ORIGINAL ARTICLE

Avoidance of fisheries-induced evolution: management implications for catch selectivity and limit reference points

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Abstract

I examined how the fitness (r) associated with early- and late-maturing genotypes varies with fishing mortality (F) and age-/size-specific probability of capture. Life-history data on Newfoundland's northern Atlantic cod (*Gadus morhua*) allowed for the estimation of r for individuals maturing at 4 and 7 year in the absence of fishing. Catch selectivity data associated with four types of fishing gear (trap, gillnet, handline, otter trawl) were then incorporated to examine how r varied with gear type and with F. The resulting fitness functions were then used to estimate the F above which selection would favour early (4 year) rather than delayed (7 year) maturity. This evolutionarily-sensitive threshold, F_{evol}, identifies a limit reference point somewhat similar to those used to define overfishing (e.g., F_{msy}, $F_{0.1}$). Over-exploitation of northern cod resulted in fishing mortalities considerably greater than those required to effect evolutionary change. Selection for early maturity is reduced by the dome-shaped selectivities characteristic of fixed gears such as handlines (the greater the leptokurtosis, the lower the probability of a selection response) and enhanced by the knife-edged selectivities of bottom trawls. Strategies to minimize genetic change are consistent with traditional management objectives (e.g., yield maximization, population increase). Compliance with harvest control rules guided by evolutionarily-sensitive limit reference points, which may be achieved by adherence to traditional reference points such as F_{msy} and $F_{0.1}$, should be sufficient to minimize the probability of fisheries-induced evolution for commercially exploited species.

Introduction

The premise that predators can generate evolutionary change in their prey has been persuasively demonstrated in natural systems (e.g., Reznick et al. 2008) and some anthropogenically influenced systems (e.g., Grift et al. 2003; Hard 2004; Swain et al. 2007; Coltman 2008). Nonetheless, the hypothesis that fishing can effect genetic responses by fish prey, having been seriously considered since the late 1970s (Handford et al. 1977; Ricker 1981), is one that remains controversial despite its logical premises (Dieckmann and Heino 2007; Marshall and McAdam 2007; Hutchings and Fraser 2008). It has been argued that the question of whether fishing effects evolution is moot and that the key question is whether the

consequences of such changes are likely to significantly influence population growth rate (Hutchings and Fraser 2008), which would then have consequences for sustainable rates of harvesting and rates of recovery following depletion. Given the high probability that evolutionary responses to fishing are unlikely to generate rates of population increase higher than those generated under natural selection in the absence of fishing, there is a need to explore the management implications of fisheries-induced evolution, focussing in particular on the means by which the probability of harvest-induced genetic change can be minimized.

The likelihood that fishing will generate an evolutionary response depends primarily on the heritability and genetic variance/covariance matrix of the trait(s) under

selection, the age-/size-specific magnitude of fishing mortality, and the age-/size-specific probability of being captured by fishing gear (Law 1991; Walsh et al. 2006). Clearly, management can have no direct influence on trait heritability or genetic covariance, but it can influence fishing mortality and catch selectivity. Fishing mortality can be modified by some combination of catch or effort controls. Arguably the best form of control is that encompassed by a management regime that utilizes reference points (Cadrin and Pastoors 2008). Reference points specify levels of stock biomass and fishing mortality that managers aim either to achieve and maintain ('target' reference points) or to not exceed ('limit' or 'threshold' reference points). Catch selectivity is a function of the type of fishing gear deployed. For example, bottom otter trawls (nets towed along the bottom from the stern of a vessel, i.e., mobile gear) typically have catch selectivity curves that resemble a logistic function, or a threshold curve, such that the probability of capture increases quite rapidly with size from 0 to a value near or at 1, remaining at that value with further increases in size. These curves are often termed knife-edged selectivity curves. The other common type of curve is a dome-shaped selectivity curve (typically characteristic of gillnets, hook-and-line fisheries, and traps, i.e., fixed gear), which reflects size-specific probabilities of capture that increase from near 0 to a maximum before declining (often) symmetrically with further increases in size to values near or equal to 0.

When considering the management implications of harvest-induced evolution, most studies have remarked upon the fact that the probability of genetic change by the prey increases with the level of predator-induced mortality (e.g., Dieckmann and Heino 2007; Hutchings and Fraser 2008). Noting the influence on evolutionary change generated by differential fishing mortality with respect to size or age, several researchers have commented on the need to maintain a breadth of size variation in a population (e.g., Conover and Munch 2002; Hutchings and Rowe 2008) and the need to ensure that larger and older fish have high probabilities of reproduction before they are captured (e.g., Law 2007; Hutchings and Fraser 2008). One means of increasing the probability of surviving to older ages would be to establish maximum (and minimum) size thresholds above which fishing would be prevented (Conover and Munch 2002). It has been argued that this objective could be achieved by dome-shaped selectivity curves (Law 2007). Alternatively, one could establish a fishing strategy that avoided the harvest of immature fish but that targeted large, mature fish (e.g., Law and Grey 1989; Heino 1998; Ernande et al. 2004). Although this second option might seem counter-intuitive, such a strategy increases the probability of survival

to older ages by minimizing fishing mortality at younger ages.

