

Nonrandom mating in a broadcast spawner: mate size influences reproductive success in Atlantic cod (*Gadus morhua*)

Sherrylynn Rowe, Jeffrey A. Hutchings, and Jon Egil Skjæraasen

Abstract: We tested the hypothesis that reproductive success in Atlantic cod (*Gadus morhua*) is random with respect to similarity in body size between mates. Immediately prior to their natural breeding periods, groups of 52–93 cod from three Northwest Atlantic populations were transported to a large (15 m diameter, 4 m deep) tank where they spawned undisturbed at densities similar to those in nature. Based on microsatellite DNA-parentage assignment of 8913 offspring from four spawning groups, females and males achieved their highest reproductive success when breeding with mates that were larger than themselves. Our observations are consistent with the hypothesis that some form of intrasexual competition or mate choice is a constituent of the mating system of this species and that this can have an important influence on individual fitness. Our results further suggest that reductions in the mean and variance in body size of commercially exploited marine fishes concomitant with size-selective harvesting may have greater negative consequences for population recovery than previously thought.

Résumé : Nous éprouvons l'hypothèse qui veut que le succès reproductif chez la morue franche (*Gadus morhua*) soit aléatoire en ce qui a trait à la similarité de taille corporelle des partenaires. Immédiatement avant leur période de reproduction naturelle, nous avons placé des groupes de 52–93 morues provenant de trois populations du nord-ouest de l'Atlantique dans de grands bassins (diamètre de 15 m, profondeur de 4 m) dans lesquels ils ont frayé à loisir à des densités semblables à celles trouvées en nature. D'après la détermination de la filiation de 8913 rejetons de quatre groupes de fraye par l'analyse des microsatellites de l'ADN, les femelles et les mâles atteignent leur succès reproductif maximal lorsqu'ils s'accouplent avec des partenaires qui leur sont supérieurs en taille. Nos observations s'accordent avec l'hypothèse selon laquelle le système de reproduction de l'espèce inclut une forme quelconque de compétition intrasexuelle ou de choix de partenaire et que cela peut avoir un effet important sur la fitness individuelle. Nos résultats laissent croire, de plus, que les réductions de la moyenne et de la variance de la taille corporelle chez les poissons marins exploités commercialement qui coïncident avec les récoltes sélectives en fonction de la taille peuvent avoir des conséquences négatives plus importantes sur la récupération des populations qu'on ne le croyait jusqu'ici.

[Traduit par la Rédaction]

Introduction

It has been hypothesized that the resistance and resilience of a species to environmental perturbation can be affected by that species' mating system (Møller and Legendre 2001; Rowe and Hutchings 2003; Quader 2005). The link between population dynamics and components of mating systems may be particularly important among severely depleted species (Kokko and Rankin 2006), such as many marine fishes, subject to past and present exploitation. Fishing, for example, by preferentially harvesting individuals by size, age, growth rate, behaviour, or some combination thereof has the potential to impose strong differential mortality, and selection among heritable characteristics, within exploited populations (Stokes et al. 1993; Law 2000; Conover and Munch

2002). If this differential mortality should negatively affect mate choice, the structure of dominance hierarchies, or other constituents of a species' mating system, then rates of population decline attributable to exploitation may increase, and subsequent rates of recovery may decrease, with increased mating system complexity.

Reproduction in commercially exploited marine fishes is often portrayed as a behaviourally vacuous process in which individuals mate with one another largely at random (Breder and Rosen 1966; Nordeide and Folstad 2000). Support for this depiction is usually derived from the observation that these species are often broadcast spawners, releasing large numbers (typically hundreds of thousands and often millions) of very small (typically less than 1.5 mm diameter) eggs directly into the water column, often in several batches

Received 8 March 2006. Accepted 17 October 2006. Published on the NRC Research Press Web site at <http://cjfas.nrc.ca> on 14 February 2007.
J19212

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throughout a breeding season, and providing them with no parental care (Hutchings 2002; Rowe and Hutchings 2003). Because energetic investment per gamete is likely to be extremely low for both sexes, and the probability of survival to maturity for each egg is typically less than 1×10^{-6} (Chambers 1997), the fitness benefits of aggressively competing for mates or exerting mate choice may be negligible. Consequently, it might not be unreasonable to predict that breeding groups of marine fishes lack the behavioural complexity seen in bird and mammal mating systems and, instead, reproduce in an unstructured manner.

