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Potential consequences of reproductive behaviour and mating system complexity on fishery-induced evolution

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Abstract

Reproductive behaviour and mating system complexity may influence the rate of evolutionary change in exploited populations. Data on Atlantic cod (*Gadus morhua*) suggest that both sexes may prefer spawning with larger mates. In addition to potential mate selection, fecundity selection might also favour late-, large-maturing genotypes, in contrast to the selection imposed by many fisheries. Estimates of evolutionary change in fished populations have tended to exclude the possibility that reproductive success is influenced by the trait(s) under fisheries-induced selection. Here, we simulate changes to the mean and variance in body size concomitant with increased fishing intensity. Then, based on empirical data from the laboratory, we compare selection differentials (S) for length under the assumptions that size does and does not affect reproductive success. We find that the rate of decline in S with increased fishing pressure depends on: (a) the initial variance in body size; (b) changes to the variance in body size with increasing fishing intensity; and (c) the influence of size on reproductive success. If the initial variation in size is sufficiently high, and if the coefficient of variation (CV) in size increases with fishing intensity, the rate of change in S is less than that expected under the assumption that size has no effect on reproductive success. However, if the CV in body size remains constant, or declines, as fishing pressure increases, genetic change is predicted to be faster than that estimated under the assumption that size has no effect on reproduction. Our work underscores the potential importance of incorporating the consequences of reproductive behaviour and mating system complexity in estimates of evolutionary change in exploited resources.

Keywords: mate choice, mate competition, spawning behaviour, Atlantic cod, life history

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Introduction

Evolution by natural selection typically involves pressures that kill off individuals with ‘unfavourable’ inherited traits, while those with more ‘favourable’ features survive and reproduce. Fisheries would seem to provide such a pressure: most fisheries target the largest, oldest, or fastest-growing individuals, such that fish genetically predisposed to mature at larger sizes and older ages are more likely to be caught before they can reproduce (Stokes et al. 1993; Law 2000). In response to these exploitation pressures, whose effects are non-random with respect to the age, size and growth rate of the captured fish, selection would be expected to favour genotypes that mature earlier, at a smaller size, and that experience slower rates of growth.

The high number of over-fished or depleted marine fishes worldwide (FAO 2004) has created multiple opportunities to examine whether the collapse of fish populations has been associated with genetic responses to fishing. One of the best examples is that of Atlantic cod (*Gadus morhua*) that inhabit Northwest Atlantic waters extending from Labrador south and east to the northern half of the Grand Bank off Newfoundland, Canada. The northern cod stock (delineated by Northwest Atlantic Fishery Organization divisions 2J, 3K, and 3L), estimated to have declined more than 99% between the early 1960s and the early 1990s (Hutchings and Myers 1994; COSEWIC 2003), remains at historically depleted levels and has exhibited no signs of recovery (DFO 2006; Lilly et al. 2006). Concomitant with this historically unprecedented decline in abundance, both age and size at maturity of northern cod have exhibited declines that have been explained as evolutionary responses to exploitation (Hutchings 1999; Olsen et al. 2004). Similar responses in these and other life-history traits have been attributed to fisheries-induced genetic change amongst a growing number of exploited fishes (e.g., Handford et al. 1977; Ricker 1981; Stokes et al. 1993; Rijnsdorp 1993; Sinclair et al. 2002; Grift et al. 2003; Hard 2004; Olsen et al. 2004).

Having been documented repeatedly in exploited populations, it is incontestable that fishing can lead to significant changes in life history traits, such as age and size at maturity (Hutchings & Baum 2005). If the traits in question are heritable (as life history traits are; Roff 2002), a genetic response to selection will be realised. Given the high probability that intensive and prolonged fishing pressure will almost certainly exact a selection response to exploitation, the key questions concern (a) the magnitude of the response, (b) the reversibility of the response, and (c) the consequences of the response to rates of population growth and, thus, rates of population recovery. Of these three key areas, the second and third have probably received the least attention. Potential consequences to recovery associated with fishery-induced changes to life history traits have been explored (Hutchings 2005; Walsh et al. 2006) as have questions pertaining to the rate at which genetic responses to fisheries-induced selection are reversible (Rowell 1993; Law 2000; Conover et al. 2005; de Roos et al. 2006).

