Sound Production by Atlantic Cod during Spawning

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Abstract.—Using captive groups of Atlantic cod *Gadus morhua* from two Northwest Atlantic populations (western Scotian Shelf and southern Gulf of St. Lawrence), we quantified the temporal patterns and behavioral contexts of sound production during the spawning season. We found that sound production occurs most frequently during the peak of the spawning period, particularly after the onset of darkness. The rate of sound production by males in the western Scotian Shelf group was 8.4 times greater on average than that of the southern Gulf of St. Lawrence group, and this corresponded to differences in the mass of the sound-producing musculature. Based on behavioral observations during daylight hours, we found that sounds were associated with both courtship behavior and agonistic displays. Although sounds were produced on only 14.5% of the occasions in which a male and female swam together in a "ventral mount," limited data suggest that ventral mounts accompanied by sound were more likely to lead to spawning. While almost all sounds produced by Atlantic cod in our study matched the short "grunt" type previously documented for this species, we report evidence for another sound, described as a "hum," which occurs during the ventral mount immediately before gamete release. We hypothesize that sound production is related to competition among males for access to females and may help synchronize gamete release, underscoring the potential importance of sound production to Atlantic cod spawning behavior.

Many fishes produce sounds to communicate information to other individuals as part of their social behavior. One of the most common contexts of sound production is during reproduction (Hawkins 1993). Under these circumstances, sounds are typically produced by males, often during agonistic interactions that may ultimately reflect competition among males for access to females. For example, territorial male bicolor damselfish *Stegastes partitus* produce "pops" when approached by another male (Myrberg 1972), and high-amplitude sounds are produced by male croaking gourami *Trichopsis vittata* during agonistic encounters (Ladich et al. 1992). In both cases, sounds are typically accompanied by agonistic behaviors such as chases, lateral displays, and circling, and may induce withdrawal of the opponent.

Reproductive sounds may also serve to advertise the presence and reproductive readiness of males to females and may even arouse reproductive activity in the latter. During the spawning season, male oyster toadfish *Opsanus tau* occupy well-defined areas on the seabed and emit "boatwhistle" sounds that attract gravid females (Gray and Winn 1961). Similarly, male haddock *Melanogrammus aeglefinus* occupy territories during the spawning period and produce long trains of repeated "knocks" believed to be attractive to females, drawing them to male territories to engage in courtship and mating (Hawkins et al. 1967; Hawkins and Amorim 2000). When a female haddock approaches a male and as courtship proceeds, the rate of knock repetition increases so as to appear as a continuous "hum" in the courtship stages immediately prior to gamete release. The progressive increase in rate of sound production as males become increasingly aroused may indicate to females a readiness to mate and help synchronize the release of eggs and sperm (Hawkins and Amorim 2000). Sound production by males might also provide a basis for mate choice by females. For instance, female bicolor damselfish use courtship sounds of conspecific males to locate nest sites (Myrberg et al. 1986) and acoustically mediated individual recognition has been documented for this species (Myrberg and Riggio 1985), thus providing a basis for mate assessment.

Atlantic cod *Gadus morhua*, a broadcast-spawning marine demersal fish found on both sides of the North Atlantic, reproduces in water depths ranging from tens to hundreds of meters (Brander 1994; Morgan et al. 1997; Smedbol and Wroblewski 1997). Like many fishes, cod are capable of producing and detecting sound (Hawkins 1993). Atlantic cod produce sound using three pairs of drumming muscles exterior to the swim bladder wall (Brawn 1961a; Rowe and Hutchings 2004). Typically, their sounds have been described as short "grunts" (about 200 ms) with peak sound amplitudes at frequencies ranging between about 50 and 500 Hz, and the acoustic repertoire is believed to

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be simple, with one call predominantly used in a variety of contexts (Brawn 1961a; Hawkins and Rasmussen 1978; Finstad and Nordeide 2004; but see Midling et al. 2002; Nilsson 2004).

Recent studies have shown that successful reproduction in Atlantic cod involves complex behavior within and between sexes, and it has been hypothesized that acoustic displays are involved in mate competition (Brawn 1961a, 1961b; Hutchings et al. 1999). Release of sperm and eggs by Atlantic cod involves a "ventral mount" in which the male, while grasping the female with his pelvic fins and matching her swimming speed, positions himself beneath her with the urogenital openings of both fish aligned to each other. Before mounting attempts, agonistic interactions (especially chases) are often seen among males and are believed to influence access to females (Brawn 1961b; Hutchings et al. 1999). Successful ventral mounts also appear to be preceded by courtship behavior, which has been described as an intense "flaunting" display during which the courting male moves alongside and in front of the female with median fins fully erect while "swimming with an excited, jerky, undulating movement with many unnecessary circles" (Brawn 1961b). Preliminary observation has suggested that Atlantic cod produce sound most frequently during the spawning period, and although both sexes are capable of making sounds throughout the year, primarily males appear to do so during the spawning season, typically during agonistic interactions and courtship display (Brawn 1961a).

