ORIGINAL ARTICLE

Consequences of sexual selection for fisheries-induced evolution: an exploratory analysis

Jeffrey A. Hutchings[1] and Sherrylynn Rowe[2]

1 Department of Biology, Dalhousie University, Halifax, NS, Canada
2 Fisheries and Oceans Canada, Bedford Institute of Oceanography, Dartmouth, NS, Canada

Abstract

Reproductive behaviour and mating system complexity may influence fisheries-induced evolution. Mate choice and intrasexual competition might favour late-, large-maturing genotypes in contrast to the selection imposed by many fisheries. Here, we simulate changes to the mean and variance in body size of Atlantic cod (*Gadus morhua*) concomitant with increased fishing intensity. Comparing selection differentials (S) for length under the assumptions that size does and does not affect reproductive success, we find that the strength of selection for smaller body size associated with increased fishing pressure depends on: (i) the initial variance in body size; (ii) changes to the variance in size with increasing fishing intensity; and (iii) the influence of size on reproductive success. If the initial variability in length is sufficiently high and its coefficient of variation (CV) increases with fishing intensity, the predicted evolutionary shift towards smaller size generated by fishing is less than that expected under the assumption that reproductive success is independent of size. However, if size influences reproduction and if the CV in body size declines as fishing pressure increases, a trend that may be characteristic of many intensively exploited populations, the strength of selection for smaller size is predicted to be comparatively rapid. We conclude that fisheries-induced evolution can be influenced by changes to the mean and variance of traits under sexual selection, and that the benefits of maintaining broad phenotypic variability in traits such as body size may be greater than previously thought.

Introduction

The potential for fishing to cause evolutionary change is not appreciably different from other forms of predator-induced mortality, given its propensity for generating differential survival among genotypes. Typically, the probability of death by fisheries-induced predation increases with the age, size and growth rate of the prey (Law 1991; Stokes et al. 1993). Given that these traits are heritable (Roff 2002) and that fishing mortality often exceeds that effected by the predator in most natural predator-prey relationships, fishing has almost certainly generated evolutionary changes in at least some harvested populations (Stokes and Law 2000; Law 2007). Based on studies of a number of heavily fished species (Dieckmann and Heino

2007; Jorgensen et al. 2007; Hutchings and Fraser 2008), most notably Atlantic cod (*Gadus morhua*) (Law and Rowell 1993; Hutchings 1999, 2005; Heino et al. 2002; Sinclair et al. 2002; Olsen et al. 2004; Swain et al. 2007), it seems reasonable to conclude that the likelihood of fisheries-induced evolution increases with the ratio of fishing mortality (F) to natural mortality (M), the degree to which fishing is nonrandom with respect to phenotype, the heritability of the trait(s) that differentially affect an individual's probability of capture, and the length of time over which fishing has occurred.

Studies of fisheries-induced evolution have focused on traits hypothesized to differentially affect an individual's probability of capture. For example, reductions in age and size at maturity in exploited populations (Trippel

1995; Hutchings and Baum 2005) have been attributed, in part, to a direct selection response generated by harvesting (Dieckmann and Heino 2007; Hutchings and Fraser 2008). A subject that has received considerably less attention is the potential for unanticipated selection responses that may accelerate or impede the rate of evolutionary change generated by exploitation. Correlational selection can be of import such that the overall genetic response is greater or less than would be predicted from analyses of single traits in isolation (Hard 2004; Walsh et al. 2006; Law 2007).

Fisheries-induced evolution might, for example, be affected by how exploitation influences the mean and variance of traits under sexual selection. Although the question of whether fishing affects mating systems has received comparatively little attention (Vincent and Sadovy 1998; Rowe and Hutchings 2003; Kokko and Rankin 2006), there is reason to believe that the relative magnitude of phenotypic selection generated by variation in mating or reproductive success (sexual selection) is comparable to or greater than that attributable to variation in survival and/or fecundity (natural selection). Kingsolver et al. (2001), for example, reported the median magnitude of sexual selection, as reflected by directional selection gradients, to be more than twice that of natural selection among diverse plant and animal taxa.