The approach adopted here differs from previous analyses of fisheries-induced evolution in that it poses the following question: For a given population, what level of fishing mortality is required to generate evolutionary change? Using a stochastic, age-structured life-history model parameterized for northern Atlantic cod, *Gadus morhua*, off Newfoundland (Hutchings 1999, 2005; see also Arlinghaus et al. 2009 and Okamoto et al. 2009), this approach begins by estimating the fitness (defined by r, the intrinsic rate of natural increase; see also Metz et al. 1992 and Stearns 1992) associated with different life-history strategies (in this case, early versus delayed maturity, age at maturity being a clearly heritable trait; Roff 2002). Then, by applying different schedules of age-specific fishing mortality (which are determined by the age-/size-selectivities of fishing gear), one can quantify the instantaneous rate of fishing mortality F [which can be converted to a percent mortality as $100^{\star}(1-e^{-F})$] above which fisheries-induced evolution is likely to occur. I further suggest that such a threshold can be considered a limit reference point insofar as it identifies a level of fishing mortality that managers should not want to exceed. This limit reference point can be designated F_{evol}. In the context of the present study, I define F_{evol} to be the level of fishing mortality that, if exceeded, will favour early-maturing genotypes over late-maturing genotypes. More specifically, F_{evol} is defined as the F above which the fitness of individuals maturing at age 4 year exceeds the fitness of those maturing at age 7 year.

Using catch selectivity and life-history data, I examine how age- and size-specific changes in F associated with different types of fishing gear affect: (i) catch (approximated here as yield per cohort); (ii) probability of population decline; and (iii) fitness of early- and late-maturing genotypes (see Jørgensen et al. 2009 for a complementary analysis of Northeast Arctic cod). It has been hypothesized that late-20th Century reductions in age at maturity in Newfoundland's northern Atlantic cod (Fig. 1; Lilly et al. 2001, 2003) can be partly attributable to genetic responses to over-exploitation (Hutchings 1999; Olsen et al. 2004, Olsen et al. 2005). Although this hypothesis has been explored with, and supported by, probabilistic maturation reaction norm analysis (Olsen et al. 2004), others have questioned the strength of this approach (Law 2007; Marshall and McAdam 2007). Given its focus on the level of fishing mortality required to generate evolutionary change, the analysis undertaken here provides an alternative means by which one can evaluate the hypothesis that northern cod have experienced fisheries-induced evolution. It also allows one to pose generic questions concerning the fitness consequences associated
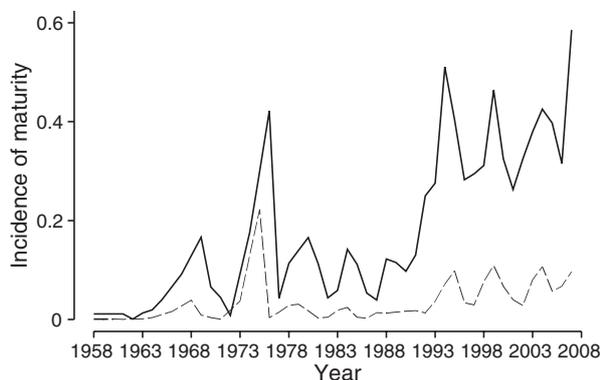
Figure 1 Temporal changes in the incidence of maturity at ages 4 (dot-dash line) and 5 years (solid line) for northern Atlantic cod, *Gadus morhua*. Data obtained from Brattey et al. (2008).

with the use of a range of gear selectivities and life-history strategies to examine the degree to which different types of fishing gear are likely to accelerate or retard fisheries-induced evolution (see also Kuparinen et al. 2009).

Materials and methods

Estimation of fitness associated with early and delayed maturity

The fitness (r) associated with early and delayed maturity was estimated with a stochastic, age-structured life-history model that has been applied previously to explore how population growth rate and recovery in Atlantic cod might be affected by changes in age and size at maturity. Given that the full details associated with the model, including details pertaining to stochasticity, are provided elsewhere (Hutchings 1999, 2005), only a summary will be provided here.

To a first approximation, the fitness associated with a particular life history, i.e., a particular age(x)-specific schedule of survival (l_x) and fecundity (m_x), is given by the intrinsic rate of increase, r, calculated from the discrete-time version of the Euler-Lotka equation $1 = \sum l_x m_x e^{-x}$, where x is summed from age at maturity, α (4 or 7 year; these ages encompass the range in α typically observed for northern cod), until an age at which the probability of postreproductive survival is nil (21 years in the present simulations). As described below, the parameters that determined l_x and m_x had their own distributions, allowing for the sampling of data from these distributions during each of the 10 000 model runs that were undertaken in each simulation. Although probability distributions of the intrinsic rate of increase cannot be described by a stochastic model (because of the analytical constraint that r can only be calculated by iteration), r

can be approximated by the natural logarithm of the net reproductive rate, R_0, discounted by generation time (G) as $r = \ln(R_0)/G$, where R_0 is given by $\sum l_x m_x$ and where $G = \sum l_x m_x x / l_x m_x$ (Roff 2002). The highly positive skew of the distributions necessitated the calculation of r from median estimates of R_0.