However, despite the comparative breadth of studies on the magnitude of potential genetic responses to fishing, few have explored the factors that might affect the *rate* at which such changes might be realised, and none has explored the degree to which the consequences of reproductive behaviour and, by implication, mating system complexity might be implicated in

such rates (Rowe and Hutchings 2003).

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 , which can range between 0 and 1) 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 after the selection event. When quantifying S in this manner, one implicit assumption is that the reproductive success (or the probability with which the surviving individuals will contribute genes to future generations) is independent of the trait in question.

For example, one powerful means of estimating S for a trait such as growth rate is to compare the mean size-at-age of individuals within a cohort after the selection event (e.g., at an age after which the differential effects of mortality caused by fishing have been experienced) with the mean size of individuals from the same cohort at a much younger age and before the effects of fishing have been experienced. If reproductive success is random with respect to size-at-age, then a direct comparison of the means before and after selection should yield a reasonably good estimate of S . However, if the probability of contributing genes during spawning varies with size-at-age, then a simple comparison of the means might lead to an under- or over-estimate of S , depending on the ways in which the mean and variance in size-at-age affect reproductive success.

Here, we simulate changes to the mean and variance in body size concomitant with increases in 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 in this species (Rowe et al. submitted, Rowe and Hutchings, unpublished data).

Methods

Frequency 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., Figure 1a). The minimum length of spawning individuals was set at 20 cm.

We examined changes to selection differentials under 8 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 (Figure 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; Figure 1 b-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, implying that relatively large individuals persist in the population despite increases in fishing intensity. 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.

Incorporating an effect of body size on reproductive success

Our assumption that body size influences reproductive success in Atlantic cod is based on data on individual reproductive success obtained from several spawning experiments, the details of which are provided by Rowe and Hutchings (2006), Sjkaeraasen et al. (2006), Hutchings et al. (submitted), and Rowe et al. (submitted). 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 m³). Group sizes ranged between 52 and 93 individually tagged cod. Parentage was determined from microsatellite DNA analyses (based on allelic variability at 7 microsatellite loci) undertaken on random samples of eggs collected daily throughout the experimental spawning periods in 2001, 2002, and 2003.

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 and Hutchings, unpublished data). 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 6 standard deviation categories) is shown in Figure 2. Based on the curvilinear function that best fit these data (Figure 2), we estimated individual reproductive success (Y , number of eggs), as a function of body size (X , in cm), to be:

Equation (1)
$$Y = \exp(0.0864 + 0.0648X) \quad .$$

(Note that an alternative approach would have been to fit the curvilinear function to all of the data. One significant drawback to this approach is that the best-fitted line would have been unduly influenced by those lengths best represented in the analysis (e.g., estimates of reproductive success for cod between 80 and 110 cm would have been significantly underestimated because of the preponderance of cod less than 60cm, many of which had exceedingly

low reproductive success).)

Based on the relationship described by Equation (1), the reproductive success for a 100 cm individual would be 711 eggs, that of a 50 cm cod would be 28 eggs, whereas that for the minimum sized individual (20 cm) considered in our simulations would be 4 eggs. 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 would be 1.000, 0.039, and 0.006, respectively.

Our estimates of the mean size of potential spawners at fishing intensity i ($\mu_{P(i)}$) was 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.

Results and Discussion

Influence of non-random 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 fishing 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 rate of change of selection differentials

We considered three means by which the coefficient of variation (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_P and S_A initially declined at similar rates (Figure 3). However, as the mean length of potential spawners declined to less than 60 cm, the rates of decline in selection differential diverged, with S_A declining at a greater rate than S_P . These patterns of divergence were not influenced by the initial CV in body size of the unfished population.

Increases in the CV for body size with the reductions in mean body size concomitant with increased fishing pressure imply that larger individuals are being removed from the population at a slower rate than comparatively smaller individuals, resulting in an increasingly positive skew in body size as fishing intensity increases. Under these circumstances, the rate of change in selection differentials depends on the CV in body size of the unfished population (Figure 4). At the lower of the two initial CVs that we considered (0.25), S_P and S_A declined in a similar manner as fishing intensity increased. However, at the higher of the initial CVs (0.33), the selection differentials among actual spawners (S_A) declined at a much slower rate than those

among potential spawners (S_p).