Atlantic cod have been harvested for hundreds of years and are now at historic population lows in many areas, having decreased by almost 90% since the 1970s in the North Sea (ICES 2002) and by more than 99% off the coast of northeastern Newfoundland since the 1960s (COSEWIC 2003). Despite being of theoretical interest and practical importance, the spawning behavior of Atlantic cod is poorly understood; spawning has rarely been observed, and earlier descriptions of behavior and sound production have been brief and anecdotal. Having recently reexamined the behavior of Atlantic cod in some detail (Rowe and Hutchings 2003; Rowe 2004), here we quantify temporal patterns of sound production by cod within large captive spawning groups and relate sounds to patterns of fish behavior. Specifically, our objectives were to (1) describe daily and diel variation in the rate of sound production, (2) determine whether sound production is associated with egg production, and (3) identify the behavioral contexts in which sounds are produced. In addition, because we had the opportunity to assess groups of cod from two distinct populations, we were also able to examine potential differences in the rate of sound production

and drumming muscle investment at the population level.

Methods

To assess patterns of sound production by Atlantic cod, we examined fish from two spatially distinct areas in the Northwest Atlantic: the western Scotian Shelf and the southern Gulf of St. Lawrence, identified by the Northwest Atlantic Fishery Organization (NAFO) as divisions 4X and 4T, respectively. Mature adults from each population were collected 2 to 3 weeks prior to their annual spawning season, individually tagged, and placed in the 684-m^3 pool tank at Dalhousie University where spawning occurred. Indoor concrete aquaria, such as the pool tank, are not well suited for making the high quality acoustic recordings that are necessary for detailed analyses of sound characteristics. Nonetheless, the pool tank was chosen for this study because Atlantic cod grunts would still be audible and its large volume made it an ideal aquarium for examining cod spawning behavior. Cod from the western Scotian Shelf typically spawn during December–March, and their behavior was observed in 2 years: 2001 (25 females and 27 males, ranging 42–78 cm in length) and 2002 (25 females and 29 males, ranging 54–105 cm in length). By comparison, cod from the southern Gulf of St. Lawrence spawn during May–July and they were observed only in 2001 (41 females and 18 males, ranging 50–70 cm in length). Cod were maintained at densities similar to those reported for spawning individuals in the wild (Rose 1993; Morgan et al. 1997). They experienced water temperatures of approximately 8°C as well as ambient photoperiods, and were fed Shurgain 8-mm fish feed daily. A plankton net covered the tank outflow and was checked daily at approximately 1600 hours for the presence of eggs, the volume of which we quantified during 2002 as an indicator of spawning activity. Fish were sacrificed at the end of the spawning periods so that they could be sexed and measured. We recorded total length of each individual to the nearest millimeter, as well as total mass and gonad mass to the nearest 0.5 g. Somatic mass was calculated as total mass less the gonad mass. In addition, in the 2001 protocol, the three pairs of drumming muscles were extracted by forceps from the surrounding tissue and their combined dry mass was measured to the nearest 0.0001 g for each fish.

Sounds were recorded on Maxell T160 cassettes using a hydrophone (Vemco VHLF-10: built-in pre-amplifier, sensitivity of −147 dB re 1 V for a sound pressure of 1 µPa, and a flat frequency response from 10 to 20 kHz) suspended in midwater at the center of the tank and a Sony SVO-1630 videotape recorder. For western Scotian Shelf and southern Gulf of St.

Lawrence fish in 2001, sounds were recorded continuously from approximately 2 to 3 weeks after the start of spawning until the time when no eggs had been collected for 5 d. For western Scotian Shelf fish in 2002, we only recorded sounds during the last 8 h of daylight each day (0800–1600 hours) but started to monitor sound production approximately 2 weeks before spawning began. In addition, behavior was documented daily during the last 8 h of daylight for fish from western Scotian Shelf in 2002 (0800–1600 hours) and southern Gulf of St. Lawrence in 2001 (1200–2000 hours) by four video cameras mounted above the tank and the videotape recorder that also recorded audio information. Unfortunately, this camera array was not available for data collection during 2001 for western Scotian Shelf fish.