The change in a trait resulting from selection, i.e. the selection response (R), is a function of the heritability of the trait (h^2) and the selection differential, S, i.e. the difference in the mean trait value amongst individuals prior to the selection event and the mean trait value amongst those that survive the selection event. When quantifying S in this manner, one implicit assumption is that the probability that surviving individuals contribute genes to future generations is independent of the trait in question. However, if the probability of contributing genes during spawning is influenced by a trait under fisheries-induced selection, such a simple comparison might lead to an under- or over-estimate of S, depending on the ways in which the mean and variance of the trait in question affect reproductive success.

Here, we simulate changes to the mean and variance in body size concomitant with increased fishing intensity. One of our primary objectives is to compare selection differentials estimated under the assumption that body size has no influence on reproductive success with those estimated under the assumption that body size does affect the probability of passing one's genes on to future generations. Thus, we are interested in comparing the selection differentials of *potential* spawners (S_P) with the selection differentials of *actual* spawners (S_A). We used Atlantic cod as the species of interest in our simulations, in part because of empirical evidence that body

size influences reproductive success (Rowe et al. 2007, in press) and because of the considerable amount of work that has focused on the conservation biology and potential for fisheries-induced evolution in this species (Hutchings and Myers 1994; Heino et al. 2002; Barot et al. 2004; Hutchings and Reynolds 2004; Swain et al. 2007).

Materials and methods

Distributions of body size in the absence and presence of fishing

To examine the influence of fishing on the body sizes of potentially spawning individuals, we compared the mean of the size frequency distribution in the absence of fishing with those under increasingly intense levels of fishing, i. In all scenarios, the sizes of spawning individuals were sampled from a lognormal distribution to reflect the observation that sizes of reproductive individuals tend to be positively skewed (e.g. Fig. 1A). The minimum length of spawning individuals was set at 20 cm.

We examined changes to selection differentials under eight levels of fishing intensity. In the absence of fishing ($i = 0$), the mean size of potentially spawning individuals was set at 75 cm and the standard deviation set at either 18.7 or 25.0 cm, which correspond to coefficients of variation (CVs) of 0.25 and 0.33 (Fig. 1A) respectively. Increases in fishing intensity (i) were modelled by incrementally decreasing the mean size of potential spawners, after fishing, in 5 cm intervals from 70 (at $i = 1$) to 40 cm (at $i = 7$). The length-frequency distributions of spawners, from which the means reported in Table 1 were estimated, were determined by 10 000 samples taken at random from these lognormal distributions.

Changes to the variance in body size with changes to fishing intensity

As fishing intensity increased, the CV in body size was either held constant, allowed to increase, or allowed to decrease (Table 1; Fig. 1B–D). When the CV for body size is allowed to increase with increased fishing intensity, this implies that the distribution of body sizes takes on an increasingly positive skew. Such a trend in CV might be expected in fisheries for which the probability of capture declines with body size. Such a change in catchability might be attributable to the type of fishing gear deployed or to a refuge (natural or regulated) that provides increasingly greater protection with increased body size. By contrast, reductions in CV for body size with increased fishing intensity imply that relatively large individuals are being removed at a faster rate from the population than are comparatively small individuals.
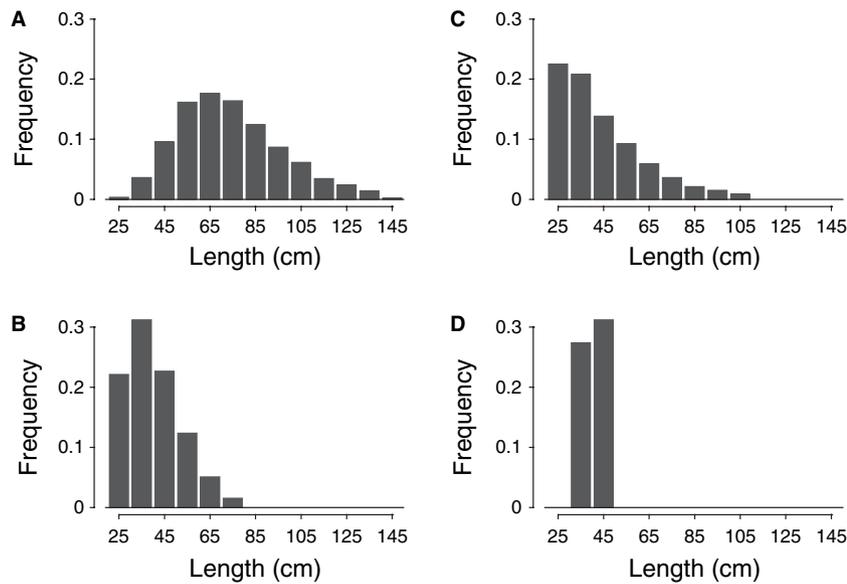
Figure 1 Simulated length-frequency distributions of Atlantic cod under four fishing intensity scenarios (see text for full details). (A) No fishing (fishing intensity, $i = 0$), coefficient of variation (CV) in body size = 0.33; (B) Fishing intensity, $i = 7$ (maximum level), CV(body size) = 0.33, having remained constant with increases in fishing intensity; (C) Fishing intensity, $i = 7$ (maximum level), CV(body size) = 0.62, having increased with increases in fishing intensity; and (D) Fishing intensity, $i = 7$ (maximum level), CV(body size) = 0.04, having declined with increases in fishing intensity.