A reduction in the CV for body size with increased fishing pressure implies that larger individuals are being removed at a faster rate than comparatively smaller individuals. Under these circumstances, the selection differentials among actual spawners declined at a faster rate than those among potential spawners (Figure 5). At the higher of the two initial CVs for body size (0.33), the increased rate of decline in S_A was not evident until the average size of potential spawners was less than 65 cm.

Summary and implications

Our primary objective was to undertake an exploratory analysis to examine how an effect of body size on reproductive success might influence the rate at which heavily fished populations respond to size-biased exploitation. Our simulations suggest that, as fishing intensity increases, selection differentials for body size are influenced primarily by three factors: (a) the initial variance in body size; (b) changes to the variance in body size; and (c) incorporation of an effect of body size on reproductive success. If the initial variation in size is sufficiently high, and if the coefficient of variation (CV) in size increases with fishing intensity, the rate of change in S is less than that expected under the assumption that size has no effect on reproductive success. However, if the CV in body size remains constant or declines as fishing pressure increases, the rate of genetic change is predicted to be faster than that estimated under the assumption that body size has no effect on reproduction.

As with all modelling analyses, the validity of our results depends on the strengths and weaknesses of our approach, our assumptions, and of the empirical basis of our model parameter estimates. Our modelling approach is a technically simple one that seems to be intuitively reasonable. One alternative would have been to model changes in an age-specific trait (e.g., size-at-age) or a life-history trait (e.g., size at maturity). Although we would not anticipate the qualitative nature of our results to differ significantly under these alternative approaches, we have not undertaken these analyses. Perhaps one important assumption we have made is 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. Based on the data summarised in Figure 2, our assumption seems to be a reasonable one. We would also note that our interest lies in the qualitative nature of our results, rather than in our quantitative estimates (which have almost certainly produced unduly high selection differentials).

If there is merit to our approach, our work has implications for the study of fishing-induced evolution in exploited populations. One prediction to emerge from our research is that the effects of body size on reproductive success can significantly influence the rate of evolutionary change in exploited populations. This finding underscores the value of behavioural and genetic research on reproductive success, and draws attention to the limitations of implicitly assuming that reproductive success is random among the potential breeders that survive a selection event. Importantly, we find, under some circumstances, that the rate of evolutionary change can

accelerate as fishing intensity increases. This conclusion is consistent with that reached by de Roos et al. (2006) who used a size-structured, consumer-resource model to examine genetic responses in age and size at maturity in exploited fish populations. They reported that exploitation of late-maturing populations can, in effect, accelerate genetic change in age at maturity by generating stepwise, 1-year reductions in this life history trait.

A second prediction is that the rate of evolutionary change in traits linked to reproductive success, such as size and age at maturity, may be more rapid than previously thought when the CV for these traits declines with increases in fishing mortality. Newfoundland's northern stock of Atlantic cod, for example, whose reductions in age and size at maturity have been attributed to fisheries-induced evolution (Hutchings 1999; Olsen et al. 2004), experienced a reduction in the CV for body size with the commercial catches of 55% between 1962 and 1991 (Rowe and Hutchings 2003), the last full year of an offshore and inshore fishery on this stock.

A third prediction is that the greater the variation in body size, the slower the rate of evolutionary change in body size. This draws attention to the fundamental importance of maintaining large individuals within fished populations.

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References

- Conover, D.O., Arnott, S.A., Walsh, M.R., and Munch, S.B. 2005. Darwinian fishery science: lessons from the Atlantic silverside (*Menidia menidia*). *Can. J. Fish. Aquat. Sci.* 62: 730-737.
- COSEWIC. 2003. COSEWIC assessment and update status report on the Atlantic cod *Gadus morhua* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa.
- de Roos, A.M., Boukal, D.S., and Persson, L. 2006. Evolutionary regime shifts in age and size at maturation of exploited fish stocks. *Proc. R. Soc. B* 273: 1873-1880.
- DFO. 2006. Stock assessment of northern (2J3KL) cod in 2006. Department of Fisheries and Oceans Can. Sci. Advis. Sec. Sci. Advis. Rep. 2006/015.
- FAO. 2004. The state of world fisheries and aquaculture. Food and Agricultural Organization of the United Nations, Rome.

