

Spawning behaviour of Atlantic cod, *Gadus morhua*: evidence of mate competition and mate choice in a broadcast spawner

Jeffrey A. Hutchings, Todd D. Bishop, and Carolyn R. McGregor-Shaw

Abstract: We quantified individual differences in Atlantic cod, *Gadus morhua*, reproductive behaviour at a field-reported spawning density under experimental conditions. Marked individuals (nine females, seven males) were observed twice daily and videotaped continuously for 9 weeks at ambient photoperiod and temperature in a large tank (60 m³). Agonistic interactions appeared to maintain a size-based dominance hierarchy among males. Multiple paternity per spawning bout, revealed by microsatellite DNA analysis, suggested a link between dominance and fertilization success. Interactions between sexes were dominated by the circling of females by males. Predicated by vertical separation from males, and after descending to the bottom, a motionless female would be circled up to 17 times, often by one male per circling bout but by several males throughout the spawning period. Although circling frequency increased with male dominance and male body size, initiation and termination of this behaviour appeared to be under female control. Circling provides opportunities for males to gain individual access to reproductive females and for females to assess the quality of potential mates. Our evidence for nonrandom mate choice and for male–male competition and display has implications for Atlantic cod mating systems and effects of fishing on their reproductive success.

Résumé : Nous avons quantifié les différences individuelles dans le comportement reproducteur chez la morue franche, *Gadus morhua*, dans des conditions expérimentales à des densités de géniteurs correspondant aux observations faites sur le terrain. Les individus marqués (neuf femelles, sept mâles) ont été observés deux fois par jour et filmés sur vidéo en continu pendant 9 semaines dans des conditions ambiantes de photopériode et de température créées dans un grand bassin (60 m³). Les interactions agonistiques semblaient maintenir parmi les mâles une hiérarchie de dominance basée sur la taille. La paternité multiple par épisode de fraye, révélée par l'analyse de l'ADN microsatellite, permet de penser qu'il existe un lien entre la dominance et le succès de fécondation. Les interactions entre les sexes étaient dominées par la rotation des mâles autour des femelles. On observe une séparation verticale des mâles et des femelles et, après être descendue sur le fond, une femelle immobile peut avoir jusqu'à 17 fois un mâle qui lui tourne autour. Il s'agit souvent du même mâle lors d'un épisode de rotation, mais plusieurs mâles peuvent tourner autour de la même femelle au fil de la période de fraye. Bien que la fréquence de rotation augmente avec la dominance et la taille corporelle des mâles, l'amorce et l'interruption de ce comportement semblent être régis par les femelles. La rotation donne l'occasion aux mâles d'avoir accès individuellement aux femelles génitrices, et aux femelles d'évaluer la qualité des partenaires potentiels. Les indices recueillis qui montrent que le choix du partenaire n'est pas aléatoire et qu'il y a compétition et parade chez les mâles fournissent des informations utiles concernant les systèmes de fraye de la morue franche et les effets de la pêche sur le succès de reproduction de cette espèce.

[Traduit par la Rédaction]

Introduction

Despite being of theoretical and practical import, the spawning behaviour of marine demersal fishes on continental shelves is poorly known. From an ecological perspective, there are no data on potential associations between mating behaviour and reproductive success in "broadcast" spawners, i.e., fish that release hundreds of thousands, often millions, of very small eggs (<3 mm in diameter), for which no paren-

tal care is provided, directly into oceanic waters, e.g., Atlantic cod, *Gadus morhua*, and haddock, *Melanogrammus aeglefinus*. This strategy of maximizing the production of eggs the sizes of which approach, or attain, the physiological minimum for survival has been interpreted as an adaptive response to environments in which egg size confers no consistent, intergenerational advantage to survival in early life (Hutchings 1997).

The complexity of mating behaviour, or lack thereof, associated with broadcast spawning cannot be predicted from theories of life history, parental care, or mating systems. Are the structured behavioural repertoires typically associated with mate competition (e.g., agonistic interactions) and mate choice (e.g., displays) evident in broadcast-spawning, demersal marine fish? Or, is the apparent lack of parental control of the spatial location of offspring immediately after

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J.A. Hutchings,¹ T.D. Bishop, and C.R. McGregor-Shaw.
Department of Biology, Dalhousie University, Halifax,
NS B3H 4J1, Canada.