Incorporating an effect of body size on reproductive success

Our assumption that body size influences reproductive success in Atlantic cod is based on data obtained from several spawning experiments, the details of which are provided elsewhere (Rowe et al. 2007, in press). In brief, four groups of Atlantic cod from three geographically disparate regions of the Northwest Atlantic were allowed to spawn undisturbed in a very large tank (684 m^3). Group sizes ranged between 52 and 93 individuals. Parentage was determined from microsatellite DNA analyses (based on allelic variability at seven microsatellite loci) undertaken on random samples of eggs collected daily throughout the experimental spawning periods in 2001 and 2002.

To model the influence of body size on reproductive success, we pooled data on body length and reproductive success (defined as the total number of genotyped offspring) for all individuals from all four spawning groups (Rowe et al. 2007, in press). This yielded data for 258 individuals and 8913 offspring. We then grouped length data based on the number of standard deviations (SDs) they fell from the mean (i.e. mean − 2SD, mean − 1SD, mean + 1SD, mean + 2SD, mean + 3SD, mean + 4SD). The resulting plot of reproductive success against body size (the mid-points of the binned body sizes within each of the six standard deviation categories) is shown in Fig. 2. Based on the curvilinear function that best fit these

data, we estimated individual reproductive success (Y, number of offspring), as a function of body size (X, in cm), to be:
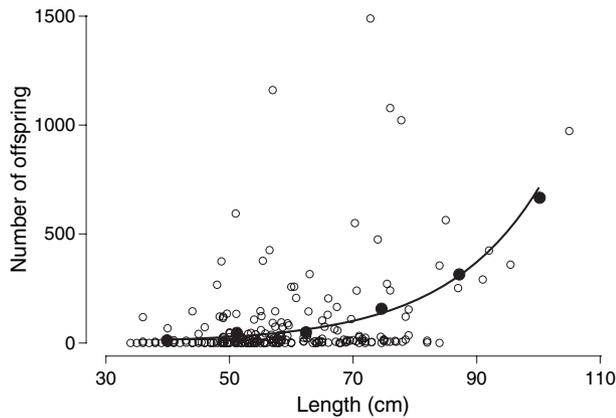
$$Y = \exp(0.0864 + 0.0648X) \qquad (1)$$

Based on the relationship described by Eqn (1), the reproductive success of a 100 cm individual would be 711 offspring, that of a 50 cm cod would be 28 offspring, whereas that for the minimum sized individual considered in our simulations (20 cm) would be four offspring. We arbitrarily set the maximum reproductive success to be that estimated for 100 cm individuals. However, rather than use these absolute values, we calculated the reproductive success of each individual relative to that of a 100 cm individual. Thus, the estimates of relative reproductive success for individuals 100, 50 and 20 cm in length were 1.000, 0.039 and 0.006 respectively.

Our estimates of the mean size of potential spawners at fishing intensity i ($\mu_{P(i)}$) were calculated from the frequency distribution of 10 000 randomly drawn samples from lognormal distributions whose mean and variance were those specified by the parameters in Table 1. The mean size of actual spawners at fishing intensity i ($\mu_{A(i)}$) was calculated from the same distributions, but the frequencies of each body size were weighted by their estimated relative reproductive success.