- Grift, R.E., Rijnsdorp, A.D., Barot, S., Heino, M., and Dieckmann, U. 2003. Fisheries-induced trends in reaction norms for maturation in North Sea plaice. *Mar. Ecol. Prog. Ser.* 257: 247-257.
- Handford, P., Bell, G., and Reimchen, T. 1977. A gillnet fishery considered as an experiment in artificial selection. *J. Fish. Res. Board Can.* 34: 954-961.
- Hard, J.J. 2004. Evolution of chinook salmon life history under size-selective harvest. *In* Evolution illuminated: salmon and their relatives. *Edited by* A.P. Hendry and S.C. Stearns. Oxford University Press, Oxford, pp. 315-337.
- Hutchings, J.A. 1999. The influence of growth and survival costs of reproduction on Atlantic cod, *Gadus morhua*, population growth rate. *Can. J. Fish. Aquat. Sci.* 56: 1612-1623.
- Hutchings, J.A. 2005. Life history consequences of overexploitation to population recovery in Northwest Atlantic cod. *Can. J. Fish. Aquat. Sci.* 62: 824-832.
- Hutchings, J.A. and Myers, R.A. 1994. What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. *Can. J. Fish. Aquat. Sci.* 51: 2126-2146.
- Hutchings, J.A., and Baum, J.K. 2005. Measuring marine fish biodiversity: temporal changes in abundance, life history and demography. *Phil. Trans. R. Soc. B* 360: 315-338.
- Hutchings, J.A., Swain, D.P., Rowe, S., Eddington, J.E., Puvanendran, V., and Brown, J.A. Submitted. Genetic variation in adaptive phenotypic plasticity among populations of Atlantic cod. *Nature*.
- Law, R. 2000. Fishing, selection, and phenotypic evolution. *ICES J. Mar. Sci.* 57: 659-668.
- Lilly, G.R., Murphy, E.F., Healey, B.P., and Bratley, J. 2006. An assessment of the cod (*Gadus morhua*) stock in NAFO Divisions 2J3KL in April 2006. Department of Fisheries and Oceans Can. Sci. Advis. Sec. Res. Doc. 2006/043.
- Olsen, E. M., Heino, M., Lilly, G. R., Morgan, J., Bratley, J., Ernande, B., and Dieckmann, U. 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature* 428: 932-935.
- Ricker, W.E. 1981. Changes in the average size and average age of Pacific salmon. *Can. J. Fish. Aquat. Sci.* 38: 1636-1656.
- Rijnsdorp, A.D. 1993. Fisheries as a large-scale experiment on life history evolution: disentangling phenotypic and genetic effects in changes in maturation and reproduction of North Sea plaice, *Pleuronectes platessa* L. *Oecologia* 96: 391-401.

- Roff, D.A. 2002. Life history evolution. Sinauer, Sunderland, Mass.
- Rowe, S., and Hutchings, J.A. 2003. Mating systems and the conservation of commercially exploited marine fish. *Trends Ecol. Evol.* 18: 567-572.
- Rowe, S., and Hutchings, J.A. 2006. Sound production by Atlantic cod during spawning. *Trans. Am. Fish. Soc.* 135: 529-538.
- Rowe, S., Hutchings, J.A., and Skjaeraasen, J.E. Submitted. Non-random mating in a broadcast spawner: mate size influences reproductive success in Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.*
- Rowell, C.A. 1993. The effects of fishing on the timing of maturity in North Sea cod (*Gadus morhua* L.). *In* The exploitation of evolving resources. *Edited by* T.K. Stokes, J.M. McGlade and R. Law. Springer-Verlag, Berlin, pp. 44-61.
- Sinclair, A.F., Swain, D.P., and Hanson, J.M. 2002. Measuring changes in the direction and magnitude of size-selective mortality in a commercial fish population. *Can. J. Fish. Aquat. Sci.* 59: 361-371.
- Skjaeraasen, J.E., Rowe, S., and Hutchings, J.A. 2006. Sexual dimorphism in pelvic fin length of Atlantic cod. *Can. J. Zool.* 84: 865-870.
- Stokes, T.K., McGlade, J.M., and Law, R. 1993. The exploitation of evolving resources. Springer-Verlag, Berlin.
- Walsh, M.R., Munch, S.B., Chiba, S., and Conover, D.O. 2006. Maladaptive changes in multiple traits caused by fishing: impediments to population recovery. *Ecol. Lett.* 9: 142-148.