An emerging view is that the mating systems of marine fishes might be considerably more complex. For example, based on studies of spawning behaviour, it has been hypothesized that mate choice may be integral to the mating systems of marine fishes such as Atlantic cod (*Gadus morhua*) (Engen and Folstad 1999; Hutchings et al. 1999; Rowe and Hutchings 2006). In this species, release of gametes occurs during a ventral mount, in which the male positions himself directly beneath the female while grasping her with his pelvic fins and matching her swimming speed (Brawn 1961). Under these circumstances, it may be beneficial for mates to be similar in body size, such that their urogenital openings are aligned directly opposite one another during gamete release and that high fertilization success is achieved, a benefit that might be expected to favour size-based, positive assortative mating (Hutchings and Myers 1993; Rakitin et al. 2001; Bekkevold et al. 2002). Alternatively, it could also be argued that this pattern of assortative mating, commonly observed in salmonids (Foote 1988), could arise if individuals of both sexes prefer large individuals as mates. Given that fecundity and sperm volume increase with body size in fishes (Trippel and Morgan 1994; Wootton 1998; McIntyre and Hutchings 2003), selection might be expected to favour individuals that mate with larger fish than themselves if male and female reproductive success is limited primarily by the number of gametes with which individuals come into contact during spawning. This prediction is based on the analogy that the probability that a fertilized egg produced by a broadcast-spawning marine fish will survive to attain maturity is akin to winning a lottery; the greater the number of gametes, the greater the number of "lottery tickets", and the greater the probability of success. Surprisingly, notwithstanding its intuitive nature, the prediction that reproductive success increases with body size has rarely been empirically tested for broadcast-spawning marine fishes.

The potential for mating system complexity to influence the degree to which intense exploitation affects population growth rate led Rowe and Hutchings (2003) to articulate two predictions. Firstly, the probability that exploitation negatively affects reproductive success is predicted to increase with the prevalence of dominance hierarchies, territorial behaviour, and mate choice in mating systems. Secondly, rate of population decline and time to population recovery is predicted to increase with (i) intensity of mate competition, (ii) importance of mate choice to fitness, and (iii) the magnitude of sex bias and differential mortality with respect to phenotype in commercial harvests. Irrespective of the precise mechanism(s) resulting in individual variation in reproductive success, these predictions centre ultimately on the question of whether reproduction is random or biased with

respect to phenotype, a question that has received little attention in broadcast-spawning, commercially exploited marine fishes such as Atlantic cod, haddock (*Melanogrammus aeglefinus*), and European plaice (*Pleuronectes platessa*).

We established experimental spawning groups to examine whether reproduction in Atlantic cod is random with respect to phenotype. In contrast with previous work (Hutchings et al. 1999; Rakitin et al. 2001; Bekkevold et al. 2002), our experimental facilities provided an unprecedented opportunity to study the breeding dynamics of a broadcast-spawning marine fish within large groups of individuals and, thus, at a scale that potentially allowed for more biologically meaningful behavioural interactions. Immediately prior to their natural spawning periods, Northwest Atlantic cod from geographically distinct regions were transferred to a large aquarium where they were allowed to spawn undisturbed in breeding groups of more than 50 individuals. Based on information obtained from four such groups, we partitioned data on individual body size and reproductive success by sex to test several hypotheses. Firstly, we tested the null hypothesis that individual reproductive success is independent of the body size similarity of potential mates. Upon rejection of this hypothesis, we then examined whether reproductive success was greatest when cod spawned with individuals smaller than, similar to, or larger than themselves. We tested this hypothesis separately for both sexes. Lastly, we examined the degree to which variability in a prominent mating behaviour of Atlantic cod is a reliable metric of individual reproductive success.

Materials and methods

Examination of parental fish and sampling of offspring

We examined fish from three spatially distinct areas in the Northwest Atlantic: Western Scotian Shelf, Southern Gulf of St. Lawrence, and Eastern Scotian Shelf, identified by the Northwest Atlantic Fishery Organization (NAFO) as divisions 4X, 4T, and 4W, respectively. Fish from each NAFO area were captured approximately 2–3 weeks prior to their annual spawning periods, individually tagged (using unique combinations of 7.5 cm long coloured T-bar anchor tags) and taken to the 684 m³ Pool Tank at Dalhousie University (Halifax, Nova Scotia), where they were allowed to spawn undisturbed. Cod experienced water temperatures of ~8 °C, ambient photoperiods, and were fed Shurgain[®] 8 mm fish feed daily.

We quantified reproductive success of four groups of spawning cod (Table 1). Groups 1 and 3 were composed of cod from Western Scotian Shelf that spawned in 2001 and 2002, respectively. The spawning period for Western Scotian Shelf cod encompassed December through March. Group 2 comprised Southern Gulf of St. Lawrence cod that spawned from May through July 2001. Group 4 comprised cod from Eastern Scotian Shelf that spawned in November and December 2002.