Table 1. Output from the modelling analyses. Parameters: CV = coefficient of variation in length of potential spawners; fishing intensity, ranging from 0 (no fishing) to 7 (highest fishing intensity); mean length (cm) of potential spawners after experiencing fishing at intensity i, $\mu_{P(i)}$; mean length (cm) of actual spawners after experiencing fishing at intensity i, $\mu_{A(i)}$; selection differential (cm) after fishing at intensity i, but prior to spawning, $S_{P(i)}$; selection differential (cm) after fishing at intensity i and after spawning, $S_{A(i)}$.

| Change in CV (body size) with fishing intensity (i) | CV | Fishing intensity (i) | Mean size of potential spawners $\mu_{P(i)}$ | Mean size of actual spawners $\mu_{A(i)}$ | Selection differentials | |
					Post fishing $S_{P(i)}$	Post spawning $S_{A(i)}$
Constant	0.33	0	74.2	97.3	0	0
		1	68.6	91.2	−5.6	−6.1
		2	63.7	87.1	−10.5	−10.2
		3	59.4	82.5	−14.8	−14.8
		4	54.3	75.2	−20.0	−22.1
		5	49.3	67.7	−24.9	−29.6
		6	44.6	58.9	−29.6	−38.4
		7	39.9	50.4	−34.3	−46.9
Constant	0.25	0	74.0	90.3	0	0
		1	69.3	85.8	−4.7	−4.5
		2	64.5	80.3	−9.5	−10.0
		3	59.7	74.8	−14.3	−15.5
		4	54.3	66.6	−19.7	−23.7
		5	49.6	59.5	−24.4	−30.8
		6	44.6	52.4	−29.4	−37.9
		7	39.5	45.7	−34.5	−44.6
Increasing	0.33	0	74.3	97.1	0	0
	0.36	1	68.6	94.1	−5.7	−3.0
	0.38	2	63.7	91.9	−10.5	−5.2
	0.42	3	58.5	88.7	−15.8	−8.4
	0.45	4	54.6	87.3	−19.7	−9.8
	0.50	5	49.5	83.9	−24.8	−13.2
	0.56	6	46.8	81.1	−27.5	−16.0
	0.62	7	42.3	75.6	−32.0	−21.5
Increasing	0.25	0	74.1	93.5	0	0
	0.27	1	69.3	87.6	−4.8	−5.9
	0.29	2	64.4	84.2	−9.7	−9.3
	0.31	3	59.1	80.5	−15.0	−13.0
	0.34	4	54.2	76.2	−19.9	−17.3
	0.37	5	49.2	71.8	−24.9	−21.7
	0.42	6	44.3	65.9	−29.8	−27.6
	0.47	7	41.1	62.2	−33.0	−31.3
Decreasing	0.33	0	73.7	96.5	0	0
	0.30	1	68.8	89.6	−4.9	−6.9
	0.28	2	64.4	82.4	−9.3	−10.4
	0.24	3	59.5	72.8	−14.2	−23.7
	0.21	4	54.6	63.5	−19.1	−33.0
	0.16	5	49.9	54.1	−23.8	−42.4
	0.10	6	44.9	46.2	−28.8	−50.3
	0.04	7	40.0	40.1	−33.7	−56.4
Decreasing	0.25	0	74.2	90.8	0	0
	0.23	1	69.2	83.7	−5.0	−7.1
	0.21	2	64.7	76.4	−9.5	−14.4
	0.19	3	59.6	68.0	−14.6	−22.8
	0.16	4	54.6	59.4	−19.6	−31.4
	0.13	5	49.9	52.5	−24.3	−38.3
	0.08	6	44.9	45.7	−29.3	−45.1
	0.03	7	40.0	40.1	−34.2	−50.7

Figure 2 Relationship between Atlantic cod length and number of randomly genotyped offspring, based on data obtained for individuals (open circles) from genetic and behavioural spawning experiments undertaken in the laboratory. Length data were pooled, based on the number of standard deviations (SDs) they fell from the mean (i.e. mean − 2SD, mean − 1SD, mean + 1SD, mean + 2SD, mean + 3SD, mean + 4SD). The average length of cod corresponding to these SD groupings, and the average number of offspring produced by these six groups, are presented as solid circles. The curved function represents the relationship between number of offspring (Y) and length (X) fitted to the solid circles, i.e. $Y = \exp(0.0864 + 0.0648X)$.