¹Author to whom all correspondence should be addressed.
e-mail: jhutch@mscs.dal.ca

Table 1. Lengths and weights of female and male Atlantic cod used in the spawning experiment.

Female ID	Length (cm)	Weight (g)	Male ID	Length (cm)	Weight (g)
1R2	66.5	3060	1L1	65.1	2925
3L1	63.0	2175	2L1	64.8	2503
2L1	61.9	2500	2R1	63.0	2291
2R2	56.2	2020	3R1	56.0	1727
2L2	55.5	1700	3L1	55.8	1664
3R1	53.7	1450	2R2	55.0	1458
1R1	53.0	1620	2R2D	53.5	1335
1L2	51.8	1562			
2R1	51.7	1646			

Note: See text for explanation of identification (ID) codes.

fertilization associated with a similar lack of control of mate choice?

From an applied perspective, the highest catch rates in many commercial fisheries are achieved by mobile fleets that target spawning aggregations (e.g., Beverton 1990; Hilborn and Walters 1992; Hutchings 1996). It is therefore of practical importance to determine whether fishing deleteriously influences the reproductive success of mature individuals not caught during the fishing of spawning aggregations (Hutchings 1996; Morgan et al. 1997).

Populations of Atlantic cod, for which age at maturity ranges between 2 and 7 years (Myers et al. 1997), typically spawn over a period of <3 months (Brander 1994; Chambers and Waiwood 1996; Kjesbu et al. 1996) in water that may vary in depth from tens (Smedbol and Wroblewski 1997) to hundreds of metres (Brander 1994; Morgan et al. 1997). Population differences in egg diameter can vary from 1.25 to 1.75 mm (Chambers and Waiwood 1996), with fecundity ranging from hundreds of thousands to millions of eggs (Chambers and Waiwood 1996; Kjesbu et al. 1996). Although individuals are presumed to breed annually, Atlantic cod are described as batch spawners because of the observation that only 5–25% of a female's egg complement is released at any given time during her 3- to 6-week spawning period (Chambers and Waiwood 1996; Kjesbu et al. 1996).

The behaviour that immediately precedes the release of sperm and eggs was initially documented at nineteenth century Atlantic cod hatcheries in Newfoundland (Templeman 1958) and Norway (Dannevig 1930). These observations, and those of Brawn (1961), describe a "ventral mount" in which the male, while grasping the female with his pelvic fins and matching her swimming speed, positions himself beneath the female with the urogenital openings of both fish opposite one another. The ventral mount has also been observed in captive breeding haddock (Hawkins et al. 1967), suggesting that it may be a general reproductive characteristic of gadid fish.

Brawn's (1961) laboratory work constitutes the only published account of cod spawning behaviour. She documented agonistic interactions and territoriality among the five males she held with seven females in a 1.3-m-deep, 10.8-m³ tank. Her descriptions suggest that successful ventral mounts are preceded by male courtship behaviours, e.g., flaunting (exaggerated lateral bends of the body with median fins fully erect), grunting (sound production from the swim bladder), prodding (the male's snout nudges the female's ventral trunk

region), and "swimming with an excited, jerky, undulating movement with many unnecessary circles" (Brawn 1961). Expanding upon Brawn's (1961) work, our objectives were to describe behavioural interactions within and between sexes and to quantify individual variation in Atlantic cod spawning behaviour.

Materials and methods

Atlantic cod were collected by baited hook near Sambro, Nova Scotia, Canada (44°25'N, 63°30'W), in late October 1995 and transported to 600-L holding tanks at Dalhousie University. Individuals were physically examined to determine sex and to ensure that they were in spawning condition, following the cannulation technique described by Larsson et al. (1997), as modified from Shehadeh et al. (1973). Atlantic cod were individually marked with 2-cm-long, coloured tags. Tags were inserted into the dorsal musculature of anaesthetized fish in unique locations that could be described by a three-digit alphanumeric code. The first digit of the code indicated the number of the dorsal fin (1 = anterior fin, 2 = middle fin, 3 = posterior fin), the second indicated whether the tag was on the left (L) or right (R) side of the fish, and the third indicated whether the tag was positioned near the anterior (1 = origin) or posterior (2 = insertion) fin rays. For example, the code 2L1 indicates that the tag was positioned near the origin of the second dorsal fin on the left side of the fish.

