

A link between sound producing musculature and mating success in Atlantic cod

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Individual variability in the mating success of male Atlantic cod *Gadus morhua* was quantified within an aggregation ($n = 59$) breeding undisturbed in a large (684 m³) mesocosm tank. Observational and morphometric data were examined to assess the degree to which this mating variation could be explained by aspects of morphology, condition and spawning behaviour. The number of ventral mounts initiated (*i.e.* mating success) was highly variable; most mounts were initiated by a very small percentage of available males. The significant correlate of male mating success was mass of the sound producing musculature, *i.e.* drumming muscles. Neither body size, condition, pelvic and median fin morphology nor aggression influenced the number of ventral mounts initiated by a male. The present study suggests a possible link between sound production and mating success in Atlantic cod.

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INTRODUCTION

It has been demonstrated in a number of fishes that processes such as mate choice and intrasexual competition can lead to high variability in mating success that is non-random with respect to individual morphology or behaviour (Andersson, 1994). For example, females have been shown to prefer to mate with males that have the most exaggerated features, such as the largest body size (*e.g.* broad-nosed pipefish *Syngnathus typhle* L.; Berglund *et al.*, 1986), the most conspicuous colouration (*e.g.* guppy *Poecilia reticulata* Peters; Houde, 1997), the longest fins (*e.g.* green swordtail *Xiphophorus hellerii* Heckel; Basolo, 1990) or the lowest pitch acoustic displays [*e.g.* bicour damselfish *Stegastes partitus* (Poey); Myrberg *et al.*, 1986]. Some of these traits, particularly large body size, may also be advantageous when males compete aggressively for access to females (*e.g.* Atlantic salmon *Salmo salar* L.; Fleming, 1998). Unfortunately, much of the present knowledge of fish mating systems has been derived

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from studies of relatively few species with a taxonomic bias towards freshwater spawning fishes, typically those depositing gametes in nests (Andersson, 1994; Amundsen, 2003). In contrast, there have been very few studies of the mating behaviour of broadcast spawning marine species which release large numbers (typically hundreds of thousands, often millions) of very small (typically <1.5 mm diameter) eggs directly into the water column, often in several batches throughout a breeding season, and provide them with no parental care (Hutchings, 2002; Rowe & Hutchings, 2003).

Reproduction in broadcast spawning marine fishes, particularly those that do not inhabit coral reefs, has been portrayed as a behaviourally vacuous process in which individuals mate with one another largely at random (Breder & Rosen, 1966; Nordeide & Folstad, 2000). Because energetic investment per gamete is extremely low for both sexes, and the probability of survival to maturity for each egg is typically $<1 \times 10^{-6}$ (Chambers, 1997), the fitness benefits of exerting mate choice or aggressively competing for mates may be negligible. Therefore, it might not be unreasonable to predict that breeding groups of broadcast spawning marine fishes lack the behavioural complexity seen in the mating systems of freshwater fishes and, instead, reproduce in an unstructured manner.

An emerging view is that the mating systems of broadcast spawning marine fishes may be considerably more complex. For example, based on studies of spawning behaviour, it has been hypothesized that intrasexual competition and mate choice may be integral to the mating systems of broadcast spawners such as Atlantic cod *Gadus morhua* L. (Brawn, 1961a; Hutchings *et al.*, 1999; Nordeide & Folstad, 2000; Rowe & Hutchings, 2003, 2006). 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, 1961a). Before mounting attempts, agonistic interactions (especially chases) are often seen among males and may allow behaviourally dominant individuals to establish 'territories' (Brawn, 1961a; Hutchings *et al.*, 1999). Successful ventral mounts also appear to be preceded by courtship behaviour, 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, 1961a). Both agonistic and courtship behaviours may be accompanied by acoustic displays (Brawn, 1961b; Rowe & Hutchings, 2006) produced using three pairs of drumming muscles exterior to the swimbladder wall (Brawn, 1961b; Rowe & Hutchings, 2004). The drumming muscles of Atlantic cod are sexually dimorphic with males having drumming muscles that are larger than those of females and that increase in mass prior to the spawning period and decrease thereafter (Rowe & Hutchings, 2004). Accordingly, sound production peaks 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 (Brawn, 1961b). The acoustic displays usually consist of short (*c.* 200 ms) 'grunts' with peak amplitudes ranging between 50 and 500 Hz (Brawn, 1961b; Hawkins & Rasmussen, 1978; Midling *et al.*, 2002; Finstad & Nordeide, 2004; Rowe & Hutchings, 2006).