To facilitate the presentation of our results, we calculate S_{diff}, the difference in S between actual and potential spawners, each of which is corrected for differences in mean spawner body size in the absence of fishing ($\mu_{(0)}$), and designated S_A^* and S_P^*s respectively. That is, the difference in selection differentials at fishing intensity i is given by

$$S_{\text{diff}(i)} = S_{A(i)}^* - S_{P(i)}^* \tag{2}$$

or

$$S_{\text{diff}(i)} = ((\mu_{A(0)} - \mu_{A(i)})/\mu_{A(0)}) - ((\mu_{P(0)} - \mu_{P(i)})/\mu_{P(0)}) \tag{3}$$

Thus, in the present context, and assuming that heritability is constant, positive values of S_{diff} are interpreted to mean that the selection response for smaller body size is greater when size is assumed to influence reproductive success.

Results

Influence of nonrandom reproductive success on selection differentials

Selection differentials for body size became increasingly negative as our simulated fishing intensities increased and as the average body size among surviving individuals decreased (Table 1). Among potential spawners, S_P generally decreased by 5 cm with incremental increases in fish-

ing intensity. Although the selection differentials among actual spawners (S_A) also declined with increasing fishing intensity, the rate at which they did so often differed from the rates of decline in S_P.

Influence of variation in body size on selection differentials

We considered three means by which the CV in body size might change with changes to fishing intensity.

When the CV for body size was held constant as fishing intensity increased, S_A^* was often less than S_P^*, meaning that selection differentials for reduced body size were lower when body size influenced reproductive success than when it did not (Fig. 3). This was particularly evident at the greater of the CVs (0.33) considered here. Nonetheless, S_{diff} was relatively small compared with those estimated when the CV in size increased or declined with increased fishing.

Increases in CV concomitant with increased fishing pressure would result in an increasingly positive skew in the frequency distributions for body size. Under these circumstances, selection differentials among actual spawners (S_A^*) were always lower than those calculated for potential spawners (S_P^*) with the divergence increasing with increased fishing intensity (Fig. 4). The greater the initial CV in body size, the greater the divergence.

A reduction in the CV for body size with increased fishing pressure implies that larger individuals are
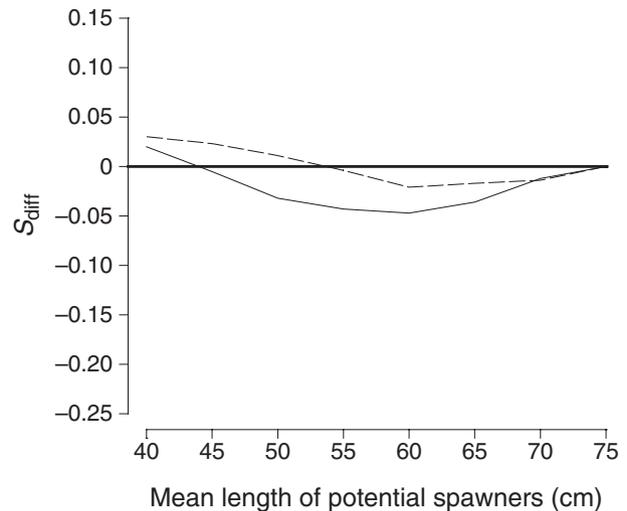
Figure 3 Difference in selection differentials (S_{diff}) for reduced body size between actual and potential spawning Atlantic cod at various levels of fishing intensity. Fishing intensity level increases from right (75 cm) to left (40 cm) along the x-axis. As fishing intensity increased, the coefficient of variation (CV) in body size remained constant (solid line: initial CV in body size = 0.33; dashed line: initial CV in body size = 0.25).
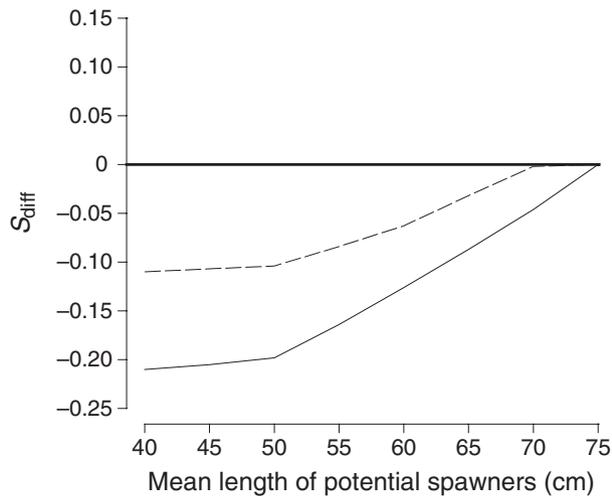
Figure 4 Difference in selection differentials (S_{diff}) for reduced body size between actual and potential spawning Atlantic cod at various levels of fishing intensity. Fishing intensity level increases from right (75 cm) to left (40 cm) along the x-axis. As fishing intensity increased, the coefficient of variation (CV) in body size also increased (solid line: initial CV in body size = 0.33; dashed line: initial CV in body size = 0.25).