Sixteen Atlantic cod (nine females, seven males) were placed in a 3-m-deep, 60-m³ experimental tank on November 14, 1995 (Table 1). This resulted in a density of spawning Atlantic cod of 0.27 fish·m⁻³, which is close to the maximum densities of 0.28–0.31 spawning fish·m⁻³ recorded by Morgan et al. (1997) under field conditions on Newfoundland's Grand Bank. The tank, part of Dalhousie University's Aquatron facility, was continuously supplied with ambient seawater. The experimental Atlantic cod, being in an outdoor tank, were exposed to a natural photoperiod.

Behaviour was monitored continuously from November 16, 1995, through January 19, 1996 (the last date upon which spawning behaviour was observed was December 13). Four underwater viewing windows, one at one end of the tank and three along one of the tank's sides, permitted individual differences in spawning activity to be recorded by direct observation and by videotape. Twice daily, at about 10:30 and 15:00, each fish was observed continuously for 3 min. The incidence of five agonistic behaviours was documented for each individual during the 3-min interval: (i) chase (swimming toward a swimming fish), (ii) approach (swimming toward a stationary fish), (iii) bite (physical contact between one fish's mouth and another fish's body or fin), (iv) nip (an attempted bite, i.e., an opening and closing of the mouth near another fish's body or fin), and (v) prod (contact between one fish's snout and another fish's body). In addition to direct observations,

Table 2. Agonistic behaviours initiated and received by male Atlantic cod during spawning under experimental conditions.

Male ID	Behavioural action	Agonistic behaviour				Total
		Chase	Approach	Nip/bite	Prod	
2R1	Initiated	30	3	2	2	37
	Received	2	2	0	0	4
1L1	Initiated	9	2	0	0	11
	Received	17	1	1	1	20
2L1	Initiated	4	1	0	0	5
	Received	11	1	0	0	12
2R2	Initiated	0	1	0	0	1
	Received	2	2	0	0	4
2R2D	Initiated	0	0	0	1	1
	Received	0	0	0	0	0
3L1	Initiated	0	0	0	0	0
	Received	5	0	1	0	6
3R1	Initiated	0	0	0	0	0
	Received	6	1	0	2	9

behavioural activity was recorded daily by two videocameras. Through one of the viewing windows, a colour videotape recorder documented behaviour continuously from 08:00 to 16:00. A black-and-white videorecorder documented behaviour continuously through day and night from a second viewing window. However, because of low ambient light conditions at night, reliable behavioural observations were limited to the hours between 07:30 and 17:30.

A random sample of eggs ($n = 27$) spawned between 17:00 on November 25 and 08:00 the following morning was sampled for pedigree analysis. After the larvae had hatched from these eggs, genotypes were determined from microsatellite DNA variation at three diallelic loci (*Gmo2*, *Gmo4*, *Gmo132*) (Doyle et al. 1995). The genetic analyses were undertaken by the Marine Gene Probe Laboratory, Dalhousie University.

All experimental animals were measured and weighed at the end of the experiment. Blood samples were obtained from each individual for the pedigree analysis. Visual examination of the gonads indicated that all individuals had spawned, i.e., ovaries were whitish grey, slack, and often wrinkled (residual eggs were often present), while testes were grey and milt was absent from the vasa deferentia (Templeman et al. 1978).

Results

Behavioural interactions among males

During the spawning period in the experimental tank (November 16 to December 13), male Atlantic cod established a hierarchy based largely on agonistic interactions between pairs of males. Of 55 aggressive behaviours recorded by direct observation, most (78.2%) were chases of one male by another (Table 2). The remaining behaviours, ranked by incidence, were approach (12.7%), prod (5.5%), and nips/bites (3.6%). The majority of these encounters (67.3%) were initiated by one "dominant" male (2R1) (Table 2). Two "subdominant" males (1L1, 2L1) contributed an additional 29.1% of aggressive interactions, with the four remaining "subordinate" males initiating fewer than 4% of all agonistic encounters observed. Agonistic interactions were not observed among females.

Behaviourally aggressive males initiated agonistic interactions with other males after the latter had entered the volume

of water in which the former generally resided. These defended "territories", distributed fairly evenly throughout the experimental facility, tended to be nearer the bottom of the 3-m-deep tank than the surface.

Male dominance was associated with body size. Those in the larger length-class (63–65 cm) (Table 1) included the dominant and subdominant males; subordinate males were in the smaller length-class (53–56 cm).