Brawn (1961a) examined the reproductive behaviour of seven female and six male Atlantic cod held captive in a 10.8 m³ tank. In that study, the largest male became dominant and aggressively excluded other fish from a territory in which all observed spawnings occurred leading the author to conclude that male body size and behavioural dominance were important determinants of male mating success. Similarly, Hutchings *et al.* (1999) reported a positive association between male rank in a size-based dominance hierarchy and mating success (frequency of ventral mounts) when observing the reproductive behaviour of nine female and seven male Atlantic cod in a 60 m³ tank. Although Atlantic cod have been reported to spawn in large aggregations (Morgan *et al.*, 1997), studies of their spawning behaviour to date have involved only small groups of individuals ($n \leq 16$; Brawn, 1961a; Hutchings *et al.*, 1999) and none has examined mating success in relation to male condition (Rakitin *et al.*, 1999) or putative sexually selected traits such as drumming muscle mass (through acoustic displays; Brawn, 1961b; Engen & Folstad, 1999; Rowe & Hutchings, 2004, 2006), pelvic fin size (Skjæraasen *et al.*, 2006) or median fin size (Engen & Folstad, 1999).

In the present study, mating success of male Atlantic cod spawning in a much larger captive group was examined in relation to individual aspects of morphology, condition and spawning behaviour. Specifically, the objectives were to (1) describe variation in seasonal mating success among males and (2) quantify associations between seasonal mating success and male body size, condition, drumming muscle mass, fin size and aggression. Based on previous research, it was predicted that mating success would be positively correlated with body size and aggression (Brawn, 1961a; Hutchings *et al.*, 1999) and possibly with some of the other morphological traits examined. To be clear, ventral mounting success by males on females was used in the present study as a proxy for male mating success. The justification for doing so was based on the observations that (1) the ventral mount is the last in a series of courtship behaviours that precedes egg release and (2) egg release does not take place in the absence of a ventral mount (Brawn, 1961a; Hutchings *et al.*, 1999).

MATERIALS AND METHODS

EXAMINATION OF SPAWNING FISH

To identify correlates of mating success, a group of Atlantic cod from the southern Gulf of St Lawrence, Canada (identified by the Northwest Atlantic Fishery Organization as division 4T), was examined. Fish were captured by bottom trawl *c.* 2–3 weeks prior to the annual spawning period and taken to the 684 m³ Pool Tank at Dalhousie University, where they were allowed to spawn undisturbed. Before spawning, Atlantic cod were anaesthetized and individually marked with one or two 7.5 cm long, coloured T-bar anchor tags which were inserted into the dorsal musculature (Hutchings *et al.*, 1999). The group comprised 41 females (range 500–697 mm in total length, L_T) and 18 males (range 535–659 mm L_T) that spawned from May to July 2001. Unfortunately, it was not possible to determine the sex of individuals in advance of the experiment and control the sex ratio. Atlantic cod were maintained at densities similar to those reported for spawning individuals in the wild (Rose, 1993; Morgan *et al.*, 1997), experienced water temperatures of *c.* 8° C and ambient photoperiods (44°38' N), and fed Shurgain® 8 mm fish feed daily. Fresh sea water was pumped continuously into the tank.

Individual behaviour was observed throughout the spawning period from a platform above the tank. During these direct observations, each individual was monitored continuously for 3 min within the last 8 h of daylight each day (1200–2000 hours) and the incidence of five agonistic behaviours was documented: (1) chase (swimming towards a swimming fish); (2) approach (swimming towards 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) (Hutchings *et al.*, 1999). Direct observations of every fish were made on 34 occasions. Individuals were examined in varying order each day. Courtship behaviour was infrequent relative to agonistic behaviour and seldom observed during 3 min focal fish watches. Therefore, to examine courtship activity, behaviour was recorded daily during the last 8 h of daylight from 15 May to 14 July 2001, using four ceiling-mounted video cameras and a colour video-tape recorder. Subsequent to the spawning season, all video-tapes were reviewed (totalling 488 h of video coverage) to document the incidence of courtship behaviour, particularly ventral mounts, as well as the identities of the fish involved (it was possible to identify the initiating male in *c.* 93% of the ventral mounts observed).