Seawater was continuously pumped into the tank, and spawned eggs were collected by a plankton net covering the single tank outflow located at the surface. The plankton net was checked daily at ~1600 h, and any eggs present were extracted. Examination of the developmental stage of random

Table 1. Average body sizes (± 1 standard error, SE) and sex ratios within four experimental groups of spawning Atlantic cod (*Gadus morhua*).

Group	Geographical location (year)	Sex	Mean length (cm)	SE	Length range (cm)	<i>N</i>
1	Western Scotian Shelf (2001)	Female	56.7	2.0	42.0–77.8	25
		Male	53.7	1.6	44.0–76.8	27
2	Southern Gulf of St. Lawrence (2001)	Female	57.9	0.7	50.0–69.7	41
		Male	58.0	0.8	53.5–65.9	18
3	Western Scotian Shelf (2002)	Female	74.9	2.2	54.0–105.0	25
		Male	72.7	1.4	62.0–92.0	29
4	Eastern Scotian Shelf (2002)	Female	49.9	1.2	35.0–84.0	56
		Male	44.9	1.2	34.0–62.0	37

samples of eggs collected indicated that almost all had been freshly spawned and fertilized within the previous 24 h. Each batch of eggs was incubated at ~ 8 °C in 20 L containers with circulating seawater and aeration. When eggs were within ~ 24 h from hatching (groups 1–3) or larvae were within 7 days after hatching (group 4), a random sample of several thousand offspring from each batch was collected and stored in ethanol for subsequent genetic analysis.

Experiments were terminated and fish sacrificed when no eggs had been collected for at least 5 days. Blood samples were obtained from each individual and preserved in ethanol for pedigree analysis. We recorded total length of each individual to the nearest millimetre. We also determined sex and stage of maturity by observation of gross morphology of the gonad (Morrison 1990).

The behaviour of Southern Gulf of St. Lawrence cod in group 2 was recorded daily during the last 8 h of daylight (1200–2000 h) from 15 May 2001 through 14 July 2001 by four video cameras mounted above the tank and by a colour videotape recorder. Subsequent to the spawning season, all videotapes were reviewed (totaling 488 h of video coverage) to document the incidence of courtship behaviour, particularly ventral mounts, in the group and identities of the fish involved (whenever possible).

Genetic analysis

DNA was extracted from blood of parental fish, using a Qiagen genomic extraction kit according to the manufacturer's protocol, and from whole offspring, following the extraction method described by Jones and Hutchings (2002). The number of daily samples for which incubated offspring were available for analysis ranged between 20 (Eastern Scotian Shelf) and 38 (Western Scotian Shelf in 2001). Given time and financial constraints and to maximize the number of samples across the spawning periods, our objective was to genotype 75 to 100 of the several thousand offspring that were usually available from each daily batch of collected eggs. On a few occasions, low egg–larval survival led to fewer than 75 offspring being available for genotyping. The number of genotyped offspring from each daily batch averaged 80.3 ± 20.3 standard deviation (SD) (range: 11–171), resulting in totals of 2931, 1633, 2652, and 1697 offspring genotyped for the full spawning period from Western Scotian Shelf in 2001, Southern Gulf of St. Lawrence, Western Scotian Shelf in 2002, and Eastern Scotian Shelf, respectively.

From a variety of available cod microsatellite DNA loci, three tetranucleotide repeat loci, *Gmo8*, *Gmo19*, and *Gmo37*, and one trinucleotide repeat locus, *Gmo35*, were chosen to be run on all samples (with the exception of those from the Western Scotian Shelf in 2002), based on their high levels of heterozygosity and genotyping reliability (Miller et al. 2000). In cases where these loci proved insufficient in determining parentage, two tetranucleotide repeat loci, *Gmo34* (Miller et al. 2000) and *Mae9* (a haddock microsatellite DNA locus; O'Reilly et al. 2002), were also examined. For cod from the Western Scotian Shelf in 2002, the following loci were run on each sample: *Gmo8*, *Gmo19*, *Gmo34*, *Gmo35*, and *Tch5* (a walleye pollock (*Theragra chalcogramma*) microsatellite DNA locus; O'Reilly et al. 2000). Loci were amplified using polymerase chain reaction conditions specified by Miller et al. (2000) and O'Reilly et al. (2000, 2002), samples were run on 6% denaturing acrylamide gels, and microsatellite alleles or bands were visualized using an FMBIO II (Hitachi, Tokyo, Japan). For parental fish, all loci were amplified and run three times to ensure correct genotyping. Standard individuals were run on all gels to check consistency in fragment lengths. Allelic data for offspring and their putative parents were analysed with PAPA 2.0 (Duchesne et al. 2002) to determine parentage assignments for fish from each of the four groups. More than 95% of the offspring were assigned parentage to both a mother and father in each group. Offspring for which full parentage could not be unambiguously established were excluded from our analyses.