Behavioural interactions between males and females

Two types of interactions between male and female Atlantic cod predominated during the spawning period. The first of these was the previously described ventral mount (Brawn 1961). Although the extrusion of eggs is always preceded by a ventral mount, we observed many such spawning attempts by males that were unsuccessful in eliciting the release of eggs by females. Given that extrusion of eggs and milt normally occurs at night (Chambers and Waiwood 1996), we observed comparatively few ventral mounts ($n = 20$) during daylight hours. For the 20 ventral mounts observed, each of which lasted an average 9.9 ± 2.8 s (\pm SE) (median of 5.5 s) in duration, there appeared to be a positive association between male dominance and frequency of ventral mounts: 55% involved male 2R1, 30% male 1L1, 10% male 2L1, and 5% male 3R1.

The second type of interaction between sexes observed throughout the spawning period was the circling of females by males. The sequence of behaviours that comprised circling bouts can be described as follows. From a midwater or near-surface position, a female would swim to the bottom where she remained motionless, moving neither her body nor her fins. Upon reaching the bottom, the female would be joined by one or more males. While the female remained motionless, the male(s) swam slowly around her in either a clockwise or a counterclockwise direction. The circling continued until the female swam off the bottom, whereafter this association between male(s) and female ended. Of the few (six of 20) ventral mounts for which the coupling male and female could be reliably identified, all occurred within 24 h

Fig. 1. Temporal changes in intra- and inter-sexual behavioural interactions in spawning Atlantic cod in an experimental facility. The number of aggressive interactions initiated by males is represented on the left ordinate, and the number of circling bouts received by females is indicated on the right ordinate. Day 1 represents November 16, 1995.

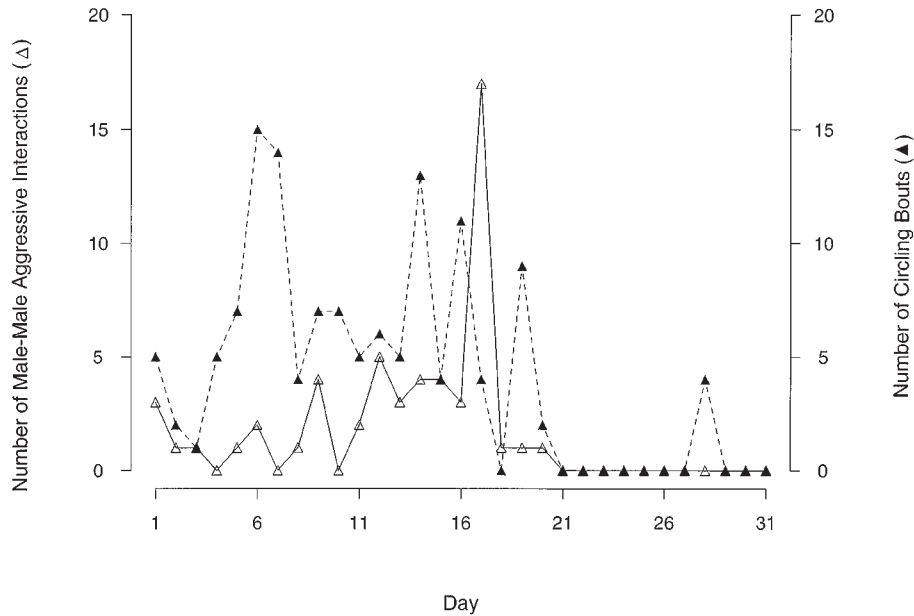
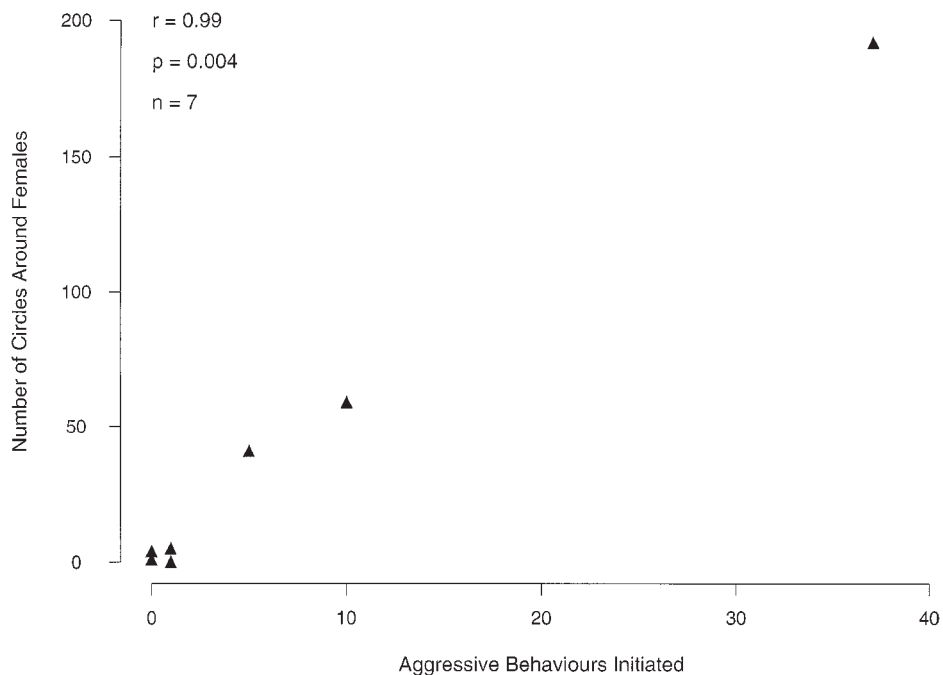