Out-flowing surface water was sieved through a plankton net which was checked daily at *c.* 1600 hours for the presence of the positively buoyant spawned eggs. Microscopic examination of random samples of eggs collected in this manner indicated that almost all had been fertilized during the previous 24 h. The experiment was terminated and fish sacrificed when no eggs had been collected for at least 5 days. The L_T of each individual to the nearest mm was recorded, as well as total mass (M_T) and gonad mass (M_G) to the nearest 0.5 g. Somatic mass (M_S) was calculated as $M_S = M_T - M_G$. Sex was determined by observation of gross morphology of the gonad (Morrison, 1990). Estimates of pelvic fin size were obtained by measuring the length of the longest ray in the pelvic fin. In addition, the lengths of the longest fin rays of all median fins were determined. All aspects of fin size were measured to the nearest mm, using a calliper. Drumming muscles were extracted by forceps from the surrounding tissue (Rowe & Hutchings, 2004) and dried at *c.* 60° C until reaching a constant mass which was measured to the nearest 0.0001 g for each fish.

DATA ANALYSES

Differences among males in the number of mounts initiated on females during the spawning season were assessed in relation to aspects of morphology, condition and behaviour using a generalized linear model of count data with Poisson error (Crawley, 2002). Using S-Plus (Version 6.1), a maximal model was fitted and then simplified by sequentially removing non-significant ($\alpha = 0.05$) explanatory variables to obtain a minimal adequate model. To adjust for overdispersion of the data (dispersion parameter for minimal adequate model = 5), model simplification was conducted using an *F*-test instead of a χ^2 -test (Crawley, 2002).

Mating success was considered to be reflected by the total number of ventral mounts initiated by individual males on females in the video recordings. The L_T was included in the maximal model as a metric of body size. The residuals of the regression of M_S and L_T were included in the maximal model as a standard metric of condition. This metric of condition is based on the premise that a heavier M_S for a given L_T corresponds to increased general well-being of individuals. The M_S was selected for use in this analysis because it excluded M_G , which can vary significantly and independently of fish condition between seasons and within populations. In addition, because available energy reserves will be located in somatic tissues as opposed to germ cells, M_S may be considered a good reflection of condition (Lambert & Dutil, 1997). To examine the association between mating success and drumming muscle investment, the influence of body size on drumming muscle mass (Rowe & Hutchings, 2004) was controlled by using the residuals of the regression of drumming muscle mass and M_S in the maximal model.

To assess the association between mating success and median fin size, a principal component (PC) analysis was first undertaken to construct a variable that represented an amalgamation of the sizes of the median fins thought to be of importance during courtship displays (Brawn, 1961*a*). Following Engen & Folstad (1999), the lengths of the longest fin rays of the two most anterior dorsal fins and of the two ventral fins were included in the analysis. The loadings of the anterior and posterior ventral fins on PC1 (83% of the explained variation) were very high (0.88 and 0.44, respectively), suggesting a separation of males that possessed relatively tall ventral fins from those with relatively short ventral fins (the loadings of the two dorsal fin lengths were <0.20). The influence of body size on fin size was controlled by using the residuals of the regression of fin length (pelvic fin length or PC1 describing median fin lengths) and L_T in the maximal model.

In cases where residuals were derived using ANOVA, mass and L_T data were \log_{10} -transformed to meet the assumptions of normality and to linearize allometric relationships otherwise described by a power function; an exception was the regression of PC1 (describing median fin lengths) and L_T as some of the PC1 scores comprised negative values.

The aggression of each male was based on the number of agonistic interactions observed initiated by that male towards other fish during the sum of all daily 3 min focal fish watches for which he was monitored; this value was also included in the maximal model.

RESULTS

The number of ventral mounts initiated during the spawning season was highly variable among males. The most successful male initiated *c.* 48% of the ventral mounts (Fig. 1). The three most successful males initiated >88% of the ventral mounts, while 10 of the 18 males (56%) initiated no ventral mounts.

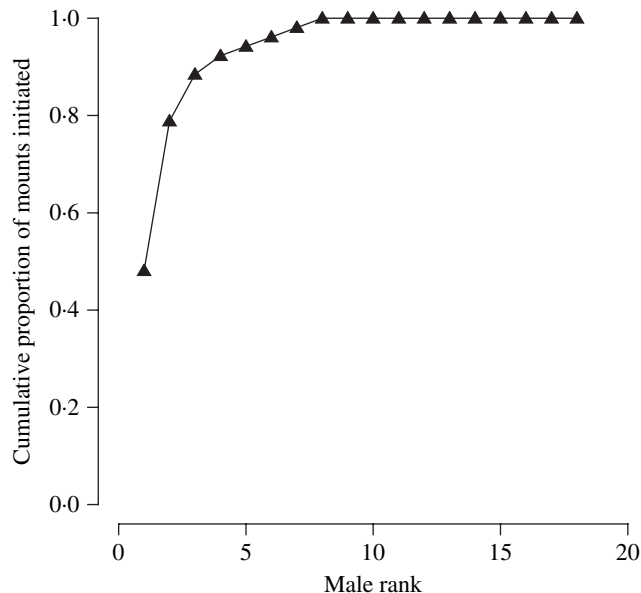


FIG. 1. Cumulative proportion of ventral mounts initiated on females by male Atlantic cod from the southern Gulf of St Lawrence, Canada, ranked from most to least successful.

