 95% confidence intervals. Horizontal lines indicate the range of cohorts grouped together for an estimate.
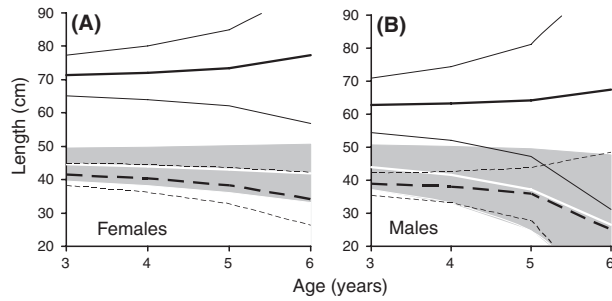
Figure 4 Maturation reaction norms for the 1950–1956 (solid lines), 1973–1977 (grey shading, white line) and 1990–1992 (dashed lines) cohorts of cod in the southern Gulf of St. Lawrence. Lines or shading show the lengths at which the probability of maturing is 25%, 50% and 75%.

Table 1. Rates of change in life-history traits of southern Gulf of St. Lawrence cod.

Trait	Sex	Time period	Time (years)	Rate (10^3 darwins)
A_{50}	F	1953–2001.5	48.5	−9.25
A_{50}	F	1953–1976	23.0	−22.83
A_{50}	F	1976–2001.5	25.5	3.00
A_{50}	M	1955.5–2001.5	46.0	−8.49
A_{50}	M	1955.5–1976	20.5	−19.91
A_{50}	M	1976–2001.5	25.5	0.69
L_{50}	F	1953–2001.5	48.5	−9.86
L_{50}	F	1953–1976	23.0	−17.65
L_{50}	F	1976–2001.5	25.5	−2.83
L_{50}	M	1955.5–2001.5	46.0	−8.19
L_{50}	M	1955.5–1976	20.5	−14.41
L_{50}	M	1976–2001.5	25.5	−3.19
PMRN	F	1954.2–1998.5	44.3	−11.98
PMRN	F	1954.2–1975	20.8	−23.77
PMRN	F	1975–1998.5	23.5	−1.55
PMRN	M	1954.2–1998.5	44.3	−10.14
PMRN	M	1954.2–1975	20.8	−20.10
PMRN	M	1975–1998.5	23.5	−1.32

The PMRN trait is the length at 50% maturation probability for 4-year-old cod. Time period is denoted by the midpoints of the cohort groups at the start and the end of the period.

Figure 5 Instantaneous rate of natural mortality (M) of cod in the southern Gulf of St. Lawrence. Heavy horizontal line is an assumed value; circles are estimates for the periods delimited by light horizontal lines. Vertical lines are ±2 SE. Grey lines show the trend in length at 50% maturity for females (solid line) and males (dashed line). M fixed at 0.1 (A) or 0.2 (B) in 1971–1975.

Figure 6 Survival rate of southern Gulf of St. Lawrence cod from 3 to 8 years of age.