Age-specific survival and fecundity

The basic model incorporated observed or estimated variability in (i) survival from birth to age 3 year (the age at which Northwest Atlantic cod are initially recruited to fishing gear), (ii) instantaneous rate of prereproductive mortality, M_{imm}, and (iii) mortality of mature, postreproductive individuals, M_{mat}. Distinguishing mortality prior to and following maturation acknowledges, and allows for the inclusion of, a survival cost of reproduction (Beverton et al. 1994; Roff 2002). Survival from birth to age 3 year was quantified from abundance estimates of northern cod (Lilly et al. 2001) and from age-specific fecundities, as described below, such that survival from birth to age 3 year in year t can be calculated as $l_{3(t)} = n_{3(t)}/\sum n_{x\ (t-3)}\ m_{x\ (t-3)}$, where n represents the number of 7- to 11-year-olds in year $t-3$ multiplied by their average fecundity. Survival from birth to age 3 year estimated in this manner for the 1962 through the 1988 year classes of northern cod was weakly density-dependent (see Myers et al. 1995) and averaged $1.13 \times 10^{-6} \pm 1.11 \times 10^{-6}$ (SD). I assumed that variation in annual mortality attributable to factors unrelated to reproduction, e.g., predation, was best reflected by a beta distribution, with the scale parameter of this distribution set to 1.0 (the upper bound of the distribution) and the mean of the distribution set to an annual survival probability of exp $(-M_{imm}) = 0.91$, which corresponds to $M_{imm} = 0.10$. As a consequence, survival was approximated by a negatively skewed distribution.

Postreproductive mortality, M_{mat}, was assumed to vary with age at maturity because of empirical and theoretical support for the hypothesis that earlier maturing individuals experience higher survival costs of reproduction than later maturing individuals, particularly when maturing at a smaller size, possibly because of energetic constraints imposed by metabolic allometry and proportionately smaller lipid reserves (e.g., Beverton et al. 1994; Schultz and Conover 1999; summarized by Hutchings 2005). In Northeast Arctic cod, for example, Beverton et al. (1994) concluded that natural mortality declined with increasing age at maturity, such that M for cod maturing at ages 6, 7, and 8 years was equal to 0.25, 0.17, and 0.15, respectively. Given the absence of such estimates for northern cod, I used Beverton et al.'s (1994) estimates to incorporate a higher postreproductive mortality

for early maturing individuals, such that M for cod maturing at age 7 year was 0.20 (the presumed natural mortality rate prior to the collapse of the northern cod fishery in the early 1990s; e.g., Pinhorn 1975), whereas M for cod maturing at age 4 years was 0.34 (Hutchings 1999, 2005).

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

and 7 were 0.83 and 2.50 kg, respectively. The natural variability associated with individual increases in weight, ε_w, was assumed to be normally distributed with the standard deviation of each age-specific error distribution set equal to the standard deviation of the observed annual mean increases in weight-at-age (w_{x+1}/w_x). Fecundity estimates were based on May's (1967) fecundity:weight relationship for cod and modified, as described by Hutchings (1999, 2005), to yield the following association between age-specific fecundity, m_x, and age-specific weight: $m_x = (0.48((w_x + 0.37)/1.45) + 0.12) \times 10^6$.

Fishing mortality, catch, and probability of population decline

Data on the size-selectivity of four prevalent types of fishing gear in the northern cod fishery were used to incorporate the effects of fishing on age-specific survival. Based on mark-recapture studies, Myers and Hoenig (1997) provided point estimates of the probability of capture, as a function of body length, for cod captured by otter trawl (i.e., a net towed along the bottom from the stern of a vessel), gillnet, handline (comprised of a baited hook at the end of a line held by a fisherman), and trap (a box-like net from which a leader is attached; Hutchings and Ferguson (2000) provide a full description of the gillnets and cod traps used in the Newfoundland fishery). Continuous length-based selectivity functions (Fig. 2) were converted to age-selectivities by first transforming length to
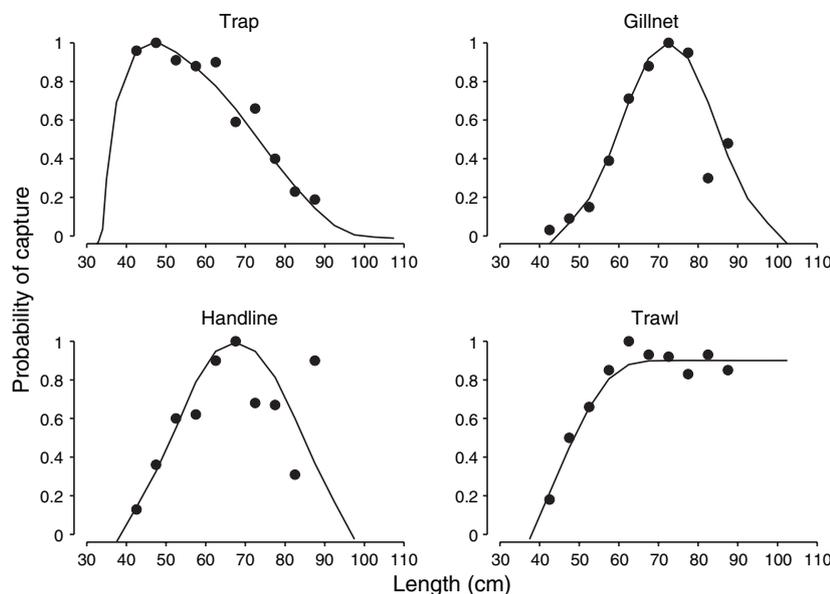