being removed at a faster rate than comparatively small individuals. Under these circumstances, S_A^* always exceeded S_P^* in our simulations (Fig. 5). The divergence in selection differential increased with fishing intensity,
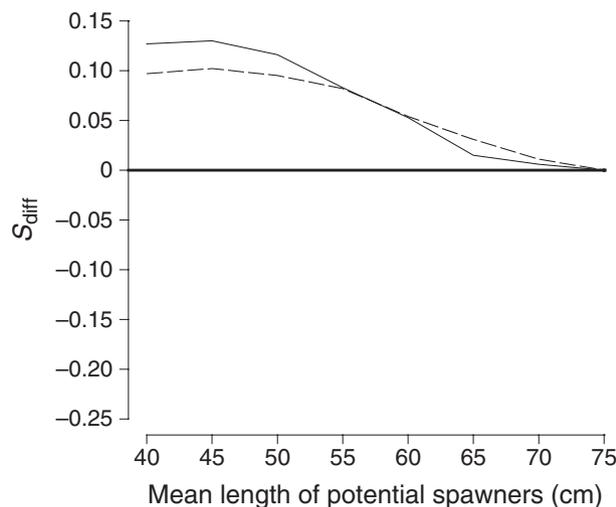

Figure 5 Difference in selection differentials (S_{diff}) for reduced body size between actual and potential spawning Atlantic cod at various levels of fishing intensity. Fishing intensity level increases from right (75 cm) to left (40 cm) along the x-axis. As fishing intensity increased, the coefficient of variation (CV) in body size decreased (solid line: initial CV in body size = 0.33; dashed line: initial CV in body size = 0.25).

implying that the selection for smaller body size imposed by fishing is greater when reproductive success increases with body size then when it does not. The initial CV in body size in the absence of fishing had relatively little effect at the lower fishing intensities. At high intensities, the greater the initial CV in body size, the greater the divergence.

Discussion

The primary objective of this exploratory analysis was to examine the potential for sexual selection to accelerate or decelerate fisheries-induced evolution. Our simulations suggest that, as fishing intensity increases, selection differentials for body size can be influenced by: (i) the variance in body size in the absence of fishing; (ii) changes to the variance in body size with increased fishing pressure; and (iii) incorporation of an effect of body size on reproductive success. If the initial variation in size is sufficiently high, and if the CV in size increases with fishing intensity, the strength of fisheries-induced selection for smaller body size is predicted to be less than that under the assumption that size has no effect on reproductive success. However, if the CV in size declines as mean body size decreases with increased fishing pressure, a trend that may not be uncommon within intensively harvested populations, e.g. Newfoundland's northern cod (Rowe and Hutchings 2003), the strength of selection for smaller size is predicted to be greater than that estimated under the assumption that size has no effect on reproduction. By comparison, estimates of S were relatively insensitive to a size effect on reproduction when the CV remained constant with increased fishing pressure. Although our work pertained to a single trait (body size) modelled for a particular species of fish (Atlantic cod), our finding that fisheries-induced evolution can be affected by the variance of a trait hypothesized to be under sexual selection may have general implications.