Data analyses

We quantified two metrics of size similarity between mates. The first reflected the proportional difference in body size between mates and was calculated as L_M/L_F , i.e., the length of the male divided by the length of the female. The second metric, $L_M - L_F$, reflected the absolute difference in body length (cm) between mates. To test the null hypothesis that reproduction was random with respect to body size similarity between mates, we compared observed frequency distributions of size similarity for both metrics with those expected by chance, using *G* tests. The latter null distributions represented the frequencies in size similarity between all possible breeding pairs. Observed distributions represented the size similarities between successfully reproducing individuals (as determined by the parentage analyses) of those breeding pairs for which each individual had its greatest reproductive success.

We also examined the degree to which ventral mounts of females by males reflected reproductive success. Firstly, we compared the frequency distribution of size similarity among those pairs for which ventral mounts were observed with that expected by chance, weighting the size similarity for each pair by the number of ventral mounts observed for that pair. Secondly, we compared this observed distribution of size similarities for pairs in which mounts were observed with the distribution of size similarities between pairs that produced offspring, weighting the size similarity for each pair by the number of offspring produced.

Results

Average body size ranged between 45 and 75 cm among the four spawning groups of Atlantic cod (Table 1). There were substantive differences (≥ 28 cm) in body length among individuals within sexes in all groups, with the exception of Southern Gulf of St. Lawrence cod in group 2, for which the range in body size was less than 20 cm for both sexes. The number of individuals per group ranged between 52 and 93, which corresponds to spawning densities between 0.08 and 0.14 fish·m⁻³, densities which fall within the range of estimates of cod spawning density in the wild (Rose 1993; Morgan et al. 1997). Based on *G* tests, sex ratio did not differ among spawning groups 1, 3, and 4 ($p > 0.05$); cod in group 2 were significantly biased towards females ($p < 0.05$). Pooling data from all four groups, thus including all possible pair combinations of mates within each group ($n = 4210$), males were found to be, on average, 4% smaller (3.3 ± 0.2 cm standard error (SE) in absolute terms) than females (Table 2). However, based on the results of a two-way analysis of variance (ANOVA), neither this difference in body size nor those between the sexes within each spawning group were statistically significant ($p > 0.05$). Based on linear regression analyses, there was no association between body size and the dates on which individuals initiated and terminated spawning ($p > 0.05$).

Reproductive success was not random with respect to size similarity between mates. The frequency distribution of size similarity at which individual reproductive success was maximal differed significantly from that expected by chance for both females ($p < 0.001$) and males ($p < 0.01$) (Fig. 1), irrespective of the metric of size similarity used in the analysis. For both sexes, reproductive success was highest when an individual's mate was, on average, larger than themselves (Fig. 1). Pooling data from all four experimental groups, female reproductive success was highest when individuals mated with males that were an average 5% greater in length (ranging from 1% to 20% larger at the level of spawning group) (Table 2). In absolute terms, females achieved their highest reproductive success when they spawned with males similar to (group 2) or as much as 9.9 ± 3.7 cm longer (group 1) than themselves (Table 2). By contrast, males achieved their highest reproductive success when spawning with females that were, on average, 14% larger than they were, a proportional difference that corresponded to 10.5 cm in length (Table 2).

Our observation that reproductive success was highest when individuals mated with fish larger than themselves was evident within three of the four experimental spawning

Table 2. A comparison of two metrics of body size similarity within and among four experimental groups of spawning Atlantic cod (*Gadus morhua*): relative length of male to female (L_M/L_F) and absolute difference (in cm) between length of male and length of female ($L_M - L_F$).