Figure 2 Catch selectivities in the trap, gillnet, handline, and otter trawl fisheries for northern Atlantic cod from 1979 to 1990. Circles identify the estimates provided by Myers and Hoenig (1997) to which the curves were fitted by eye.

weight, using a length:weight regression provided by McIntyre and Hutchings (2003), and then transforming weight to age using data on northern cod documented by Lilly et al. (2003).

Yields were calculated for each of the types of fishing gear used to catch northern cod and for each of the two ages at maturity. The ages at which fish were fully recruited to the gear were those corresponding to the data provided by Myers and Hoenig (1997). The total catch provided by each cohort was calculated by taking the product of harvest rate $(1-e^{-F})$, weight at age, and numbers at age (the number of eggs per cohort, n_0, was arbitrarily set to 10^{12} to obtain numerically tractable values). The probability of population decline associated with early and delayed maturity, and for each type of fishing gear, was estimated from the probability distributions of R_0 used to estimate fitness and was simply the expected probability of negative population growth per generation, i.e., $\Pr(R_0 < 1)$.

In addition to estimating catch and decline probabilities for the selectivities actually experienced by northern cod (Myers and Hoenig 1997), one can vary the ages at which fish are fully recruited to the various types of fishing gear to identify those combinations of gear and fishing mortality most likely to achieve the following fisheries management objectives considered desirable from a traditional and evolutionary perspective: (i) maximize yield; (ii) minimize probability of population decline; and (iii)

maximize F_{evol}, thus minimizing the likelihood of fisheries-induced evolution.

Results

Fishery yields and probability of population decline

Simulated fishery yields and probabilities of per-generation population decline revealed similar patterns within and between ages at maturity, independent of fishing gear, for values of F ranging between 0 and 0.6 (Figs 3 and 4). As predicted from yield-per-recruit analyses (Hilborn and Walters 1992), catch initially increased with fishing mortality with the rate of increase (i.e., the slope) declining as F increased further (Fig. 3). Catch reached a maximum, for the fishing mortalities considered here, for cod maturing at age 7 year in all gears, except gillnets, but for none of the gears for cod maturing at age 4 year. Yields were consistently higher among late-maturing cod relative to early-maturing cod, for all types of fishing gear.

The probability of population decline between generations was greater for late-maturing cod relative to early-maturing cod with the difference increasing with increases in F (Fig. 4). Among cod maturing at age 4 year, the likelihood of decline remained low across all fishing mortalities considered here for each type of gear except the trap, for which $\Pr(R_0 < 1)$ increased steadily at $F > 0.2$. For cod maturing at age 7 year, the likelihood of decline also
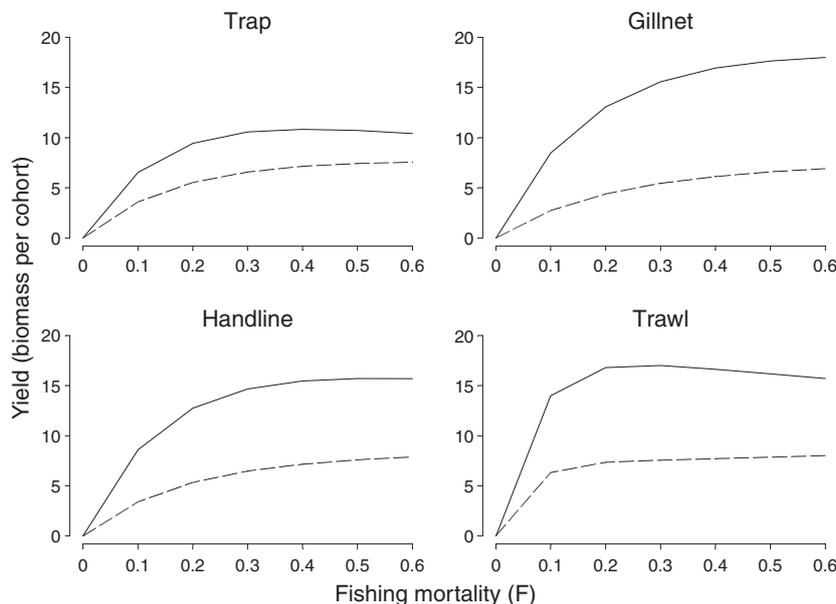

Figure 3 Estimated yield per cohort (thousand tonnes per 10^{12} eggs) from northern Atlantic cod maturing at ages 4 year (dashed line) and 7 year (solid line) in trap, gillnet, handline, and otter trawl fisheries, as a function of the fully recruited fishing mortality.