Estimated survival from 3 to 8 years of age declined over the time period (Fig. 6). Survival was over 25% for the earliest cohort observed and under 5% for recent cohorts. Survival declined more or less steadily over time, though there was some improvement in survival for cohorts produced in the 1970s. This reflected a decline in fishing mortality in the early- to mid-1980s (Fig. 1A). However, even for these cohorts, survival was only about half that observed at the beginning of the time series. These calculations assume an M of 0.2 for the period 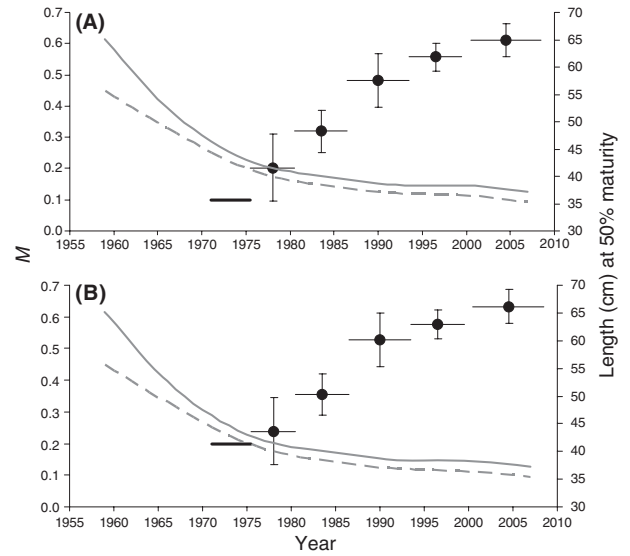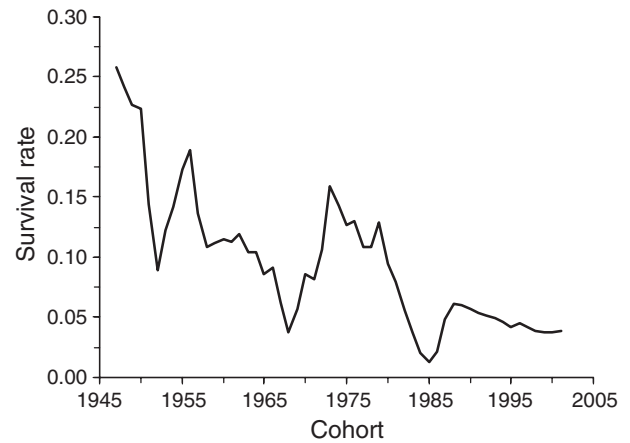prior to 1976, a value near the upper limit of plausible values for this period (about 0.1–0.2). Even greater declines in survival would be estimated assuming a lower plausible M for this period.

Discussion

Life-history traits are expected to evolve in response to changes in mortality schedules. An increase in the mortality of older individuals is predicted to favour an earlier age at maturation (e.g. Law 1979). This prediction is

supported by extensive studies of life-history variation in wild populations of the guppy, *Poecilia reticulata* (Reznick and Ghalambor 2005; and references therein). These studies compare life-history traits between populations occurring at high- and low-predation sites. The predators characteristic of high-predation sites have been reported to prey predominantly on the reproductive size classes of guppies (Reznick and Endler 1982), and the estimated increase in mortality at high-predation sites is proportionally greater at these larger sizes (Reznick and Ghalambor 2005). As predicted by theory, guppies from high-predation sites mature at an earlier age and a smaller size than those from low-predation sites. These differences in life history have a genetic basis (Reznick and Ghalambor 2005), and transplant experiments between high- and low-predation sites have demonstrated that the evolutionary response in life-history traits to changes in mortality schedules can be rapid (Reznick et al. 1997).

Like selective predators, fisheries can profoundly alter the mortality schedules of exploited populations. Fisheries typically target the larger adult size classes. A decline in age and size at maturation is the expected evolutionary response to the increase in mortality at larger sizes imposed by fishing (Law and Grey 1989; Law 2000). (An exception occurs when fisheries are confined to the spawning grounds, targeting spawners and thus generating an advantage to delayed maturation.) Length and age at 50% maturity of SGSL cod declined dramatically in the 1960s and early 1970s, following large increases in fishing mortality. These changes are in the direction expected for evolutionary responses to fishing. However, fishing may also generate non-genetic changes in life history due to phenotypic plasticity in growth and maturation (e.g. Kuparinen and Merilä 2007). Reduced competition for resources in populations depleted by fishing may result in an increase in the growth rate of individuals and thus lead to early maturation. Beacham (1983b) reported declines in length and age at maturity of cod in the neighbouring Scotian Shelf population, similar to those observed in SGSL cod (Beacham 1983a), and noted that it was not clear whether these declines reflected fishing-induced genetic changes or phenotypic responses to increases in growth rate as cod biomass decreased. Subsequent to the studies by Beacham (1983a,b), there was a decrease in the growth rate of SGSL cod as the population recovered in the late 1970s and early 1980s (Sinclair et al. 2002b; Swain et al. 2003). There was no return to an older age and greater length at maturity as growth rate declined, suggesting that the changes in maturation schedules were genetic in origin. Moreover, analyses presented here demonstrate that changes in PMRNs underlie the changes in maturity of SGSL cod. Because PMRNs control for effects of variation in average growth rates,