As with all such analyses, the confidence one can have in our results depends on the strengths and weaknesses of our approach, our assumptions and the empirical basis of our parameter estimates. Although the modelling approach is technically simple, it seems intuitively reasonable. Nonetheless, the model structure could be made more complex, the number of estimated parameters increased, and a variety of other traits examined. We have assumed that the influence of body size on reproductive success is based on absolute rather than relative body size. That is, we have assumed that large individuals have higher reproductive success because they are large in absolute terms, rather than simply being larger than others in the population. If we had undertaken our analyses on a cohort basis, we would anticipate that our estimates

of S would have been less than those calculated here, but the qualitative nature of our results should remain unchanged. Similarly, the analyses might have been partitioned by sex. Our work suggests that the influence of sexual selection for body size on the rate of fisheries-induced evolution would be greater in the sex for which size is the greater determinant of reproductive success. The demographic consequences to exploited populations of such a sex bias in evolutionary change warrant study.

Our work may have implications for the study of fisheries-induced evolution insofar as our simulations draw attention to the potential limitations of implicitly assuming that reproductive success is random amongst the breeders that survive a selection event. Swain et al. (2007) explicitly identified this assumption, and its potential caveats, in their recent exploratory analysis of fisheries-induced evolution on the growth rate of cod in the Southern Gulf of St Lawrence (Canada). Their means of estimating S was to compare the mean size-at-age of individuals within a cohort after the selection event with the mean size of individuals from the same cohort at a much younger age before the effects of fishing had been experienced. If reproductive success is random with respect to size-at-age, then a comparison of the means before and after selection should yield a reasonably good approximation of S. If reproductive success increases with size, however, our work suggests that sexual selection for increased body size might counter or offset (to varying degrees) the selection against larger size effected by fishing, depending on how the CV in size changes with fishing mortality.

One important prediction to emerge from our work is that maintenance of variability in body sizes, particularly the maintenance of large individuals, might serve to reduce the strength of fisheries-induced selection for smaller body size. Our simulations indicate that the greater the variation in length, relative to the mean, the slower the rate of evolutionary change in body size. This draws attention to the fundamental importance of maintaining, or rebuilding, a breadth of body sizes and age classes within exploited populations. The necessity of doing so has been articulated by others as a means of reducing the influence of fisheries-induced evolution (Conover and Munch 2002; Law 2007) and as a means of increasing the probability of persistence of harvested populations (e.g. Birkeland and Dayton 2005).

Importantly, we find, under some circumstances, that the evolutionary response in a trait influenced by fisheries can be exacerbated by other forms of selection. This conclusion is consistent with that reached by De Roos et al. (2006) who provide another example of how additional factors might alter the evolutionary response expected from fishing selection alone. They used a size-structured, consumer-resource model that incorporated quantitative genetics and life history to examine genetic responses in age and size at maturity in exploited populations. Based on their finding that evolutionary trends to earlier maturity resulting from fisheries that target late-maturing individuals can be associated with step-wise, 1-year shifts in age at first reproduction, De Roos et al. (2006) hypothesized that early maturation at small sizes and late maturation at large sizes may represent alternative evolutionarily and ecologically stable states.

Our simulations suggest that the rate of evolutionary change in traits linked to reproductive success may be more rapid than previously thought when the CV for these traits declines with increased fishing mortality. This might account for the comparatively rapid reductions in age and size at maturity that have been documented in many exploited fishes (Trippel 1995; Hutchings and Baum 2005). Newfoundland's northern cod, for example, experienced substantive reductions in both of these life-history traits (Olsen et al. 2004; Hutchings 2005) during a period when the population declined more than 99% (Hutchings and Myers 1994; Hutchings and Reynolds 2004). Between 1962 and 1991, the CV for body size, as determined from commercial fishery catches, is estimated to have declined 55% (Rowe and Hutchings 2003), and northern cod continue to exhibit no substantive signs of recovery (DFO 2007).

We conclude that the rate of harvest-induced evolution can be affected by fishery-generated changes in the mean and variance of traits under sexual selection. In this regard, our work contributes to an emerging body of literature that is examining how correlational selection can generate unanticipated responses to the rate of evolutionary change effected by exploitation (Hard 2004; Walsh et al. 2006; Law 2007).