Figure 4 Estimated probabilities of per-generation population decline, $Pr(R_0 < 1)$, for northern Atlantic cod maturing at ages 4 year (dashed line) and 7 year (solid line) in trap, gillnet, handline, and otter trawl fisheries, as a function of the fully recruited fishing mortality.
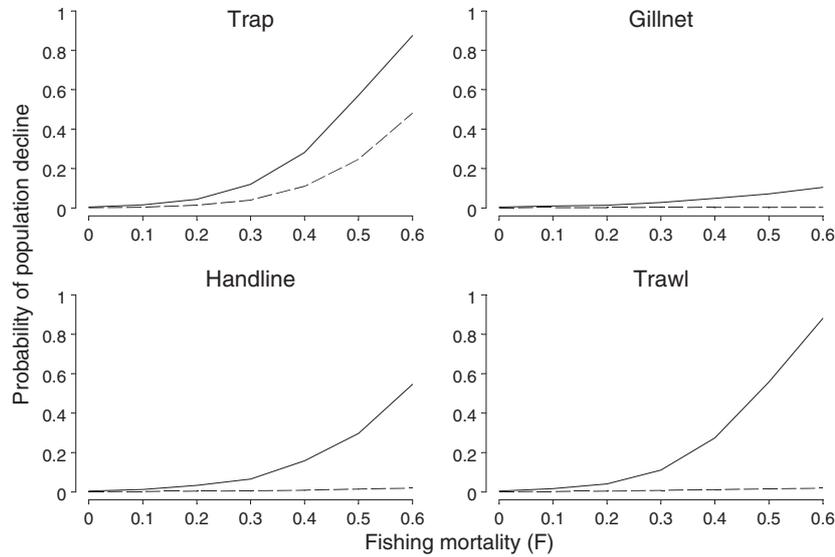
increased steadily with increases in F, with the rate of increase being comparatively high for traps and trawls, somewhat lower for handlines, and lowest for gillnets.

Estimates of F_{evol} for the northern cod fishery

The proposed limit reference point for fisheries-induced evolution differed among the four types of fishing gear used

to prosecute the fishery for northern cod. The value of F above which the fitness of early-maturing (4 years) genotypes is predicted to exceed that of late-maturing (7 years) genotypes was lowest for the otter trawl ($F_{evol} = 0.13$) and highest for the trap and gillnet ($F_{evol} = 0.22$ for both); that for the handline fishery was intermediate ($F_{evol} = 0.18$) (Fig. 5). By comparison, the fishing mortality experienced by northern cod from 1962 through 1991 was always well
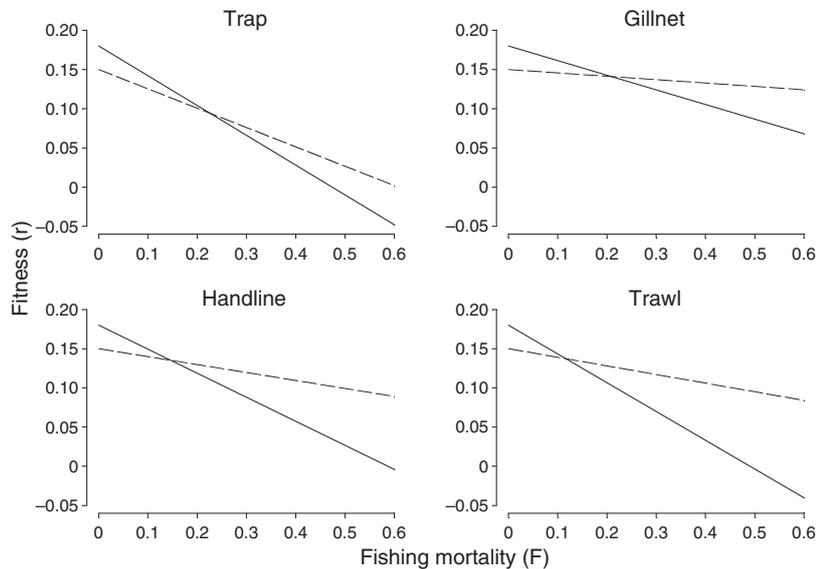