this result further strengthens support for the hypothesis that the trend in maturation schedules of SGSL cod reflects fisheries-induced evolution.

The PMRNs used here do not account for other potential plastic effects on maturation, such as effects of variation in ambient temperature or fish condition (e.g. Dieckmann and Heino 2007; Marshall and McAdam 2007). However, the alternate hypothesis that the trends in maturation reflect such unaccounted plastic effects is not supported by the time trends in the forcing factors associated with these effects. For example, high fish condition may increase the probability of being mature at a given age or length (see references in Marshall and McAdam 2007), leading to the expectation of an inverse relationship between condition and size or age at maturity. Condition of SGSL cod in September, shortly before the onset of gonad maturation in late fall, was high in the mid-1970s, low in the early to mid-1980s, and at an intermediate level since then (Swain et al. 2009; their fig. 18). Instead of the expected inverse pattern, length at maturity showed little variation over this period (Fig. 5). Temperature may also directly affect the probability of maturing independent of its indirect effects via growth, with the probability of maturing increasing with temperature (Grift et al. 2003; Kraak 2007). Consistent with such an effect, SGSL cod matured at a relatively old age and large size in the early 1960s when the bottom water layer in the SGSL was relatively cold (Gilbert and Pettigrew 1997; Galbraith et al. 2008). However, inconsistent with such an effect, cod matured at an early age and small size during the cold period in the mid-1970s and during the coldest period on record, from the late 1980s to the mid-1990s. Thus, the available evidence suggests that the dramatic decline in age and size at maturation of SGSL cod during the 1960s and early 1970s (in cohorts produced in the 1950s and 1960s) was in large part an evolutionary response to increasing fishing mortality.

Fisheries-induced evolution may be slow to reverse after fishing pressure is relaxed (e.g. Law 2000; Stokes and Law 2000; Hutchings and Fraser 2008). This may occur because of an erosion in additive genetic variation in severely depleted populations, or because the selection differentials imposed by fishing are likely to be stronger than those expected in the absence of fishing. For example, expected lifetime egg production estimated from a growth model for North Sea cod indicated strong selection favouring early maturity at high exploitation rates but little selection for age at maturation in the absence of fishing (Rowell 1993). Recent eco-genetic models of fish populations also predict that recovery of life-history traits from fisheries-induced evolution may be very slow to non-existent after fishing has ceased (Dunlop et al. 2009; Enberg et al. 2009). The slow recovery observed in these

models resulted from weak natural selection rather than reduced genetic variance. An alternative modelling approach suggests that in some situations fisheries-induced evolutionary changes may become irreversible due to a shift to an alternative evolutionarily stable state (de Roos et al. 2006). On the other hand, in laboratory populations, recovery from evolutionary change can be moderately rapid after size-selective harvesting ceases, with recovery occurring at about half the rate of the original change in large-harvested populations (Conover et al. 2009).