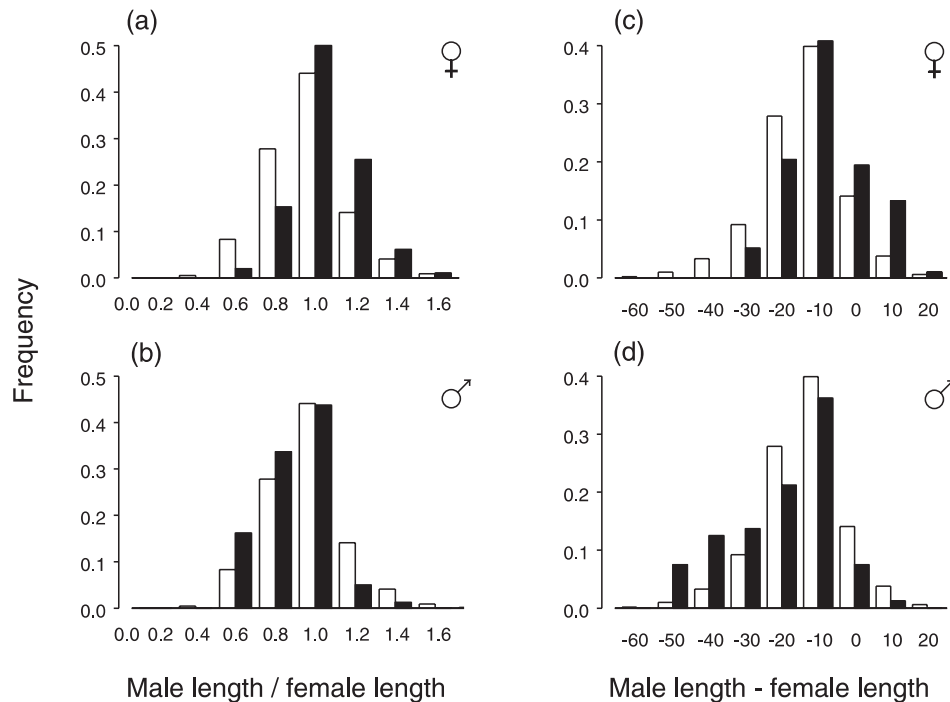
Metric of size similarity	Group	Sex	Mean	SE	<i>n</i>
L_M/L_F	All	Both	0.96	0.01	4210
		Female	1.05	0.02	98
		Male	0.88	0.02	80
	1	Both	0.97	0.01	675
		Female	1.20	0.07	10
	2	Male	0.89	0.05	19
		Both	1.01	0.01	738
	3	Female	1.01	0.02	37
		Male	0.99	0.02	16
	4	Both	0.99	0.01	725
		Female	1.07	0.04	25
	4	Male	0.80	0.02	28
Both		0.93	0.01	2072	
4	Female	1.03	0.04	26	
	Male	0.89	0.03	17	
$L_M - L_F$	All	Both	-3.3	0.2	4210
		Female	2.4	1.1	98
		Male	-10.5	1.6	80
	1	Both	-3.0	0.5	675
		Female	9.9	3.7	10
	2	Male	-8.9	3.5	19
		Both	0.1	0.2	738
	3	Female	0.3	1.1	37
		Male	-1.1	1.3	16
	4	Both	-2.2	0.5	725
		Female	3.4	2.8	25
	4	Male	-19.2	2.9	28
Both		-5.0	0.2	2072	
4	Female	1.5	2.0	26	
	Male	-6.6	2.1	17	

Note: For each group, the size similarity data for both sexes represent the average for all possible pairs in that group. When reported for each sex separately, the metrics represent the average similarity in body sizes between successfully reproducing individuals of those breeding pairs for which each individual had its greatest reproductive success, i.e., greatest number of offspring produced for both females and males.

groups (Fig. 2). For Southern Gulf of St. Lawrence cod (group 2), there were no discernible differences when comparing the size similarity of individuals that reproduced successfully with the size similarity of those individuals with whom they could have reproduced. Interestingly, however, the variability in body size within this group was the smallest among the four groups, the coefficient of variation (CV) in size similarity (9.3) being considerably less than the CV in size similarity in the other groups (ranging between 17.3 and 22.9). Although sample sizes were relatively small within groups, the size similarity between mates during their most successful breeding events differed statistically from that expected by chance for females in group 1 ($p < 0.05$) and males in group 3 ($p < 0.0001$).

Egg release by individual female Atlantic cod typically occurs during a ventral mount in which the male, while

Fig. 1. Comparisons between observed (solid bars) frequency distributions of mate size similarity at which individual reproductive success was maximal and those expected by chance (open bars). Data on proportional size similarity (length of male divided by length of female, L_M/L_F) are presented for females and males in panels (a) and (b), respectively. Data on absolute size similarity ($L_M - L_F$) are presented for females and males in panels (c) and (d), respectively.



grasping the female with his pelvic fins and matching her swimming speed, positions himself directly beneath the female, such that their urogenital openings are approximately aligned with one another (Brawn 1961). Among the Southern Gulf of St. Lawrence cod in spawning group 2, males did tend to mount females that were most similar in body size, but the frequency with which they did so did not differ from that expected by chance ($p > 0.05$; Fig. 3a). There was, however, a highly significant ($p < 0.0001$) difference between the relative sizes of females with whom males mounted and the relative sizes of mating pairs that produced offspring (Fig. 3b). Although the average size similarity did not differ between pairs in which mounts were observed (0.99 ± 0.07 SD) and pairs that produced offspring (0.97 ± 0.12 SD), the variation in size similarity was significantly greater (Bartlett's test for homogeneity of variances; $p < 0.01$) among the latter pairs than it was among the former.