Fig. 2. The number of circles undertaken by a reproductive male around female Atlantic cod during the spawning period increases with the number of aggressive interactions initiated by that male towards other males.



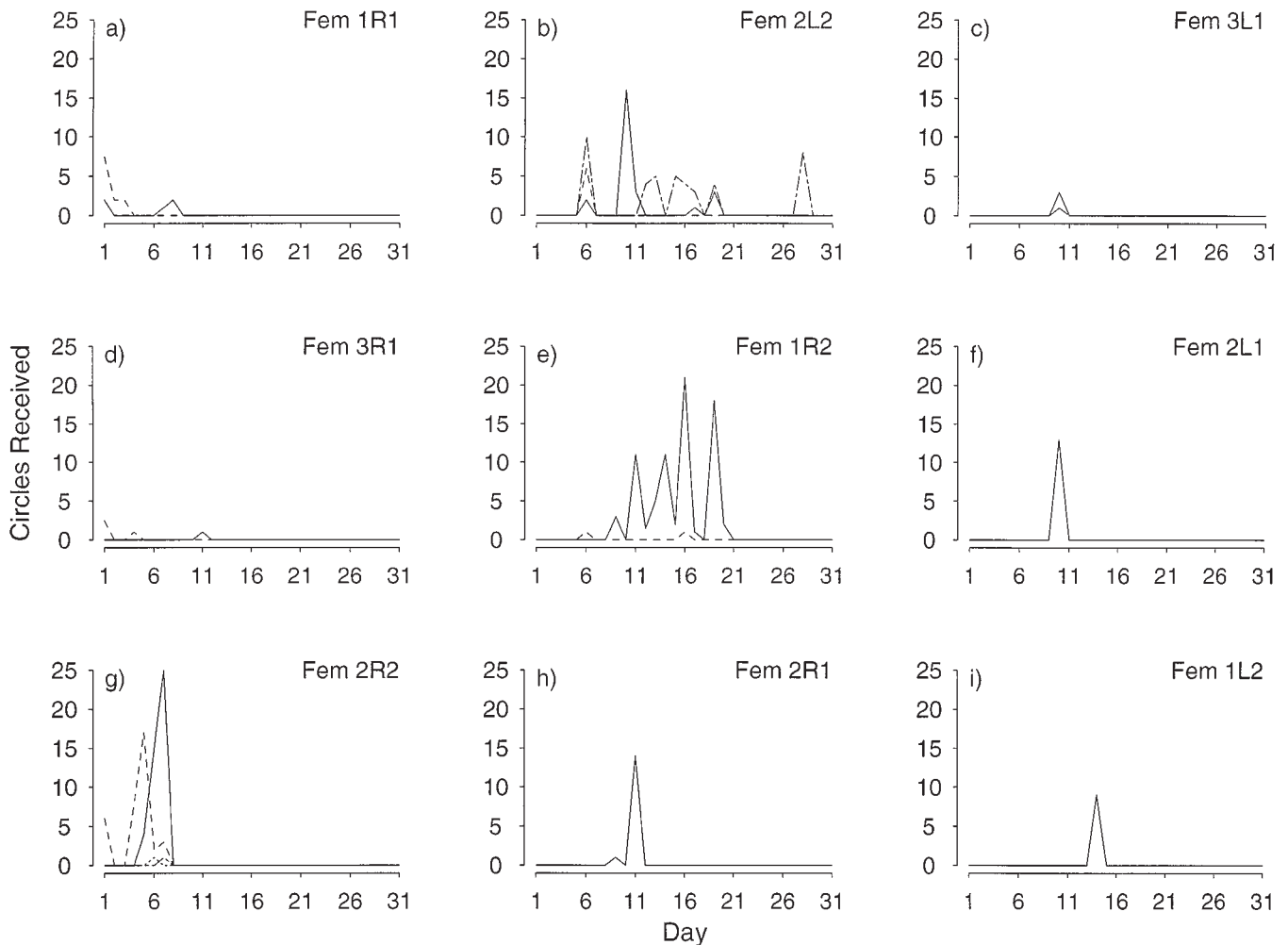
of that male (either 2R1 or 2L1), and one or two other males (including 2R1, 1L1, 2L1, 3R1), having circled the female.