In contrast to the rapid decline in length and age at maturation observed in cohorts of SGSL cod produced in the 1950s and 1960s, there has been little change in maturation schedules since then, despite the population recovery in the late 1970s and early 1980s and 15 years with very low fishing mortality following the second collapse of this stock. At first glance, this appears consistent with the hypothesis that reversal of fisheries-induced evolution may be slow when selection for early maturation is relaxed by reducing fishing mortality. However, in this case, it appears that selection in favour of early maturation has not been relaxed. The population recovery in the late 1970s was due to unusually strong recruitment (Swain and Sinclair 2000) rather than a reduction in fishery landings. Fishing mortality did decline in the early to mid-1980s due to the increase in abundance (Fig. 1), but overall survival remained low compared to that experienced by cohorts produced in the late 1940s (Fig. 6). Despite very low fishing mortality since 1994, survival has now decreased to even lower levels due to elevated natural mortality. Preliminary analyses of the age-dependence of changes in natural mortality of SGSL cod indicate that the increased natural mortality in the 1990s and 2000s is restricted to the older ages classes (5 years and older; Swain et al. 2009, see their appendix III). Thus, elevated natural mortality appears to be focussed on the same age classes that had been targetted by the fishery, with high natural mortality now replacing fishing mortality as an agent of selection favouring early maturation.

Can life-history evolution provide an explanation for the high natural mortality of SGSL cod? Individuals maturing at an earlier age and smaller size are expected to experience higher survival costs to reproduction (Roff 2002; Hutchings 2005; e.g. Hutchings 1994). The sharp decline in age and size at maturation in cohorts produced in the 1950s and 1960s appeared to be associated with an increase in M by 0.05–0.1 to a level near 0.2–0.25. This is similar to results reported by Beverton et al. (1994), who concluded that M of Northeast Arctic cod appeared to increase from about 0.15 to 0.25 as age at maturation declined from 8 years or older to 6 years. However, the much larger increase in M from 0.2–0.25 in the late 1970s

to 0.6–0.65 in recent years is not associated with any substantial change in age or size at maturity. Costs to reproduction may be more evident under stressful physiological or ecological conditions (Reznick 1985; Roff 2002). Perhaps, the lag of about 15 years between the main declines in age and size at maturation and the main increases in M reflects a shift from optimal to stressful conditions. The condition of cod did decline from the mid-1970s to the mid-1980s (Swain et al. 2009), consistent with the hypothesis that the further increase in M in the early to mid-1980s may reflect an interaction between early maturation and harsh conditions (e.g. low per capita food resources). However, inconsistent with this hypothesis, cod condition subsequently increased and has been at average levels since the late 1980s but, instead of declining, M has increased further. The high estimates for M in the 1980s, particularly during the intense fishery in the 1987–1993 period, may be partly due to unreported catch, though this is clearly not the case after 1993 when fishing effort was very low (Swain et al. 2009). If so, the discrepancy in timing between the change in maturation and the main increases in M is even greater. Possibly, increased reproductive investment beyond that associated with earlier maturation (e.g. increased size-specific fecundity) contributes to the increases in M in the 1980s and 1990s. However, the limited evidence available does not support this hypothesis. Reproductive allotment does appear to be relatively high for SGSL cod, but if there has been a change over time, the evidence points to a decrease in size-specific fecundity between the mid-1950s and the late 1990s (McIntyre and Hutchings 2003). Finally, high M is the main factor contributing to the low productivity and apparent inviability of this population (Swain and Chouinard 2008). If early maturation were a major cause of this high M, there would be very strong selection favouring a return to later maturation. Thus, the increase in M of SGSL cod in the 1970s may be related to increased costs of reproduction associated with early maturation, but the greater increases in M since then appear to be associated with some other factor external to the population, such as increased predation by the expanding grey seal herd (Chouinard et al. 2005; Benoît and Swain 2008). For the most part, the current high natural mortality of SGSL cod appears to be a cause, rather than a consequence, of the continued early maturation in this population.