Discussion

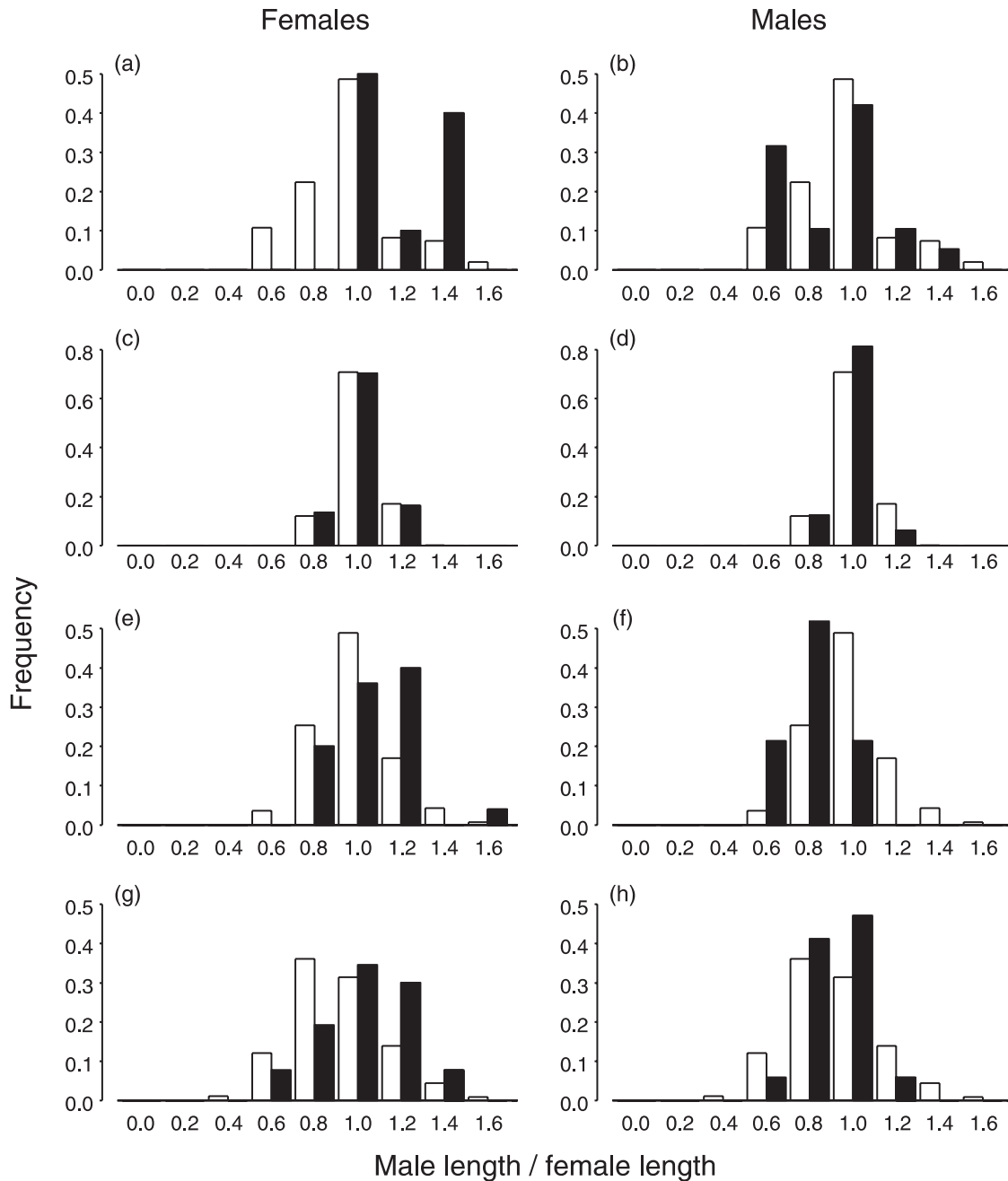
We established experimental spawning groups of Atlantic cod to examine whether reproductive success is random or biased with respect to the similarity in body size between potential mates. Our data suggest that reproductive success in cod depends on the relative sizes of spawning individuals. Both females and males achieved their highest success when breeding with mates that were, on average, larger in body size than themselves. To our knowledge, this is the first empirical support for the prediction that both female and male reproductive success increase with body size in broadcast-spawning marine fishes. These observations are consistent with the hypothesis that some form of intrasexual competi-