More than 2 h was required to extract information on sound production from each 1 h of videotape. Therefore, we examined only a subset of the recordings to investigate patterns of sound production. To examine daily variation in sound production by fish from the western Scotian Shelf in 2002, we reviewed 2 h (1100–1200 and 1500–1600 hours) of audio recordings approximately every fourth day during the spawning season and quantified the number of grunts heard. To examine diel variation in sound production by western Scotian Shelf and southern Gulf of St. Lawrence fish in 2001, we reviewed 6 h (0300–0400, 0700–0800, 1100–1200, 1500–1600, 1900–2000, and 2300–2400 hours) of audio recordings approximately every fourth day during the spawning season and quantified the number of grunts heard. Using the total number of grunts heard on each day of observation during 2001, we compared the rate of sound production between groups from the western Scotian Shelf and southern Gulf of St. Lawrence, controlling for the number of males in the tank by reporting the number of grunts per hour per male (most sound production during the spawning season is assumed to be by males [Brawn 1961a; Rowe and Hutchings 2004]). An analysis of covariance (ANCOVA) with somatic mass (a metric of body size) as the covariate was used to test for differences in drumming muscle mass in relation to population origin and sex. Initial models included all interaction terms, although nonsignificant interaction terms were removed from subsequent models. Both drumming muscle and somatic mass were log transformed to meet the assumptions of normality.

We examined videos recorded during the last 30 min of daylight every fifth day during the spawning season and documented any behavioral interactions visible in the group when sounds were produced. We focused our observation effort on the time close to dusk because cod activity levels appeared slightly higher during this period than other daylight hours. Nonetheless, behavioral interactions and sound production were infrequent events, and the chance of them occurring simultaneously solely by chance was very small. Interactions considered included five agonistic behaviors: (1) chase (swimming toward a swimming fish), (2) approach (swimming toward a stationary fish), (3) bite (physical contact between one fish's mouth and another fish's body or fin), (4) nip (an attempted bite [i.e., an opening and closing of the mouth near another fish's body or fin]), and (5) prod (contact between one fish's snout and another fish's body; Brawn 1961c; Hutchings et al. 1999). We also considered courtship behaviors (flaunting and ventral mounts; Brawn 1961b), as well as spawning events (indicated by the appearance of a cloud of milt in the water around a pair of fish engaged in a ventral mount). As part of a related study, all video recordings of southern Gulf of St. Lawrence fish in 2001 were reviewed to document the incidence of ventral mounts and spawning events in the group. In this case, we noted the identities of the fish involved (whenever possible) and whether the behavior was accompanied by sound production.

Results

Although we recorded sounds beginning approximately 2 weeks after the onset of egg production and did not quantify the volume of eggs collected during 2001, qualitative observations suggested that sound production occurred most frequently during the peak of the spawning season. This hypothesis was supported when we monitored sounds starting approximately 2 weeks before spawning began and quantified the volume of eggs collected daily for western Scotian Shelf cod during 2002 (Figure 1). To determine whether egg production increased with the production of sound, we regressed the volume of eggs produced on a given day against the number of grunts recorded on the same day between 1100 and 1200 hours and between 1500 and 1600 hours. Egg production was significantly associated with the production of sound during the former time period ($n = 15$; $r = 0.74$; $P = 0.001$). The number of grunts produced between 1500 and 1600 hours was also positively associated with egg production ($n = 15$; $r = 0.39$; $P = 0.15$), although not significantly so. However, exclusion of one outlying datum (the 146 grunts produced on day 21; Figure 1) did yield a highly significant correlation ($n = 14$; $r = 0.77$; $P = 0.001$).

During the spawning season, there was considerable variation in the occurrence of sound production in relation to time of day. For both populations, sound was produced at all times of day but was most frequent shortly after sunset, continuing at high levels through-
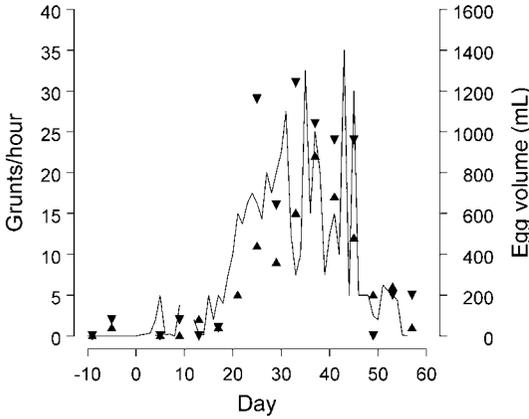
FIGURE 1.—Variation in sound and egg production by 25 female and 29 male Atlantic cod from the western Scotian Shelf during the 2002 spawning period. Day 1 represents the first day that fish spawned. Upward-pointing triangles indicate the number of grunts recorded from 1100 to 1200 hours, downward-pointing triangles the number of grunts recorded from 1500 to 1600 hours; the solid line indicates the volume of eggs collected. On day 21, 146 grunts were recorded between 1500 and 1600 hours, but this point was excluded from the graph.

out the night, and tapering during daylight hours (Figure 2). Most spawning events are also believed to have occurred at night as recently spawned eggs were collected most every day during the spawning season despite very few spawning events having been observed during daylight hours (see below).