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)		Fishing intensity (i)	Mean size of potential spawners $\mu_{P(i)}$	Mean size of actual spawners $\mu_{A(i)}$	Selection differentials	
	CV				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	545.7	-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

Table 1 continued

Change in CV (body size) with fishing intensity (<i>i</i>)	CV	Fishing intensity (<i>i</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 $S_{A(i)}$
increasing	0.25	0	74.1	96.5	0	0
	0.27	1	69.3	87.6	-4.8	-8.9
	0.29	2	64.4	84.2	-9.7	-12.3
	0.31	3	59.1	80.5	-15.0	-16.0
	0.34	4	54.2	76.2	-19.9	-20.3
	0.37	5	49.2	71.8	-24.9	-24.7
	0.42	6	44.3	65.9	-29.8	-30.6
	0.47	7	41.1	62.2	-33.0	-34.3
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	86.1	-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

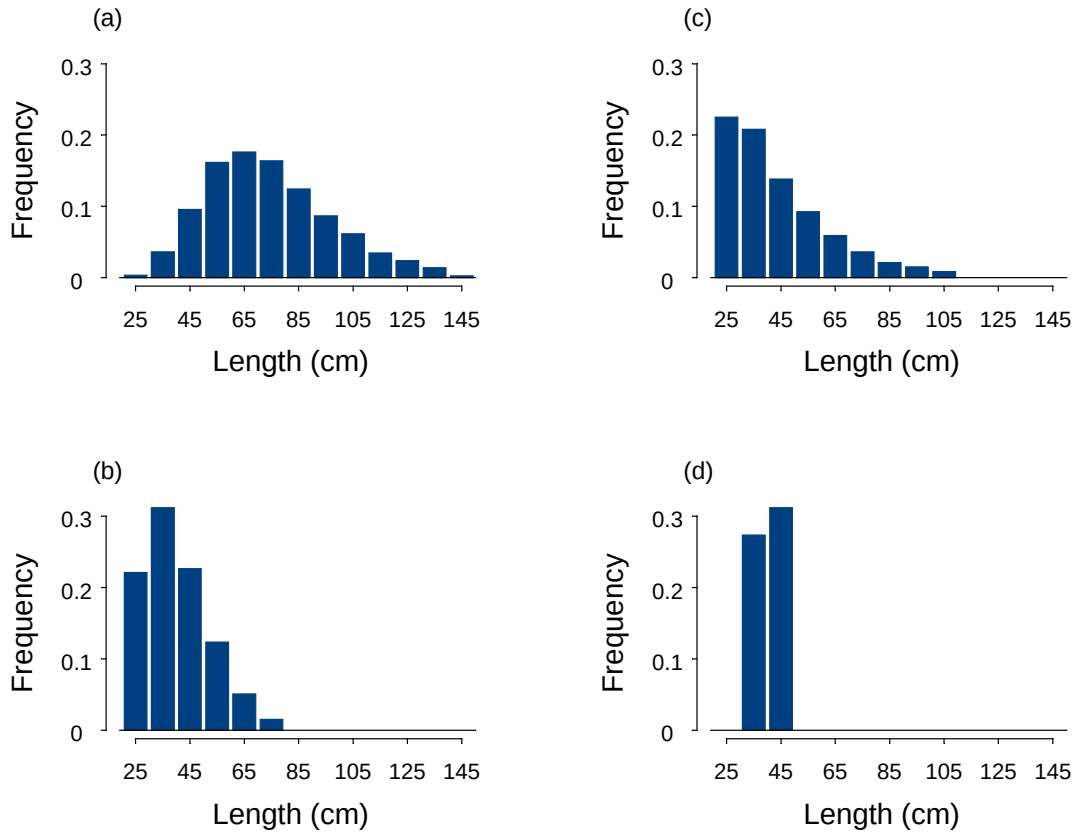


Figure 1. Simulated length-frequency distributions of Atlantic cod under four fishing intensity scenarios (see text for full details). (a) No fishing (fishing intensity, $i=0$), coefficient of variation (CV) in body size=0.33; (b) Fishing intensity, $i=7$ (maximum level), $CV(\text{body size})=0.33$, remaining constant with increases in fishing intensity; (c) Fishing intensity, $i=7$ (maximum level), $CV(\text{body size})=0.62$, increasing with increases in fishing intensity; and (d) Fishing intensity, $i=7$ (maximum level), $CV(\text{body size})=0.04$, decreasing with increases in fishing intensity).