tion or mate choice is a constituent of the mating system of this species and that this can have an important influence on individual fitness. Experimental data also suggest that estimates of mating success (based solely on behavioural observations, such as ventral mounts) may underestimate variability in individual reproductive success, one of the key parameters that influence effective population size. The existence of nonrandom mating in Atlantic cod has conservation implications for commercial fisheries that selectively harvest individuals on the basis of size, growth rate, and sex.

The scale of our analysis, in terms of the size of experimental spawning groups and the number of offspring examined for parentage assignment, is unprecedented among studies of marine fishes. Comparing our work with other studies of Atlantic cod, the only species that has been examined previously, each of our spawning groups was composed of at least 50 individuals, whereas those studied by Rakitin et al. (2001) and Bekkevold et al. (2002) consisted of 3 and 8 individuals (on average), respectively. Our parentage analyses were based on the genotyping of almost 9000 offspring, compared with the 1340 and ~4100 offspring genotyped by Bekkevold et al. (2002) and Rakitin et al. (2001), respectively. One particular strength of our analysis was that we were able to compare our results among three geographically distinct populations, including a comparison of two separate years for one population. The fact that the relationships between body size and reproductive success reported here were temporally replicated for one population and spatially replicated among three populations suggests that these patterns may be general ones for this species.

However, notwithstanding these experimental differences, our finding that reproductive success in Atlantic cod is not

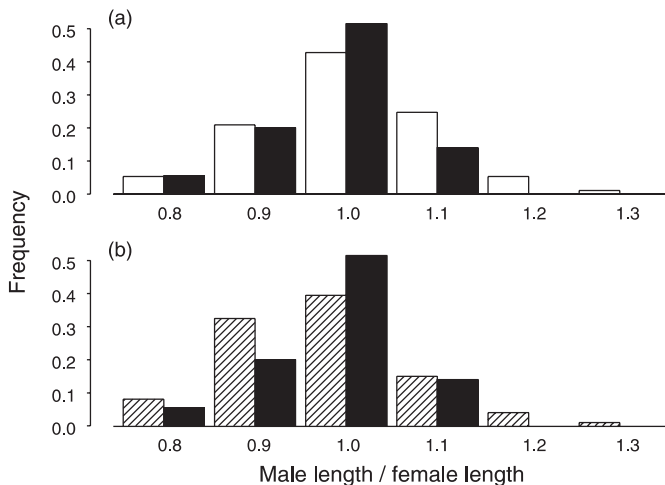
Fig. 2. Comparisons between observed (solid bars) frequency distributions of mate size similarity at which individual reproductive success was maximal and those expected by chance (open bars). Each of the four rows of figures depicts the distributions for females (left panels) and males (right panels) in a single spawning group: (a and b) group 1 (Western Scotian Shelf cod, 2001); (c and d) group 2 (Southern Gulf of St. Lawrence cod, 2001); (e and f) group 3 (Western Scotian Shelf cod, 2002); (g and h) group 4 (Eastern Scotian Shelf cod, 2002).



random with respect to body size is consistent with previous work. Rakitin et al. (2001) reported that the greater the similarity in body length between mates, the higher male reproductive success, suggesting that there might be size-based assortative mating in this species. However, as the authors noted, the number of individuals in their eight experimental groups (each of which comprised two males competing for a single female) was too small to allow for one sex to choose another within a behavioural and phenotypic milieu some-

what similar to that which exists in the wild. Bekkevold et al. (2002) examined how the proportion of offspring fertilized by males during single spawning events varied with the male's size relative to that of the female. Their data indicated that male reproductive success tended to be highest when males were similar to or larger than the female with whom they spawned, although they did not compare the observed frequency distribution of size similarity between mates with that expected by chance.

Fig. 3. Comparisons of size similarity among female–male pairs for which ventral mounts were observed (solid bars) with (a) the frequency distribution of all potential female–male pairs (open bars) and (b) female–male pairs that produced offspring, irrespective of whether mounts were observed between the pair (hatched bars), for Southern Gulf of St. Lawrence cod in spawning group 2.