Figure 5 Estimated fitness (r) of northern Atlantic cod maturing at ages 4 year (dashed line) and 7 year (solid line) in trap, gillnet, handline, and otter trawl fisheries, as a function of fishing mortality. For each fishing gear, the point of intersection of the fitness functions identifies F_{evol}.
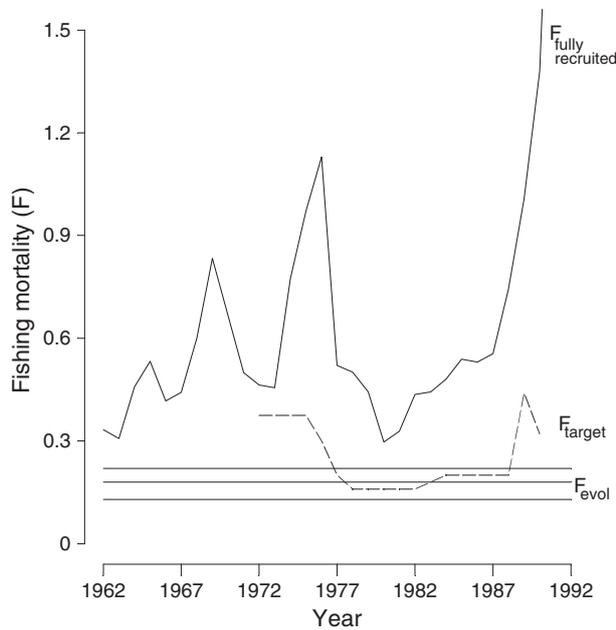
Figure 6 Temporal variation in fishing mortality and fishing mortality targets for northern Atlantic cod. Trends are shown for the estimated fully recruited fishing mortalities experienced by cod (solid line) and for management targets (F_{target}; dashed line). Data are from Shelton (1998). The horizontal solid lines depict estimates of F_{evol} for northern cod fisheries for otter trawl ($F_{evol} = 0.13$), handline ($F_{evol} = 0.18$), and gillnets/traps ($F_{evol} = 0.22$).

in excess of these estimates of F_{evol} (Fig. 6); that is, F was always greater than that required for fisheries-induced evolution to favour earlier maturity.

Avoiding fisheries-induced evolution: implications for F and gear selectivity

In addition to estimating catch and decline probabilities for the selectivities actually experienced by northern cod (Myers and Hoenig 1997), one can vary the ages at which fish are fully recruited to the various types of fishing gear to identify those combinations of gear and fishing mortality most likely to achieve traditional fisheries management objectives. The catch selectivity curves used in this analysis (Fig. 7), based on the data provided by Myers and Hoenig (1997), were such that the age at which fish were fully recruited to the fishing gear (i.e., the youngest age at which probability of capture was equal to 1) was either 4, 6, or 8 years.

For many fisheries managers, the most important of these objectives is the maximization of catch. Irrespective of the type of fishing gear, catch was highest when age at maturity equalled 7 years and when fish were fully recruited to each fishing gear at age 8 year (Table 1), the same age at which the second objective of minimizing $\Pr(R_0 < 1)$ was most likely to be attained. At this age at full-gear recruitment, the fishing mortality above which fisheries-induced evolution was predicted to occur differed considerably among gear types. F_{evol} was lowest for the knife-edged selectivity curve associated with otter trawls, intermediate for the symmetrical dome-shaped selectivities characteristic of gillnets and handlines, and highest for the asymmetrical, steeply rising dome-shaped selectivity associated with cod traps.
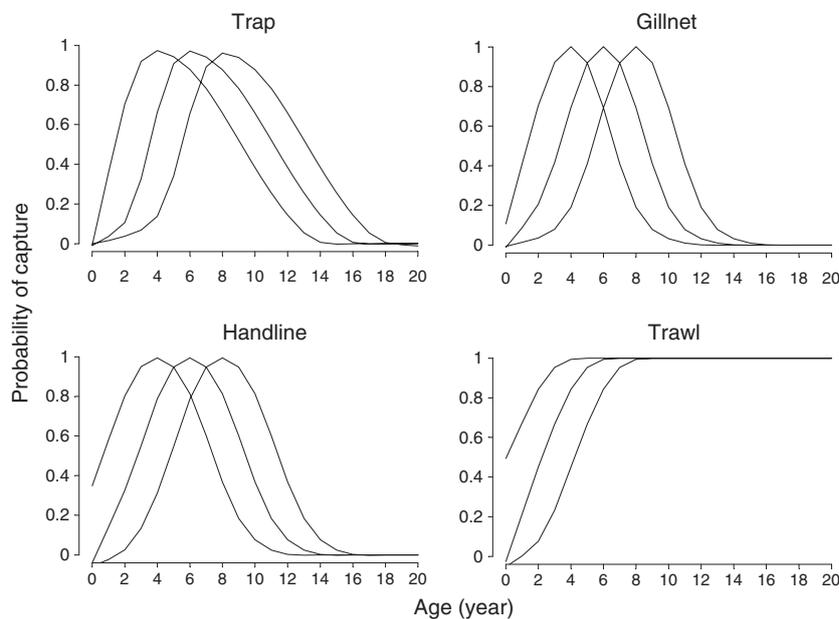

Figure 7 Simulated selectivity curves for trap, gillnet, handline, and trawl fisheries for northern Atlantic cod. The functions are based on the fitted curves shown in Fig. 2, and reflect ages of full recruitment to each fishing gear of 4, 6, and 8 years.

Table 1. Estimates of yield per cohort, probability of population decline [$\Pr(R_0 < 1)$], and F associated with four types of northern cod fishing gear, three ages at full recruitment to the gear, and ages at maturity, averaged across fishing mortalities of $F = 0.1, 0.2, 0.3, 0.4, 0.5,$ and 0.6.