There was a dramatic difference in the number of sounds produced by groups of cod from the southern Gulf of St. Lawrence and the western Scotian Shelf (Figure 2). Differences between the two groups in the number of sounds produced per hour persisted after controlling for number of males present (southern Gulf of St. Lawrence: 0.05 ± 0.01 SE grunts/h/male; western Scotian Shelf: 0.42 ± 0.11 SE grunts/h/male; analysis of variance [ANOVA]: $F_{1,25} = 11.75$, $P = 0.002$). Data available for western Scotian Shelf fish in 2002 showed high rates of sound production similar to those observed for western Scotian Shelf fish in 2001 during sessions recorded 1100–1200 hours (2001: 0.18 ± 0.07 SE grunts/h/male; 2002: 0.23 ± 0.06 SE grunts/h/male; ANOVA: $F_{1,31} = 0.35$, $P = 0.56$) and 1500–1600 hours (2001: 0.34 ± 0.15 SE grunts/h/male; 2002: 0.67 ± 0.31 SE grunts/h/male; ANOVA: $F_{1,31} = 0.95$, $P = 0.34$).

Differences in the rate of sound production by the groups of cod representing different populations corresponded to differences in drumming muscle mass (Figure 3; Table 1). Using ANCOVA with somatic mass as the covariate to test for differences in
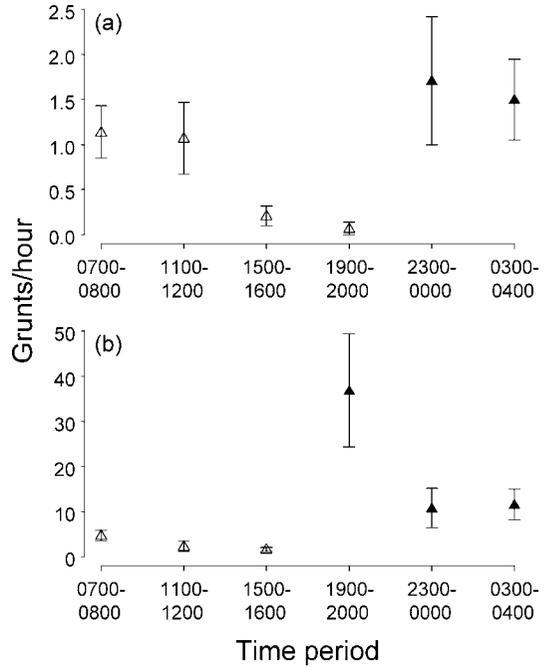

FIGURE 2.—Variation in sound production in relation to time of day for Atlantic cod from (a) the southern Gulf of St. Lawrence and (b) the western Scotian Shelf. Means ± SEs are shown. There were 14 d of sampling in the southern Gulf of St. Lawrence, 13 in the western Scotian Shelf. Open triangles represent sounds recorded during daylight, closed triangles sounds recorded during darkness.