Fisheries-induced genetic changes in life history may contribute to the lack of recovery observed for many collapsed fish populations (Hutchings and Reynolds 2004). Potential consequences of these changes include reduced productivity and lower maximum sustainable yields (Hutchings and Fraser 2008). This study presents a striking example of the failure to reverse fisheries-induced evolution by relaxing fishing pressure. The observation

that these evolutionary changes may not be readily reversible underlines the need for management strategies that minimize the chance of inducing these changes by fishing (Hutchings 2009). Reversal of fisheries-induced evolution has been predicted to be slow because, compared to the selection imposed by fisheries, natural selection in the reverse direction is expected to be weak (e.g. Law 2000; Dunlop et al. 2009). However, in contrast to this expectation, natural selection in this case appeared to be strong following the relaxation of fisheries selection, and now appears to operate in the same direction as selection by fisheries had operated. The high natural mortality of adult cod that is the source of this natural selection is also the main cause of the continued decline of the SGSL cod stock (Swain and Chouinard 2008). Increased natural mortality has also been identified as the most important factor contributing to the lack of recovery of several other collapsed cod stocks in the Northwest Atlantic (Shelton et al. 2006). Fisheries-induced evolution of early maturation, which is expected to result in a higher survival cost to reproduction, has been suggested as one possible cause of increased natural mortality in these depleted cod stocks (e.g. Hutchings 2005). However, in the case of SGSL cod, the current high and unsustainable level of natural mortality appears to be mainly due to factors external to the population, such as changes in predator-prey interactions. These changes may themselves be another consequence of overexploitation. For example, hypothesized increases in predation mortality may be partly a consequence of the sharp decline in cod abundance; that is, the current high natural mortality may be a predation-driven Allee effect (Gascoigne and Lipcius 2004). If so, this again emphasizes the need for more precautionary management regimes in order to avoid stock collapses that are not readily reversible by stopping fishing.

Acknowledgements

Literature cited

Barot, S., M. Heino, L. O'Brien, and U. Dieckmann. 2004. Estimating reaction norms for age and size at maturation when age at first reproduction is unknown. Evolutionary Ecology Research 6:659–678.

Beacham, T. D. 1983a. Growth and maturity of Atlantic cod (*Gadus morhua*) in the Southern Gulf of St. Lawrence. Canadian Technical Report of Fisheries and Aquatic Sciences 1142, iv+31 pp.

Beacham, T. D. 1983b. Variability in median size and age at sexual maturity of Atlantic cod, *Gadus morhua*, on the Scotian Shelf in the Northwest Atlantic Ocean. Fisheries Bulletin 81:303–321.

Beacham, T. D. 1987. Variation in length and age at sexual maturity of Atlantic groundfish: a reply. Environment Biology of Fishes 19:149–153.

Benoît, H. P., and D. P. Swain. 2008. Impacts of envilronmental change and direct and indirect harvesting effects on the dynamics of a marine fish community. Canadian Journal of Fisheries and Aquatic Sciences 65:2088–2104.

Beverton, R. J. H., A. Hylen, and O. J. Ostvedt. 1994. Growth, maturation, and longevity of maturation cohorts of Northeast Arctic cod. ICES Journal of Marine Science Symposium 198:482–501.

Biro, P. A., and J. R. Post. 2008. Rapid depletion of genotypes with fast growth and bold personality traits from harvested.fish populations. Proceedings of the National Academy of Sciences of the United States of America 105:2919–2922.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodel Inference, 2nd edn. Springer-Verlag, New York.

Chouinard, G. A., D. P. Swain, M. O. Hammill, and G. A. Poirier. 2005. Covariation between grey seal (*Halichoerus grypus*) abundance and natural mortality of cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. Canadian Journal of Fisheries and Aquatic Science 62:1991–2000.

Conover, D. O., and S. B. Munch. 2002. Sustaining fisheries yields over evolutionary time scales. Science 297:94–96.

Conover, D. O., S. B. Munch, and S. A. Arnott. 2009. Reversal of evolutionary downsizing caused by selective harvest of large fish. Proceedings of the Royal Society B: Biological Sciences 276:2015–2020.

Dieckmann, U., and M. Heino. 2007. Probabilistic maturation reaction norms: their history, strengths, and limitations. Marine Ecology Progress Series 335:253–269.