Although nonrandom mating in Atlantic cod could be attributable to a number of mechanisms (Andersson 1994), mate competition, mate choice, or some combination thereof may be among the most probable. Studies have shown that successful reproduction in Atlantic cod involves complex behaviour within and between sexes (Brawn 1961; Hutchings et al. 1999). Before ventral mounting attempts, agonistic interactions (especially chases) are often seen among males and are believed to influence access to females (Brawn 1961; Hutchings et al. 1999). In some species, such as Atlantic salmon (*Salmo salar*), where males compete aggressively for access to females, body size has been found to be an important determinant of male reproductive success (Hutchings and Myers 1988).

As argued previously, there may be important fitness benefits for broadcast-spawning fish that provide no parental care to mate with larger individuals because of the increased number of gametes with which they come into contact during spawning (Trippel and Morgan 1994; McIntyre and Hutchings 2003). These advantages may lead to mate choice by both females and males for larger individuals of the opposite sex.

Both sexes are afforded various opportunities to exert choice during the spawning period. Females can do so by controlling the timing of their spawning. Although egg release is preceded by the ventral mount of a single female by a single male (Brawn 1961), not every mount is followed by egg release (Rowe and Hutchings 2006), suggesting that females are capable of selecting the mounting male with whom they choose to mate. Males can exert choice in one of two ways. Behaviourally dominant males can potentially select their mates by deciding which females to court and mount ventrally. Other males, rather than engaging in courtship, may adopt a satellite-spawning strategy, releasing sperm near a spawning couple and successfully fertilizing eggs in

competition with the dominant male (Hutchings et al. 1999; Rakitin et al. 2001; Bekkevold et al. 2002). Each satellite male can potentially exert choice by selecting the spawning events in which he will participate. If smaller individuals are more likely to fertilize eggs as satellite males than larger individuals and if the majority of males achieve fertilizations by adopting the satellite spawning tactic, this type of choice could generate a frequency distribution of mate size similarity in which male reproductive success is highest when males are small relative to the size of the spawning female, a pattern documented in three of the four spawning groups that we studied. Sperm competition might also affect a male's reproductive success, although it is not clear that this would necessarily lead to the bias in size similarity between mates observed here. On the other hand, sperm competition might account, in part, for the higher variance in reproductive success relative to mating success, which we observed among Southern Gulf of St. Lawrence cod in group 2.

Most commercial fisheries are size-selective, with larger individuals more likely to be caught than smaller individuals (Law 2000). Persistent removal of larger individuals will ultimately lead to a reduction in the average size of spawners and, thus, a reduction in the total number of eggs released during the spawning period, among other negative consequences for population growth (Walsh et al. 2006). From a mate-choice perspective, regular removal of the largest individuals will also lead to a reduction in body size variability (Rowe and Hutchings 2003). Within the context of the present study, we would predict that reduced variability in body size would reduce the scope for and the effectiveness of choice, negatively affecting individual reproductive success, recruitment to the fished population, and recovery following population collapse. This prediction is consistent with the results of a modeling analysis undertaken by Bessa-Gomes et al. (2003) who describe how either acceptance or refusal of unattractive mates, two potential consequences of a reduced breadth of choice, can negatively affect population growth rate and increase the probability of extinction. If reduced variability in body size narrows the scope for mate choice in Atlantic cod, we would predict that this would be reflected by a reduction in the variance in individual reproductive success, a prediction borne out by recent experimental work (Bekkevold 2006).

Our work provides strong evidence that reproductive success in Atlantic cod, a broadcast spawner, is not random with respect to the phenotype of potential mates. The observation that reproductive success was highest when both sexes reproduced with individuals larger than themselves is consistent with the hypothesis that mate choice is exerted by both sexes in this species, although we also draw attention to the potential importance of mate competition, particularly among males. If variability in body size enhances choice and the fitness benefits derived therefrom, then the severe truncations in the size-frequency distributions of reproductive individuals typically associated with population collapse may have greater negative consequences for recovery than previously thought. Research focused on the causal basis for nonrandom mating in Atlantic cod and the incidence of such a mating pattern in other commercially exploited marine fishes is warranted.

Acknowledgements

We are grateful to Paty Avendaño, Jim Eddington, and Steve Thompson for providing support and technical assistance in the lab. Parentage analysis would not have been possible without the help of Louise Bezanson, Roxanne Gillett, Matt Jones, and Cheryl Smith. Logistic support for fish collections was provided by Fisheries and Oceans Canada and by Inshore Fisheries Limited. We thank Dorte Bekkevold and an anonymous reviewer for their insightful comments on a previous version of the manuscript. Financial support was provided by the Natural Sciences and Engineering Research Council of Canada and by the Norwegian Research Council.

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