drumming muscle mass in relation to population origin and sex, we found a significant interaction between population origin and somatic mass (two-factor ANCOVA: $F_{1,106} = 4.64$, $P = 0.03$). An additional ANCOVA involving only individuals from western Scotian Shelf revealed a significant association between drumming muscle mass and somatic mass (One-Factor ANCOVA: $F_{1,49} = 280.95$, $P = 0.0001$), as well as a significant difference in drumming muscle mass in relation to sex (males had heavier drumming muscles than females; one-factor ANCOVA: $F_{1,49} = 9.66$, $P = 0.003$). Similarly, involving only individuals from southern Gulf of St. Lawrence, we observed a significant association between drumming muscle mass and somatic mass (one-factor ANCOVA: $F_{1,56} = 94.20$, $P = 0.0001$), although there was no significant difference in drumming muscle mass between females and males (one-factor ANCOVA: $F_{1,56} = 3.20$, $P = 0.08$). That being said, the smaller range in somatic mass of individuals from the southern Gulf of St. Lawrence (Figure 3) might have reduced the power of our analysis to detect a difference in drumming muscle mass in relation to sex.
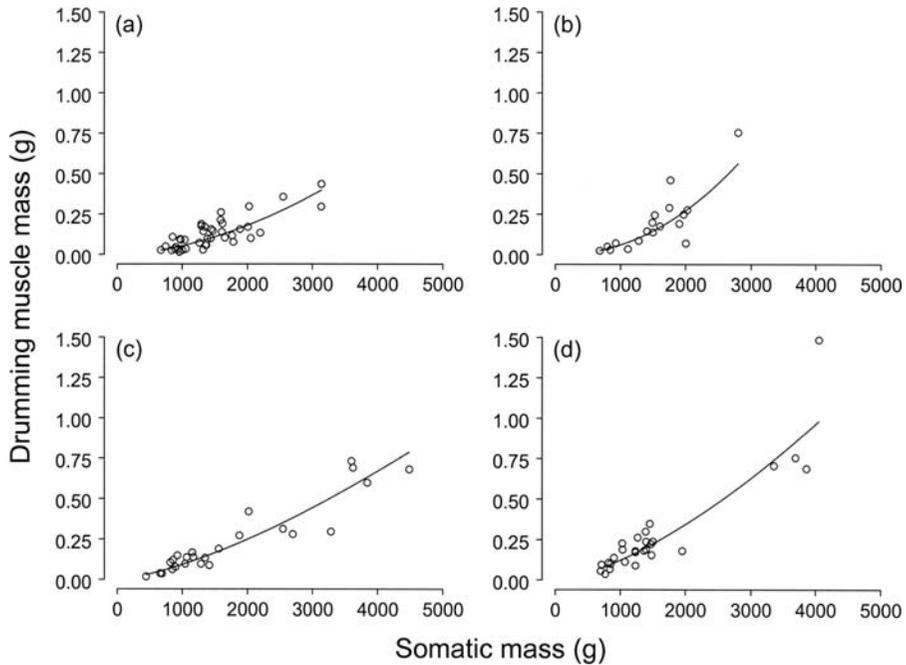
FIGURE 3.—Variation in Atlantic cod drumming muscle mass in relation to somatic mass for **(a)** southern Gulf of St. Lawrence females, **(b)** southern Gulf of St. Lawrence males, **(c)** western Scotian Shelf females, and **(d)** western Scotian Shelf males.

Sound production was associated with both agonistic interactions and courtship behavior. For example, among 425 grunts recorded during the last 30 min of daylight every fifth day during the spawning seasons, 26 (6.1%) were concurrent with an agonistic display (including 23 accompanying chases and three accompanying approaches). A total of 139 (32.7% of total) grunts were concurrent with courtship display (male flaunting, 132) and mounting attempts (seven). No discernable behavioral interactions were noted for the remaining 260 grunts. In addition, we found no evidence for a difference in the behavioral context of sound production between populations (western Scotian Shelf: 5.8% agonistic, 33.0% courtship, 61.2% no behavior, $n = 379$; southern Gulf of St. Lawrence: 8.7% agonistic, 30.4% courtship, 60.9% no behavior, $n = 46$; $G_2 = 0.59$, $P = 0.75$).

Examination of all video recordings of southern Gulf of St. Lawrence fish in 2001 revealed 106 ventral mounts, of which only six led to gamete release. We were able to identify the initiator in 104 (98.1%) of the ventral mounts observed and in all of these instances it was a male. The observed ventral mounts included 91 (85.8%) with no accompanying grunt(s) and 15 (14.2%) with grunt(s). Interestingly, among the 88 ventral mounts for which the recipient could be identified, 33 (37.5%) involved a male recipient and

55 (62.5%) involved a female recipient. However, we found no evidence for a difference in the occurrence of sound production during ventral mounts in relation to sex of the recipient (female recipient: 14.5% involved sound production, 85.5% did not involve sound production, $n = 55$; male recipient: 15.2% involved sound production, 84.8% did not involve sound production, $n = 33$; $G_1 = 0.01$, $P = 0.94$). Nevertheless, considering only instances that involved a female recipient, sound production was more likely to occur during ventral mounts that were associated with spawning (mounts associated with spawning: 50.0% were with sound, 50.0% were without sound, $n = 6$; mounts not associated with spawning: 10.2% were with

TABLE 1.—Regression equations describing drumming muscle mass (y) as a function of somatic mass (x) for female and male Atlantic cod from the southern Gulf of St. Lawrence and western Scotian Shelf. Both variables were log transformed.