Dunlop, E. S., M. Heino, and U. Dieckmann. 2009. Eco-genetic modeling of contemporary life-history evolution. Ecological Applications 19:1815–1834.

Edeline, E., S. M. Carlson, L. C. Stige, I. J. Winfield, J. M. Fletcher, J. B. James, T. O. Haugen et al. 2007. Trait changes in a harvested population are driven by a dynamic tug-of-war between natural and harvested selection. Proceedings of the National Academy of Sciences of the United States of America 104:15799–15804.

Enberg, K., C. Jørgensen, E. S. Dunlop, M. Heino, and U. Dieckmann. 2009. Implications of fisheries-induced evolution for stock rebuilding and recovery. Evolutionary Applications 2:394–414.

Galbraith, P. S., D. Gilbert, R. G. Pettipas, J. Chassé, C. Lafleur, B. Pettigrew, P. Larouche et al. 2008. Physical oceanographic conditions in the Gulf of St. Lawrence in 2007. DFO Canadian Science Advisory Secretariat Research Document 2008/001, 55 pp.

Gascoigne, J. C., and R. N. Lipcius. 2004. Allee effects driven by predation. Journal of Applied Ecology 41:801–810.

Gavaris, S. 1988. An adaptive framework for the estimation of population size. Canadian Atlantic Fisheries Stock Assessment Committee Research Document 88/29, 12 pp.

Gilbert, D., and B. Pettigrew. 1997. Interannual variability (1948-1994) of the CIL core temperature in the Gulf of St. Lawrence. Canadian Journal of Fisheries and Aquatic Science 54(Suppl. 1):57–67.

Grift, R. E., A. D. Rijnsdorp, S. Barot, M. Heino, and U. Dieckmann. 2003. Fisheries-induced trends in reaction norms for maturation in North Sea plaice. Marine Ecology-Progress Series 257:247–257.

Halliday, R. G. 1987. Size and age at sexual maturity of Atlantic argentine, *Argentina silus*: a critique. Environment Biology of Fishes **19**:139–147.

Handford, P., G. Bell, and T. Reimchen. 1977. A gillnet fishery considered as an experiment in artificial selection. Journal of the Fisheries Research Board of Canada **34**:954–961.

Haugen, T. O., and L. A. Vøllestad. 2001. A century of life-history evolution in grayling. Genetica **112**:475–491.

Heino, M., U. Dieckmann, and O. R. Godø. 2002a. Estimating reaction norms for age and size at maturation with reconstructed immature size distributions: a new technique illustrated by application to Northeast Arctic cod. ICES Journal of Marine Science **59**:562–575.

Heino, M., U. Dieckmann, and O. R. Godø. 2002b. Measuring probablistic reaction norms for age and size at maturation. Evolution **56**:669–678.

Hurlbut, T., and D. Clay. 1990. Protocols for research vessel cruises within the Gulf Region (demersal fish) (1970-1987). Canadian Manuscript Report of Fisheries and Aquatic Sciences **2082**, 143.

Hutchings, J. A. 1994. Age- and size-specific costs of reproduction within populations of brook trout, *Salvelinus fontinalis*. Oikos **70**:12–20.

Hutchings, J. A. 2005. Life history consequences of overexploitation to population recovery in Northwest Atlantic cod. Canadian Journal of Fisheries and Aquatic Science **62**:824–832.

Hutchings, J. A. 2009. Avoidance of fisheries-induced evolution: management implications for catch selectivity and limit reference points. Evolutionary Applications **2**:324–334.

Hutchings, J. A., and D. J. Fraser. 2008. The nature of fisheries- and farming-induced evolution. Molecular Ecology **17**:294–313.

Hutchings, J. A., and J. D. Reynolds. 2004. Marine fish population collapses: consequences for recovery and extinction risk. BioScience **54**:297–309.