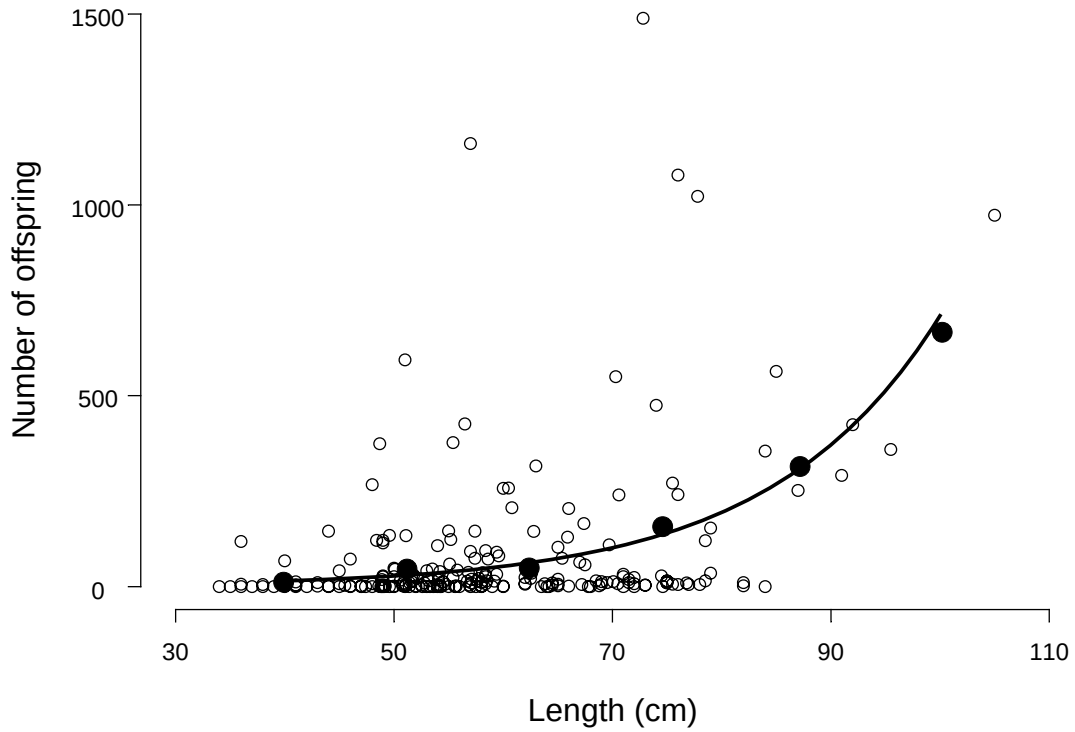


Figure 2. Relationship between Atlantic cod length and number of randomly genotyped offspring, based on data obtained for individuals (open circles) from genetic and behavioural spawning experiments undertaken in the laboratory. Length data were pooled, based on the number of standard deviations (SDs) 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., $Y = \exp(0.0864 + 0.0648X)$.