Location and sex	Regression equation	n	r^2	P
Southern Gulf of St. Lawrence				
Females	$y = 1.76x - 6.54$	41	0.58	<0.0001
Males	$y = 2.16x - 7.68$	18	0.74	<0.0001
Western Scotian Shelf				
Females	$y = 1.42x - 5.31$	25	0.88	<0.0001
Males	$y = 1.48x - 5.36$	27	0.82	<0.0001

sound, 89.8% were without sound, $n = 49$; Fisher's exact test: $P = 0.03$). In three of the six spawning events, no sounds were detected after the start of gamete release. In all cases where sounds were heard after the start of gamete release, intense male–male competition for access to the spawning female was apparent in the form of four or more males moving rapidly into the gamete cloud, sometimes displacing the male involved in the ventral mount. For instance, on one occasion, the male that initiated courtship and spawning was displaced from the female early in the spawning event, whereafter the spawning female was mounted by a second male. At this moment, two grunts were heard while the original male counterattacked the second male. The original male may have produced these grunts during his counterattack; immediately after emission of the second grunt, the second male abandoned the female, as did other satellite males, when a third grunt was emitted.

Although very few "clean" waveforms could be obtained in our study, almost all sounds produced by our cod appeared to match the short grunt type described by other investigators (Figure 4; Brawn 1961a; Hawkins and Rasmussen 1978; Midling et al. 2002; Finstad and Nordeide 2004; Nilsson 2004). However, on two occasions, we heard a sound that seemed like a very low-pitched grunt lasting several seconds and that may be similar to the "hum" reported by Nilsson (2004) in his study of sound production by cod held in a net-pen at sea. On both occasions, the hum was emitted concurrent with a ventral mount, in the final moments immediately preceding gamete release.

Discussion

The temporal resolution at which we have examined sound production and its behavioral contexts is unprecedented for Atlantic cod and rare for broadcast-spawning marine fish in general. Interestingly, we found sound production to be positively associated with the production of eggs during spawning. We also documented significant among-population differences in sound production that correspond with observed differences in the size of the sound-producing musculature, which we suggest might reflect inherent differences in acoustic communication at the population level.

The first investigation of sound production by cod was provided by Brawn (1961a). This important study described deep grunting sounds that were produced most frequently during the spawning season, typically in agonistic interactions and courtship display by males. However, this description was based on sporadic observations at variable times of day and on
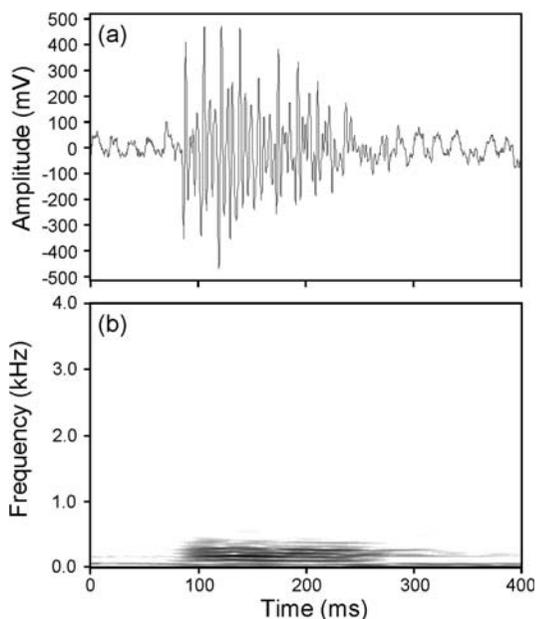

FIGURE 4.—(a) Oscillogram and (b) spectrogram of a single grunt recorded at 1900–2000 hours on 17 May 2001 from 1 of 59 Atlantic cod from the southern Gulf of St. Lawrence held in the pool tank at Dalhousie University. This is one of the best recordings achieved during the study.

an examination of a small group of captive individuals that varied in number and sex composition, potentially limiting the strength of the conclusions that could be drawn. To date, there has been no study subsequent to Brawn's (1961a) work to elucidate patterns of sound production by Atlantic cod or to determine whether they differ among populations.

We examined sound production in large groups of spawning cod from two Northwest Atlantic populations, focusing in particular on the behavioral contexts in which sounds were produced. Although sound production studies on large groups of individuals can be challenging, we found it useful to combine the recording of fish sounds with videotapes of fish behavior so that they could be observed repeatedly. Indoor concrete aquarium tanks, such as the one used in this study, are not ideal for recording fish sounds; the tank walls form reflecting boundaries that can distort sounds produced, and aquarium machinery can result in persistent low levels of background noise. Consequently, we were unable to make detailed measurements of individual sound characteristics of a nature similar to those undertaken on cod held in netting enclosures at sea (Hawkins and Rasmussen 1978; Midling et al. 2002; Nilsson 2004) or in outdoor fiberglass tanks (Finstad and Nordeide 2004). Nonetheless, sounds produced by fish in our study were audible

(even against background noise caused by machinery) and there did not appear to be discernable differences in the characteristics of grunts produced between our two populations of cod and those documented by other investigators (Figure 4; Brawn 1961a; Hawkins and Rasmussen 1978; Midling et al. 2002; Finstad and Nordeide 2004; Nilsson 2004).