Jean, Y. 1963. Abundance of Cod Eggs and Larvae in the Gulf of St. Lawrence, 1958–1962. Annual Report. Fisheries Research Board of Canada, Biological Station, St. Andrews, 1962–1963.

Kraak, S. B. M. 2007. Does the probabilistic maturation reaction norm approach disentangle phenotypic plasticity from genetic change? Marine Ecology Progress Series **335**:295–300.

Kuparinen, A., and J. Merilä. 2007. Detecting and managing fisheries-induced evolution. Trends in Ecology and Evolution **22**:652–659.

Law, R. 1979. Optimal life histories under age-specific predation. American Naturalist **114**:399–417.

Law, R. 2000. Fishing, selection and phenotypic evolution. ICES Journal of Marine Science **57**:659–668.

Law, R., and D. R. Grey. 1989. Evolution of yields from populations with age-specific cropping. Evolutionary Ecology **3**:343–359.

Lett, P. F. 1980. A comparative study of the recruitment mechanisms of cod and mackerel, their interaction and its implication for dual stock assessment. Canadian Technical Report of Fisheries and Aquatic Sciences **988**:51.

Maguire, J. J., D. Lever, and L. Waite. 1983. Assessment of cod in NAFO Division 4T and subdivision 4Vn (Jan.-Apr.) for 1983. Canadian Atlantic Fisheries Scientific Advisory Committee Research Document 83/51, 38 pp.

Marshall, C. T., and B. J. McAdam. 2007. Integrated perspective on genetic and environmental effects on maturation can reduce potential for errors of inference. Marine Ecology Progress Series **335**:301–310.

McIntyre, T. M., and J. A. Hutchings. 2003. Small-scale temporal and spatial variation in Atlantic cod (*Gadus morhua*) life history. Canadian Journal of Fisheries and Aquatic Science **60**:1111–1121.

Morita, K., and M. Fukuwaka. 2006. Does size matter most? The effect of growth history on probabilistic reaction norm for salmon maturation. Evolution **60**:1516–1521.

Nusslé, S., C. N. Bornand, and C. Wedekind. 2009. Fishery-induced selection on an Alpine whitefish: quantifying genetic and environmental effects on individual growth rate. Evolutionary Applications **2**:200–208.

Olsen, E. M., M. Heino, G. R. Lilly, M. J. Morgan, J. Brattey, B. Ernande, and U. Dieckmann. 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. Nature **428**:932–935.

Olsen, E. M., G. R. Lilly, M. Heino, M. J. Morgan, J. Brattey, and U. Dieckmann. 2005. Assessing changes in age and size at maturity in collapsing populations of Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Science **62**:811–823.

Pérez-Rodríguez, A., M. J. Morgan, and F. Saborido-Rey. 2009. Comparison of demographic and direct methods to calculate probabilistic maturation reaction norms for Flemish Cap cod (*Gadus morhua*). Evolutionary Applications **2**:291–298.

Powles, P. M. 1958. Studies of reproduction and feeding of Atlantic cod (*Gadus callarius* L.) in the southwestern Gulf of St. Lawrence. Journal of the Fisheries Research Board of Canada **15**:1383–1402.

Reznick, D. 1985. Costs of reproduction: an evaluation of the empirical evidence. Oikos **44**:257–267.

Reznick, D. N., and J. A. Endler. 1982. The impact of predation on life history evolution in Trinidadian guppies (*Poecilia reticulata*). Evolution **36**:160–177.

Reznick, D. N., and C. K. Ghalambor. 2005. Can commercial fisheries cause evolution? Answers from guppies (*Poecilia reticulata*). Canadian Journal of Fisheries and Aquatic Sciences **62**:791–801.

Reznick, D. N., F. H. Shaw, F. H. Rodd, and R. G. Shaw. 1997. Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). Science **275**:1934–1937.

Ricker, W. E. 1981. Changes in the average size and average age of Pacific salmon. Canadian Journal of Fisheries and Aquatic Science **38**:1636–1656.