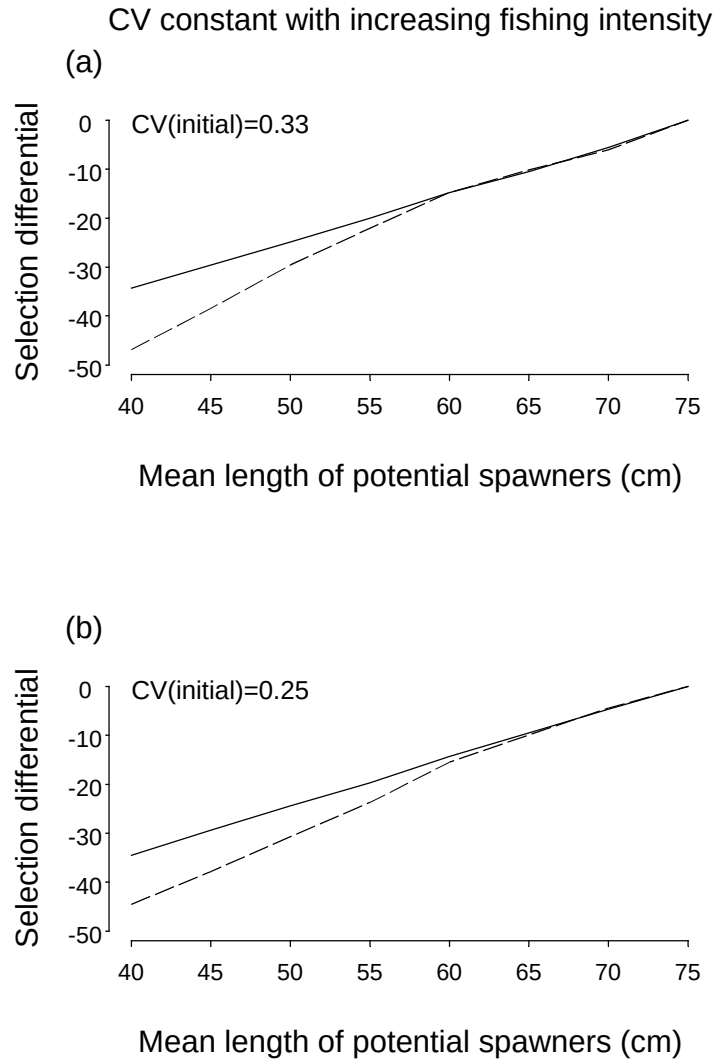


Figure 3. Estimated selection differentials for potential (S_P ; solid lines) and actual (S_A ; dashed lines) spawning Atlantic cod as functions of the mean length of potential spawners, at various levels of fishing intensity. Fishing intensity level increases from right (75 cm) to left (40 cm) along the x-axis. The coefficient of variation (CV) in body size remained constant as fishing intensity increased. (a) Initial CV in body size=0.33; (b) Initial CV in body size=0.25.