Brawn's (1961a) description of sound production by spawning cod was based primarily on observations of seven females and six males held in captivity. She reported being able to identify the sound-producing individual within the group by observing sudden movements of the body that often accompanied sound production, particularly bending of the head and tail ventrally on the trunk. Using this technique, she concluded that only males produced sound during the spawning period, and that sounds were produced during agonistic encounters with other males and unripe females and during the flaunting display characteristic of courtship of ripe females. Unfortunately, the visual resolution afforded by our overhead video cameras did not allow us to document such external body movements that would assist us in identifying the sound producer in the tank. However, consistent with Brawn's (1961a) observations, we found that sounds were associated with agonistic interactions among males and courtship, although sound production seemed to occur more often during courtship (as opposed to during agonistic encounters as reported by Brawn [1961a]) for both of the populations that we examined. Curiously, no behavioral interactions were evident during most instances of sound production (260 of 425 grunts) and it is difficult to ascertain the function of calls in these situations. Brawn (1961a) did not report sound production during the ventral mount (except when a male was mistakenly mounted and he was interpreted to have then grunted to break up the pairing). In contrast, we found that 14.2% of ventral mounts were accompanied by sounds, and we found no evidence for a difference in the occurrence of sound production during ventral mounts in relation to sex of the recipient. Although Brawn's (1961a) observations were irregularly distributed through time, they are consistent with our work indicating that most sound production occurs during the spawning period, particularly after sunset. Increased use of acoustic signals at night may not be surprising given the reduced effectiveness of visual signals at this time (Anthony 1981). Regrettably, we were unable to observe cod behavior during hours of darkness so future work should be conducted to explore whether the behavioral contexts of sound production differ between day and night.

There has been much speculation about the function

of sound production by Atlantic cod (Brawn 1961a; Engen and Folstad 1999; Hutchings et al. 1999; Nordeide and Kjellsby 1999; Nordeide and Folstad 2000; Nilsson 2004; Rowe and Hutchings 2004). Both sexes are capable of producing sounds throughout the year and often do so during agonistic behavior, causing threatened individuals to flee (Brawn 1961a). Sound production by males becomes especially frequent during the spawning period, at which time agonistic behavior accompanied by sound production may indicate competition among males for space, perhaps even particular areas on the seabed, or for females themselves. Brawn (1961a, 1961b) reported that approximately 3 weeks before spawning, males became aggressive and that, using grunting sounds to reinforce threat displays, the most aggressive male was able to establish the largest "territory" in which all observed spawning occurred. Its prevalence during male flaunting also suggests that sound might be used in mate assessment by females. Brawn's (1961a) assertion of increased sound production during the spawning period, particularly among males, is supported by the observation that males have drumming muscles that are larger than those of females and that increase in mass prior to spawning and decline thereafter (Rowe and Hutchings 2004).

Acoustic communication may be an important criterion by which females discriminate among males from different cod populations. The spawning periods of migratory and stationary populations of cod off Norway overlap and reproductive individuals from both populations mingle spatially at the same spawning grounds (Nordeide 1998). In addition, artificial crossings of eggs and sperm from the two populations have been successfully conducted in the laboratory (Godø and Moksness 1987). Nonetheless, migratory and stationary individuals do not seem to interbreed in the wild, and female assessment of potential population differences in male acoustic displays has been suggested as a premating mechanism enabling this separation (Nordeide and Folstad 2000).

Acoustic displays may also allow females to discriminate among males for assessment purposes at an individual level (Myrberg et al. 1986; Andersson 1994). Greater investment by females than males in each zygote means that females have more to lose in an unsuccessful reproductive event, a cost that should make them more cautious in their choice of mate (Clutton-Brock and Vincent 1991; Andersson 1994). In Atlantic cod, females receive nothing from males but gametes; there is no parental care and males do not occupy an area with resources necessary for female survival or reproduction. Therefore, should direct benefits result from mate choice, they would most