The period of time during which circling was observed coincided with the time frame during which aggressive interactions among males were observed (Fig. 1). With the exception of four circling bouts observed on day 28, male aggression and circling of females ended on day 21 of the spawning period. Among individual males, the total number

of circles performed during the spawning period was positively associated with the total number of aggressive behaviours initiated against other males ($n = 7$, $r = 0.99$, $p = 0.004$; p value estimated from 1000 data randomizations) (Fig. 2).

Of the 445 circles recorded on videotape, 97.1% ($n = 432$) were undertaken by males around females positioned on the bottom with the remainder experienced by females in

Fig. 3. Temporal changes in the number of circles received by reproductive female Atlantic cod in the experimental facility. Each line corresponds to the number of circles undertaken by a given male, the prominent males being 2R1 (solid line), 1L1 (long-dashed line), and 2L1 (long- and short-dashed line).



midwater. For all of the latter circles, females were circled while swimming to the bottom and were circled thereafter. Of the 141 occasions upon which a female was observed to swim to the bottom during the spawning period, circling of that female occurred 102 times (72.3%). Circles were made in both clockwise ($n = 235$, 52.8%) and counterclockwise ($n = 210$) directions. Males undertook an average 2.43 ± 0.15 circles per bout (\pm SE, range 1–17). Circles averaged 17.5 ± 0.3 s in duration (\pm SE, range 6–51).

The temporal incidence of circling and the number of circling males per female varied among individuals (Fig. 3). Females were circled by one to three males during 24-h time periods; the number of males observed to circle a given female averaged 2.1 ± 0.4 (\pm SE, range 1–4) throughout the spawning period.

Pedigree analysis

The loci *Gmo2*, *Gmo4*, and *Gmo132* were sufficient to unambiguously identify individuals. The pedigree analysis indicated that three males contributed to the fertilization of eggs from a single female (2R2) (Table 3). These were the most aggressive of the seven experimental males and their

ranks of fertilization success matched their ranks of body weight: 1L1 (2925 g), 2L1 (2503 g), and 2R1 (2291 g).

Discussion

Spawning of Atlantic cod

Coupled with that by Brawn (1961), the present study indicates, that successful reproduction in Atlantic cod involves a complex repertoire of behaviours within and between sexes. Spawning male Atlantic cod appear to establish a dominance hierarchy, with rank determined by aggressive interactions, particularly chases of one male by another, and by body size, larger individuals being dominant over smaller individuals. Agonistic interactions, continuing through the spawning season, may enable high-ranking males to defend territories. Limited genetic data suggest that male fertilization success increases with male body size and (or) behavioural dominance and that eggs from a single reproductive bout can be fertilized by more than one male (multiple paternity has also been documented by A. Rakitin, Department of Zoology, University of Guelph, Guelph, ON N1G 2W1, Canada, unpublished data). The existence of a behavioural

Table 3. Parental contributions to a random sample of eggs obtained from a single spawning event, as determined by pedigree analysis of microsatellite DNA analysis.

Sex	ID	Length (cm)	Weight (g)	Fertilization success (%)	Dominance Rank
Female	2R2	56.2	2020	—	—
Male	1L1	65.1	2925	85.2	2
Male	2L1	64.8	2503	11.1	3
Male	2R1	63.0	2291	3.7	1

dominance hierarchy and multiple paternity per spawning event raises the question of whether alternative mating strategies exist in Atlantic cod. Limited observations of multiple sperm releases in the experimental facility are consistent with this hypothesis. On three occasions, “satellite” males released milt among the female’s eggs and among the sperm released by the male involved in the ventral mount. One interpretation, then, of the paternity data is that the male involved in the ventral mount fertilized most of the eggs, while the other males achieved fertilizations as satellite individuals.