Roff, D. A. 2002. Life History Evolution. Sinauer, Sutherland, MA.

de Roos, A. M., D. S. Boukal, and L. Persson. 2006. Evolutionary regime shifts in age and size at maturation of exploited fish stocks. Proceedings of the Royal Society B: Biological Sciences **273**:1873–1880.

Rowell, C. A. 1993. The effects of fishing on the timing of maturity in North Sea cod (*Gadus morhua* L.). In T. K. Stokes, J. M. McGlade, and R. Law, eds. The Exploitation of Evolving Resources, pp. 44–61. Springer-Verlag, Berlin.

Schwalme, K., and G. A. Chouinard. 1999. Seasonal dynamics in feeding, organ weights, and reproductive maturation of Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. ICES Journal of Marine Science **56**:303–319.

Sharpe, D. M. T., and A. P. Hendry. 2009. Life history change in commercially exploited fish stocks: an analysis of trends across studies. Evolutionary Applications **2**:260–275.

Shelton, P. A., A. F. Sinclair, G. A. Chouinard, R. Mohn, and D. Duplisea. 2006. Fishing under low productivity conditions is further delaying recovery of Northwest Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Science **63**:235–238.

Sinclair, A. F. 2001. Natural mortality of cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. ICES Journal of Marine Science **58**:1–10.

Sinclair, A. F., D. P. Swain, and J. M. Hanson. 2002a. Disentangling the effects of size-selective mortality, density, and temperature on

length-at-age. Canadian Journal of Fisheries and Aquatic Science **59**:372–382.

Sinclair, A. F., D. P. Swain, and J. M. Hanson. 2002b. Measuring changes in the direction and magnitude of size-selective mortality in a commercial fish population. Canadian Journal of Fisheries and Aquatic Science **59**:361–371.

Stokes, K., and R. Law. 2000. Fishing as an evolutionary force. Marine Ecology Progress Series **208**:307–309.

Swain, D. P., and G. A. Chouinard. 2008. Predicted extirpation of the dominant demersal fish in a large marine ecosystem: Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. Canadian Journal of Fisheries and Aquatic Science **65**:2315–2319.

Swain, D. P., and A. F. Sinclair. 2000. Pelagic fishes and the cod recruitment dilemma in the Northwest Atlantic. Canadian Journal of Fisheries and Aquatic Science **57**:1321–1325.

Swain, D. P., A. F. Sinclair, M. Castonguay, G. A. Chouinard, K. F. Drinkwater, L. P. Fanning, and D. S. Clark. 2003. Density- versus temperature-dependent growth of Atlantic cod (*Gadus morhua*) in the Gulf of St. Lawrence and on the Scotian Shelf. Fisheries Research **59**:327–341.

Swain, D. P., A. F. Sinclair, and J. M. Hanson. 2007. Evolutionary response to size-selective mortality in an exploited fish population. Proceedings of the Royal Society B: Biological Sciences **274**:1015–1022.

Swain, D. P., L. Savoie, T. Hurlbut, T. Surette, and D. Daigle. 2009. Assessment of the southern Gulf of St. Lawrence cod stock, Feb-ruary 2009. DFO Canadian Science Advisory Secretariat Research Document 2009/037, vi+129 pp.

Walsh, M. R., S. B. Munch, S. Chiba, and D. O. Conover. 2006. Maladaptive changes in multiple traits caused by fishing: impediments to population recovery. Ecology Letters **9**:142–148.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. Seasonal distribution of cod in the southern Gulf of St. Lawrence.

Data S2. Summary of data sources on age and size at maturity of southern Gulf of St. Lawrence cod.

Data S3. Comparison of maturity ogives based on spring, fall and January data.

Data S4. Discontinuities in the time series of fall maturity staging data.

Data S5. Effects of size-selective mortality on estimates of PMRN midpoints.

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