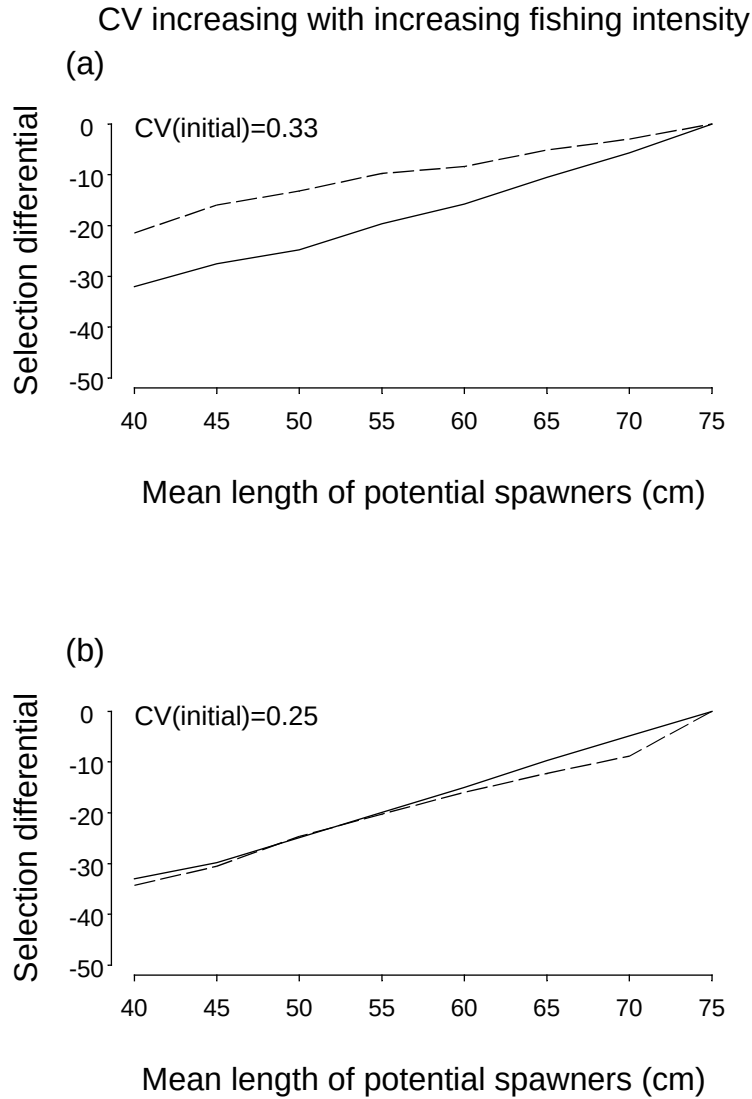


Figure 4. Estimated selection differentials for potential (S_P ; solid lines) and actual (S_A ; dashed lines) spawning Atlantic cod as functions of the mean length of potential spawners, at various levels of fishing intensity. Fishing intensity level increases from right (75 cm) to left (40 cm) along the x-axis. The coefficient of variation (CV) in body size increased as fishing intensity increased. (a) Initial CV in body size=0.33; (b) Initial CV in body size=0.25.

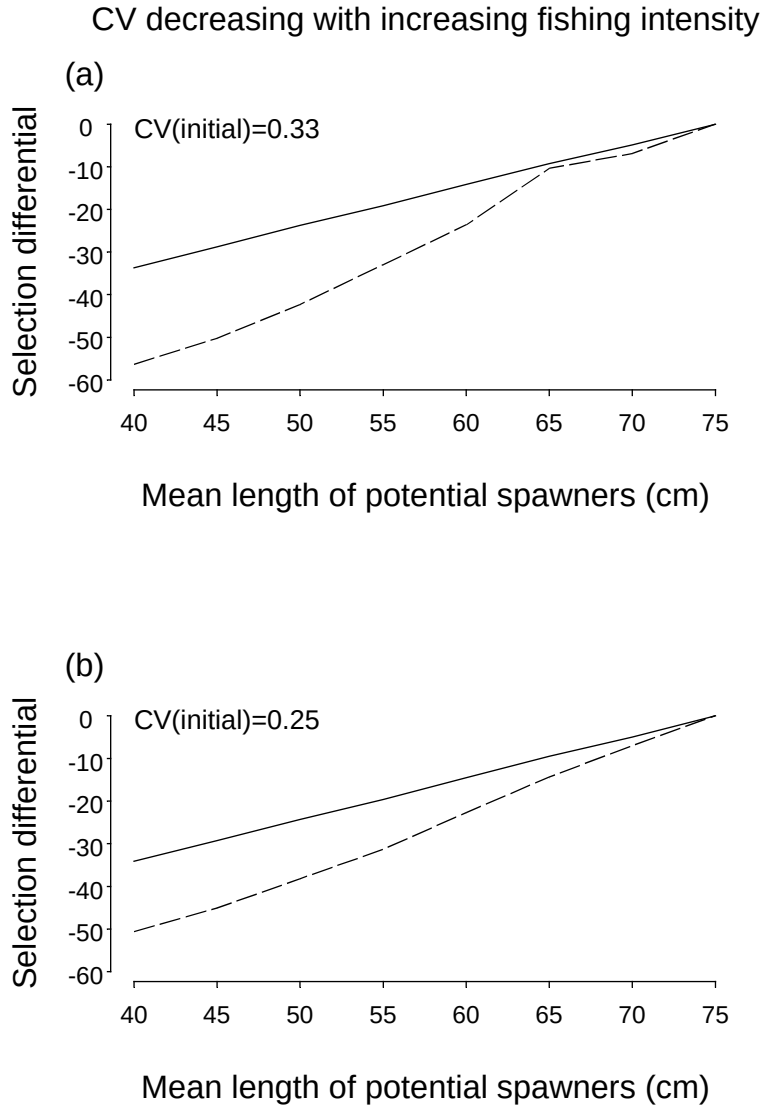


Figure 5. Estimated selection differentials for potential (S_P ; solid lines) and actual (S_A ; dashed lines) spawning Atlantic cod as functions of the mean length of potential spawners, at various levels of fishing intensity. Fishing intensity level increases from right (75 cm) to left (40 cm) along the x-axis. The coefficient of variation (CV) in body size decreased as fishing intensity increased. (a) Initial CV in body size=0.33; (b) Initial CV in body size=0.25.