Prominent among male–female interactions is the circling of females, on the bottom, by one or more males. Initiation and termination of circling bouts appear to be under female control. Circling begins when a female positions herself on the bottom and ends when the female departs from the bottom and swims vertically in the water column away from the circling male(s). The temporal pattern of circling bouts for individual females (Fig. 3), coupled with the observation that females that swim to the bottom are usually circled, suggests that the timing of a female’s circling bouts may coincide with the ovulation of her egg batches. Spawning intervals of 2–6 days appear typical of individual females held in captivity (Kjesbu 1989; Chambers and Waiwood 1996; Kjesbu et al. 1996). These intervals correspond roughly with the 2- to 4-day peaks of circling activity experienced by females in the present study for which sufficient data exist (e.g., females 1R1, 3R1, 2R2, 2L2, and 1R2 in Fig. 3).

The present study indicates that females may not be in continuous physical contact with males during the spawning season, possibly restricting such associations to circling bouts and ventral mounts. Females were observed to swim to the bottom to enable males to undertake circling bouts; otherwise, females remained in the upper waters of the experimental tank. A similar vertical separation of sexes has been reported for Norwegian cod in the wild. Hydroacoustic data, coupled with the sampling of fish from different depths by Danish seine, gill nets, and pelagic trawls, indicate that male cod in spawning condition appear to be much more active than females and are typically found associated with the bottom, while females in reproductive condition tend to be found well off the bottom (Olav Rune Godø, Institute of Marine Research, N-5024 Bergen, Norway, personal communication). Vertical separation of the sexes during spawning is also suggested by male-biased sex ratios of reproductive Atlantic cod sampled by research bottom trawls in the Northwest Atlantic (Morgan and Trippel 1996).

The behavioural data reported here, and the depth distribution of wild Norwegian cod described above, imply a strong physical association between Atlantic cod reproduction and the bottom. This conclusion is supported by the observation that Atlantic cod in spawning condition are readily

captured within a few metres of the bottom (Hutchings et al. 1993; Rose 1993; Morgan and Trippel 1996; Morgan et al. 1997; Smedbol and Wroblewski 1997). Hydroacoustic data indicate that haddock, a gadid closely related to cod, may also be closely associated with the bottom (within 2.5 m) during reproduction (Boudreau 1992). Rose (1993) suggested that hydroacoustically determined vertical scattergrams extending through depths of 50 m or more, 50–150 m off the bottom, represented spawning columns of Atlantic cod off eastern Newfoundland. However, it cannot be determined whether fish in these vertical columns were physically sampled to determine their reproductive state, nor is there evidence to indicate that these same individuals were actually spawning. Nonetheless, these echograms may indicate that some spawning by Atlantic cod occurs in midwater.

Evidence of mate choice in a broadcast spawner

Several factors associated with the circling of reproductive females by mature males are suggestive of female mate choice. Firstly, circling bouts are initiated and terminated by females, i.e., they appear to be under female control. Secondly, by restricting circling to occasions when they are positioned directly on the bottom, females can effectively prevent ventral mounts by circling and noncircling males. Thirdly, circling provides females the opportunity to be in close physical contact with, and assess the quality of, several males prior to spawning.

Although potential means by which females might assess male quality are undoubtedly varied, e.g., visual inspection of body characteristics (Atlantic cod appear able to discern silhouettes throughout the depth ranges at which they are thought to spawn (see Rose 1993)), direct physical contact, possible pheromone release, and frequency of circling by individual males, there is reason to believe that auditory stimuli may be of considerable import. Sound production by males has been documented during reproduction in cod (Brawn 1961) and in the closely related haddock (Hawkins et al. 1967). These sounds are produced through compression of the swim bladder by rapid, synchronized contractions of specialized, highly innervated “drumming” muscles of high myoglobin content and rich blood supply (Hawkins 1986). Indeed, sonograms have revealed changes in the frequency, amplitude, and pulse interval of sounds produced by spawning male haddock concomitant with changes in courtship behaviour (Hawkins 1986). Female gadids may be able to discriminate sounds produced by individual males (acoustically mediated individual recognition has been documented in other fish, e.g., the bicolor damselfish, *Pomacentrus partitus* (Myrberg and Riggio 1985)).