Gear	Age at full recruitment to gear (year)	Age at maturity (year)	Average yield for $F_{0.1-0.6}$ (tonnes per 10^{12} eggs)	Average $\Pr(R_0 < 1)$ for $F_{0.1-0.6}$	F_{evol}
Trap	4	4	6186	0.141	0.21
		7	9694	0.326	
	6	4	6243	0.005	0.19
		7	14 094	0.145	
	8	4	5092	0.003	0.31
		7	15 897	0.021	
Gillnet	4	4	5240	0.168	0.36
		7	7004	0.226	
	6	4	6180	0.079	0.20
		7	10 155	0.295	
	8	4	6069	0.006	0.21
		7	13 830	0.115	
Handline	4	4	5320	0.205	0.32
		7	7266	0.270	
	6	4	6189	0.169	0.19
		7	9868	0.381	
	8	4	6377	0.010	0.18
		7	13 810	0.187	
Trawl	4	4	7054	0.473	0.14
		7	11 600	0.612	
	6	4	7712	0.062	0.14
		7	14 385	0.485	
	8	4	7268	0.004	0.16
		7	17 442	0.105	

Discussion

The present study represents an attempt to examine the management implications of fisheries-induced evolution by integrating common fisheries management objectives with that of avoiding selection responses by fish to differential fishing mortalities. One means of achieving this was through the introduction of F_{evol}, which identifies a threshold level of fishing mortality that fishery managers should wish to avoid. As a limit reference point, F_{evol} is similar to those currently used by fisheries scientists in the US (F_{limit}) and by International Council for the Exploration of the Sea (ICES) scientists (F_{lim}) to identify the maximum fishing mortality deemed permissible under a harvest control rule (Cadrin and Pastoors 2008). Relative to knife-edged selectivities, the analysis undertaken here identifies dome-shaped selectivity curves as those less likely to effect harvest-induced evolution, with narrow selection functions (i.e., a high degree of leptokurtosis) being preferable to broad dome-shaped

curves. The application of an age-structured life-history model to estimate the fitness associated with early- and late-maturing genotypes at different fishing mortalities exacted by different fishing gears provides a novel means of exploring the degree to which changes in age at maturity may be partly attributable to a genetic response to fishing. More importantly, perhaps, is the conclusion that avoidance of fisheries-induced evolution can be achieved simply by controlling fishing mortality alone. Thus, changes to fisheries management that might be perceived to be socio-economically or politically problematic (e.g., changes to catch selectivity-functions through changes to fishing gear, or the establishment of no-take zones) may not be necessary if managers and politicians are willing to establish and adhere to harvest control rules that incorporate evolutionarily risk-averse limit reference points for fishing mortality.

The levels of fishing mortality experienced by northern cod since at least the early 1960s appear to have been more than sufficient to generate an evolutionary change in age at maturity. From 1962 to 1991, otter trawls accounted for 50% to 90% of the overall catch of northern cod (Lilly et al. 2003). The estimate of F_{evol} for trawls is 0.13, well below the fishing mortality actually experienced by this stock (range: 0.30 to 3.42; Shelton 1998), as were the estimates of F_{evol} for traps, gillnets, and handlines. This conclusion is consistent with Hutchings' (1999) hypothesis and Olsen et al.'s (2004) supportive analysis that exploitation has generated evolutionary change in northern cod. Despite minimal fishing in the offshore waters inhabited by northern cod since 1992, the levels of F generated by inshore fisheries from 1998 through 2007 (ranging between 0.02 and 0.46, depending on area; DFO 2008) may have been sufficiently high to prevent a significant relaxation of the selection pressures favouring early maturity, thus reducing the rate at which an evolutionary reversal to later maturity might occur.

The over-exploitation of northern cod resulted in fishing mortalities that appear to have been considerably greater than those required to effect evolutionary change. However, it is instructive to note that fisheries-induced evolution would have been predicted to have occurred even if the targeted fishing mortalities set by management had been attained. Between 1972 and 1992, the mortality rates set by fishery managers that were intended to provide for sustainable harvests were, for the most part, based on a percentage of two target reference points: F_{max} (the fishing mortality that maximizes yield per recruit) and $F_{0.1}$ (the fishing mortality which corresponds to a slope on the yield-per-recruit curve that is one-tenth the initial slope; $F_{0.1} = 0.2$ for northern cod) (Shelton 1998). The fishing mortalities associated with F_{max} (0.35–0.40 for northern cod) greatly exceed the estimates of F_{evol}

(0.13–0.22) for the fishing gear used to catch northern cod. By contrast, had the $F_{0.1}$ target of 0.2, or the lower target of $F = 0.16$ (1978–1983) been achieved, these fishing mortalities would have been sufficiently low to have prevented fisheries-induced evolution by all fishing gears except the otter trawl.