likely come in the form of high-quality ejaculates that assure fertilization of eggs. Indirect benefits may also be realized if females can obtain information about heritable qualities of mates. Accordingly, patterns of variation in Atlantic cod drumming muscle mass are consistent with the hypothesis that acoustic displays represent a sexually selected indicator of male size, condition, and fertilization potential (Rowe and Hutchings 2004). In the present study, the importance of sound production to male mating and reproductive success might be reflected by the fact that ventral mounts accompanied by sound were more likely to lead to spawning than those that were not accompanied by sound. The occurrence of sound production also seemed to increase as courtship behavior by males intensified and a sound appearing similar to the hum reported by Nilsson (2004) was sometimes heard immediately prior to gamete release. Assuming that these sounds were produced by the courting male, it is possible that the increase in rate of sound production as the male becomes increasingly aroused provides an indication to the female of male readiness to spawn, resulting in a synchronization of egg and sperm release, thus achieving high fertilization success. Although hums appear to be infrequently produced, our observations and those of Nilsson (2004) suggest that they coincide with ventral mounts and possibly gamete release. Our observation that cod in a controlled, captive setting are capable of producing more than one type of sound (grunts and hums) lends support to the suggestion put forth by Midling et al. (2002) and Nilsson (2004), based on field studies, that the vocal repertoire of cod may be more complex than previously believed.

It has been suggested that, during the spawning season, mature male Atlantic cod aggregate near the bottom on spawning grounds where they actively defend mating territories and that females are typically found peripherally to male aggregations (Brawn 1961b; Morgan and Trippel 1996; Nordeide 1998; Hutchings et al. 1999). When ready to spawn a batch of eggs, females enter male aggregations, returning to peripheral areas after spawning (Brawn 1961b; Hutchings et al. 1999). In addition to its apparent use as a short-range signal related to agonistic and courtship behavior, it is not unreasonable to hypothesize that the chorus of sound produced by large aggregations of Atlantic cod males on spawning grounds might serve as a long-range signal to attract females to the spawning area (Nordeide and Kjellsby 1999).

Our study is one of the few to examine sound production in more than one fish population. We found no evidence for a difference in the temporal patterns or behavioral contexts of sound production between cod from the western Scotian Shelf and the southern Gulf of St. Lawrence. Nonetheless, the rate of sound production was much higher for western Scotian Shelf cod compared with those from the southern Gulf of St. Lawrence. Furthermore, the greater sound production was reflected by differences in the mass of drumming muscles relative to body size. Unfortunately, we are unable to identify the specific factors responsible for group differences in the rate of sound production and drumming muscle investment. Most sound production occurs at night, and fish from the western Scotian Shelf might have been expected to produce more sound than those from the southern Gulf of St. Lawrence solely because they experienced longer periods of darkness by spawning in winter. However, a less than two-fold difference in the period of darkness seems an unlikely explanation for the more than eight-fold difference observed in rate of sound production per male between groups. Similarly, although differences in sex ratio between our experimental groups might have influenced male mating strategies and display rates, these also seem unlikely to explain related differences in drumming muscle mass. While it is possible that the observed differences in rate of sound production and drumming muscle investment between cod from the western Scotian Shelf and the southern Gulf of St. Lawrence were solely an artifact of sampling, we suggest that they may also reflect inherent differences between these populations.

The highest catch rates in many commercial fisheries, including those for Atlantic cod, are achieved by mobile fleets that target spawning aggregations (Hutchings 1996) and the biological consequences of such fishing practices have been of recent concern (Hutchings and Myers 1994; Myers et al. 1997; Rowe and Hutchings 2003). Growing evidence for the importance of sound production in cod spawning behavior presents a new concern relating to interference caused by noise produced during fishing activity (e.g., from engines, trawl doors, gear contact with substrate, and trawl cables) which overlaps the frequencies of sounds produced by Atlantic cod (Brawn 1961a; Hawkins and Rasmussen 1978; Nordeide and Kjellsby 1999; Midling et al. 2002; Finstad and Nordeide 2004; Nilsson 2004). Disruption of acoustic signaling associated with mating might prolong intervals between egg batch releases because of the increased time required by males to aggressively compete for females and the increased time used by females to evaluate male quality (Hutchings et al. 1999). For batch-spawning fishes such as Atlantic cod, delays in the release of eggs after ovulation of just a few hours can dramatically reduce egg viability (Kjørsvik and Lønning 1983; Kjørsvik et al. 1990).

Unfortunately, at present, there are no data to directly assess the impact of anthropogenic noise on the spawning behavior and reproductive success of Atlantic cod.

Together with previous work, our study underlines the importance of sound production to Atlantic cod spawning behavior. Further studies involving playback experiments are required to elucidate the precise role of acoustic signals in reproductive behavior. In addition, research should be undertaken to better understand the causes and consequences of variation in rates of sound production and drumming muscle investment at both the individual and population levels.

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