Sexual differences in the size of drumming muscles would be consistent with the hypothesis of female mate choice. Templeman and Hodder (1958) measured the volume of

drumming muscles from more than 500 prespawning and spawning haddock from the Grand Bank and St. Pierre Bank off the east and south coasts of Newfoundland, respectively. Their study indicated that drumming muscles in males are larger than those in females and that this difference in muscle volume increases with body size, male muscles being about four to five times larger among 40-cm fish and about nine to 10 times larger among 70-cm individuals. Thus, based on the observation that male sound production is a prominent feature of male–female courtship and male–male aggression in haddock (Hawkins 1986), sexual differences in drumming muscle size may be the result of sexual selection, providing indirect evidence of mate choice.

Given that male Atlantic cod provide neither parental care nor physical resources to females, what possible benefits to female fitness may be associated with mate preference? Firstly, given that mating involves a ventral mount, fertilization success would be expected to be maximized when the urogenital openings of both individuals are aligned with one another, an argument in favour of assortative mating (Hutchings and Myers 1993). Secondly, the larger sperm volume possessed by larger males (see Trippel and Morgan 1994) may increase the probability that a male will have sufficient sperm to fertilize the batch of eggs (tens of thousands to hundreds of thousands) released by a female. Such an explanation appears to have merit in lekking frogs (e.g., Bourne 1993). Thirdly, a female may be able to reduce the probability of a disruption in courtship by other males by choosing a male high in the dominance hierarchy. And, fourthly, females may gain indirect genetic benefits if sexual selection is strong.

Do Atlantic cod lek?

The proposed physical location of reproduction (bottom), vertical separation of the sexes (males close to the bottom, females off the bottom), and the means by which individuals appear to acquire mates (mate competition among males, mate choice by females) may provide insight into the mating system of Atlantic cod. More specifically, the mating characteristics of leks are consistent with those known or proposed for Atlantic cod: (i) large, unstable, highly dense groups of females in a large undefended area, (ii) inability of males to monopolize resources to obtain matings, (iii) defence by males of small, clustered mating territories that females visit solely for mating, (iv) self-advertisement by males in the form of visual, acoustic, or olfactory displays, (v) nonrandom mating by females, and (vi) absence of male parental care (Davies 1991; Höglund and Alatalo 1995). The conditions under which leks are thought to evolve, i.e., an inability of males to defend economically either females or the resources that females may require for reproduction (Emlen and Oring 1977), would also appear to hold for Atlantic cod. Although leks have rarely been described in fishes, they have been documented for some cichlids (McKaye 1983; Barlow 1991).

Irrespective of their mating system, it seems reasonable to assume that fishing could negatively influence Atlantic cod reproductive success, e.g., the disturbance effected by the passage of a trawl through a spawning aggregation (Morgan et al. 1997). Assuming that males establish dominance hierarchies prior to and during spawning (Brawn 1961; present

study), one consequence of fishing-induced disturbances would be the displacement, and outright removal, of individuals that were constituent members of these hierarchies. Constant “reshuffling” of the ranks and perhaps body sizes of males during extensive periods of fishing may unnecessarily prolong the spawning interval between egg batches because of continual reestablishment of the dominance hierarchy and delays imposed on the time used by females to evaluate mate quality. Prolonged spawning intervals may reduce reproductive success, given that eggs unduly retained in the ovary after ovulation become unviable. For Atlantic cod, Kjesbu (1989) estimated that eggs are released about 5 h after ovulation. Kjørsvik and Lønning (1983) determined that the viability of Atlantic cod eggs declines rapidly 9 h after ovulation. Time periods during which eggs remain viable after ovulation for other marine fishes range from 10 h for turbot, *Scophthalmus maximus*, to as long as 48 h for Atlantic herring, *Clupea harengus* (Kjørsvik et al. 1990). Thus, by directly affecting spawning behaviour and indirectly influencing egg fertilization rates, increased spawning intervals provide a potential mechanism by which fishing may reduce Atlantic cod reproductive success.

The present study provides evidence of nonrandom mate choice and of male–male competition and display in Atlantic cod. The hypotheses suggested herein regarding mate choice, mate competition, auditory displays, and mating systems, and their implications for the management of demersal, broadcast-spawning fish, merit further consideration.

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