Although the analyses presented here represent a novel approach to the study of fisheries-induced evolution, the conclusions resulting therefrom are consistent with previous research on the management implications of fisheries-induced evolution. Ernande et al. (2004), for example, emphasized the fundamental importance that fishing mortality *per se*, independent of gear selectivity, has on the magnitude of fisheries-induced evolution. They, in addition to Law and Grey (1989) and Heino (1998), argued that selection for earlier maturity can be minimized by selectively harvesting larger, older fish and concomitantly minimizing the F on immature fish. Minimal levels of fishing mortality on younger, smaller fish increases the probability that individuals will survive to reproduce and be available to the fishery in greater numbers at older ages. The simulations presented here found that catches were maximized, and selection against delayed maturity minimized, when fish were fully recruited to fishing gears at relatively old ages (8 year, as opposed to 4 or 6 year). The conclusion that selection for earlier maturity can be reduced by harvesting with gear characterized by dome-shaped selectivities has been made implicitly by Conover and Munch (2002), and explicitly by Law (2007) and Jørgensen et al. (2009). Dome-shaped selectivity curves provide protection for both younger and older fish.

A comparison of F_{evol} among gear types suggests that some are more likely to effect fisheries-induced evolution than others. This can be attributed to differences in selectivity curves and in the ages at which fish are fully recruited to the gear. In the northern cod fishery, for example, the highest yields are predicted to occur when fish are fully recruited to the gear at age 8 year. At this age of full recruitment, the highest value of F_{evol} was that associated with the cod trap ($F_{evol} = 0.31$), suggesting that this gear would be the one least likely to generate an evolutionary shift to earlier maturity. However, as promising a gear as this might seem, traps can only be deployed in comparatively shallow inshore waters; they cannot be used offshore (Hutchings and Ferguson 2000). The second highest values of F_{evol} were those associated with gillnets (0.21) and handlines (0.18). (The slightly higher estimate of F_{evol} associated with gillnets can be attributable to their steeper selectivity curve.) However, widespread use of gillnets would be unwise from a conservation perspective. Gillnets are readily lost for a variety of reasons, raising concerns that many continue to 'fish'

(as 'ghost' nets) long afterwards. In addition to the poorer quality of fish obtained from gillnets, the discarding of unwanted fish increases steadily with the time during which nets are deployed (i.e., soak time), particularly as the gear is set further and further from shore (Hutchings and Ferguson 2000), resulting in higher catch misreporting. By contrast, the quality of handline-caught fish tends to be best because the fish are alive when they are landed and their bodies are not compressed, or otherwise stressed physically, because they are landed singly rather than in the large groups characteristic of trawl and trap gear. All else being equal, otter trawls are predicted to have the highest probability of generating fisheries-induced evolution towards earlier maturity, based on their estimated F_{evol} (0.16). [Although not explicitly modelled here, the F_{evol} associated with longline gear is likely to be similar to that associated with otter trawls because of their similar, knife-edged selectivity functions (Myers and Hoenig 1997).]

The present study suggests that there is utility in developing evolutionarily-sensitive fishing mortality reference points, such as F_{evol}. Once estimated for a greater number of stocks, it would be instructive to examine how metrics of F_{evol} compare to the magnitude of traditional reference points, such as F_{msy} (the F at which maximum sustainable yields are obtained), F_{max}, and $F_{0.1}$. For northern cod, the simulations presented here suggest that F_{evol} for fixed gears is generally higher than $F_{0.1}$ (i.e., 0.2), implying that harvest control rules that utilize $F_{0.1}$ (or some percentage thereof; Walters and Maguire 1996) as a reference point may be sufficient to minimize the probability of fisheries-induced evolution. Clearly, there are alternative means of estimating F_{evol}. One could incorporate, for example, a positive association between hatching rate/egg survival and age at maturity (e.g., Trippel 1998; Murawski et al. 2001; Berkeley et al. 2004), which would likely have the effect of increasing F_{evol}, all else being equal. One could also estimate F_{evol} associated with alternative ages at maturity, alternative sizes at maturity, or alternative rates of individual growth; F_{evol} need not be linked solely with changes to particular ages at maturity, as illustrated here. And one could also examine how F_{evol} is influenced by a greater range in catch selectivity curves. It should also be acknowledged that the present analysis pertains to fisheries selection on body size, as opposed to traits related to growth rate, energy acquisition, or behaviour.

In general, it seems unlikely that fisheries-induced selection for earlier maturity will have positive consequences either for fish or for fisheries. Unless it is associated with considerably faster rates of individual growth and larger sizes-at-age (Hutchings 1999), earlier maturity will almost certainly lead to reduced yields (Law and Grey 1989; Heino 1998; Conover and Munch 2002; Ernande

et al. 2004; present study), lower rates of population growth and, thus, reduced resilience (Hutchings 2005; present study). The current work underscores the prediction that fishing gear with dome-shaped selectivities will reduce selection against late maturity; the narrower the range of age classes vulnerable to fishing, the greater the protection afforded to young and old individuals alike.

A primary finding of the present study is that management strategies designed to minimize evolutionary change (e.g., Jørgensen et al. 2007) are entirely consistent with traditional management objectives, such as the establishment of fishing mortality reference points, the maximization of yield, and the minimization of the probability of population decline. Depending on the phenotypic target(s) of fisheries-induced evolution, adherence to conventional reference points and appropriate harvest control rules may be sufficient to safeguard against evolutionary change.

Acknowledgements

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