Acknowledgements

Literature cited

Barot, S., M. Heino, L. O'Brien, and U. Dieckmann. 2004. Long-term trend in the maturation reaction norm for two cod stocks. *Ecological Applications* **14**:1257–1271.

Birkeland, C., and P. K. Dayton. 2005. The importance in fishery management of leaving the big ones. *Trends in Ecology and Evolution* **20**:356–358.

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

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* **273**:1873–1880.

DFO. 2007. *Stock Assessment of Northern (2J3KL) Cod in 2007.* Department of Fisheries and Oceans, Canadian Science Advisory Secretariat Science Advisory Report 2007/018, Ottawa, Canada.

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

Hard, J. J. 2004. Evolution of chinook salmon life history under size-selective harvest. In A. P. Hendry, and S. C. Stearns, eds. *Evolution Illuminated: Salmon and their Relatives*, pp. 315–337. Oxford University Press, Oxford.

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

Hutchings, J. A. 1999. The influence of growth and survival costs of reproduction on Atlantic cod, *Gadus morhua*, population growth rate. *Canadian Journal of Fisheries and Aquatic Sciences* **56**:1612–1623.

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

Hutchings, J. A., and J. K. Baum. 2005. Measuring marine fish biodiversity: temporal changes in abundance, life history and demography. *Philosophical Transactions of the Royal Society B* **360**:315–338.

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 R. A. Myers. 1994. What can be learned from the collapse of a renewable resource? Atlantic cod, Gadus morhua, of Newfoundland and Labrador. *Canadian Journal of Fisheries and Aquatic Sciences* **51**:2126–2146.

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

Jorgensen, C., K. Enberg, E. S. Dunlop, R. Arlinghaus, D.S. Boukal, K. Brander, B. Ernande *et al.* 2007. Managing evolving fish stocks. *Science* **318**:1247–1248.

Kingsolver, J. G., H. E. Hoekstra, J.M. Hoekstra, D. Berrigan, S.N. Vignieri, C.H. Hill, A. Hoang *et al.* 2001. The strength of phenotypic selection in natural populations. *American Naturalist* **157**:245–261.

Kokko, H., and D. J. Rankin. 2006. Lonely hearts or sex in the city? Density-dependent effects in mating systems. *Philosophical Transactions of the Royal Society B Biological Sciences* **361**:319–334.

Law, R. 1991. On the quantitative genetics of correlated characters under directional selection in age-structured populations. *Philosophical Transactions of the Royal Society B: Biological Sciences* **331**:213–223.

Law, R. 2007. Fisheries-induced evolution: present status and future directions. *Marine Ecology Progress Series* **335**:271–277.

Law, R., and C. A. Rowell. 1993. Cohort-structured populations, selection responses, and exploitation of the North Sea cod. In T.K. Stokes, J.M. McGlade, and R. Law, eds. *The Exploitation of Evolving Resources*, pp. 155–174. Springer-Verlag, Berlin.

Olsen, E. M., M. Heino, G. R. Lilly, 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.

Roff, D. A. 2002. *Life History Evolution*. Sinauer, Sunderland, MA.

Rowe, S., and J. A. Hutchings. 2003. Mating systems and the conservation of commercially exploited marine fish. *Trends in Ecology and Evolution* **18**:567–572.

Rowe, S., J. A. Hutchings, and J. E. Skjæraasen. 2007. Nonrandom mating in a broadcast spawner: mate size influences reproductive success in Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* **64**:219–226.

Rowe, S., J. A. Hutchings, J. E. Skjæraasen, and L. Bezanson. In press. Morphological and behavioural correlates of reproductive success in Atlantic cod *Gadus morhua. Marine Ecology Progress Series*, doi:10.3354/meps0717.

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

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

Stokes, T. K., J. M. McGlade, and R. Law. 1993. *The Exploitation of Evolving Resources*. Springer-Verlag, Berlin.

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* **274**:1015–1022.

Trippel, E. A.. 1995. Age at maturity as a stress indicator in fisheries. *BioScience* **45**:759–771.

Vincent, A., and Y. Sadovy. 1998. Mating systems and conservation problems. In T. J. Caro, ed. *Behavioral Ecology and Conservation Biology*, pp. 315–337. Oxford University Press, Oxford.

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.