Preliminary examination of the data suggested that the number of ventral mounts initiated might have been associated with male condition, drumming muscle mass, median fin length and agonistic interactions initiated (Table I). In particular, the most successful males in terms of mating (those that initiated $\geq 80\%$ of the ventral mounts on females) tended to have larger values for each of the above-mentioned traits than the remaining males in the spawning group. There was no apparent association, however, between L_T or pelvic fin length and male mating success (Table I).

The only explanatory variable included in the minimal adequate model describing the number of ventral mounts initiated by males during the spawning season was drumming muscle mass (residual deviance = 79.4, residual d.f. = 16, $P < 0.01$). The number of ventral mounts initiated by individual males during the spawning season tended to increase with increased drumming muscle mass relative to somatic mass (Fig. 2). The variation explained by the minimal adequate model was 49.8%. Other morphological traits (L_T , post-spawning body condition, pelvic fin length and median fin length) and the number of agonistic interactions initiated appeared to show no significant association with male mating success.

DISCUSSION

Variation in mating success of male Atlantic cod and its relation to patterns of individual morphology and social behaviour was examined using a large captive group from a north-west Atlantic population. While spawning groups under natural conditions are open systems comprised of individuals free to move in response to social or environmental cues, the experimental protocol employed here involved a closed system. Consequently, the possibility that the experimental facility may have influenced spawning behaviour and mating success cannot be excluded. Although little is known about Atlantic cod spawning behaviour in the wild, it is not unreasonable to assume that captivity may have altered female availability or male reproductive strategies. Average densities of $0.004 \text{ fish m}^{-3}$ have been reported for spawning aggregations in nature (Morgan *et al.*, 1997) which does not preclude the possibility that males establish territories of a size similar to those that have been described in captivity (Brawn, 1961a). Field recordings at natural spawning grounds when large numbers of spawning Atlantic cod are present have revealed increased sound activity within the frequency range of sounds produced by Atlantic cod in captivity (Nordeide & Kjellsby, 1999), suggesting that acoustic communication is also an important part of spawning behaviour in the wild. It is noteworthy that the tank used to conduct this experiment has the largest volume of any ever used to study the spawning behaviour of a marine fish.

Past observations of Atlantic cod spawning behaviour have suggested that male mating and reproductive success may be highly skewed (Brawn, 1961a; Hutchings *et al.*, 1999; Rakitin *et al.*, 2001; Bekkevold *et al.*, 2002). In the present study, male mating success was examined in a captive group more than three times larger than any examined in the past. Observation of this group confirms the high skew in male mating success suggested by previous studies.

TABLE I. Morphological and behavioural attributes of the most successful male in terms of mating (a), the most successful males in terms of mating (*i.e.* those that initiated $\geq 80\%$ of the ventral mounts on females) (b), and the remaining males (c) within a captive group of spawning Atlantic cod from the southern Gulf of St Lawrence, Canada

Rank	<i>n</i>	Mean \pm S.E. L_T (mm)	Mean \pm S.E. condition*	Mean \pm S.E. muscle mass†	Mean \pm S.E. drumming muscle mass†	Mean \pm S.E. pelvic fin length‡	Mean \pm S.E. median fin length§	Mean \pm S.E. agonistic interactions initiated
a	1	565	0.145	0.343	0.010	61.360	43.0	
b	3	573 \pm 5	0.060 \pm 0.043	0.202 \pm 0.082	-0.003 \pm 0.010	13.081 \pm 24.140	16.0 \pm 13.5	
c	15	581 \pm 9	-0.012 \pm 0.031	-0.040 \pm 0.052	0.001 \pm 0.006	-2.616 \pm 1.232	6.3 \pm 3.4	

L_T , total length.

*Residual somatic mass after controlling for L_T .

†Residual drumming muscle mass after controlling for somatic mass.

‡Residual pelvic fin length after controlling for L_T .

§Residual PC1 score (from a principal component analysis describing median fin lengths) after controlling for L_T .

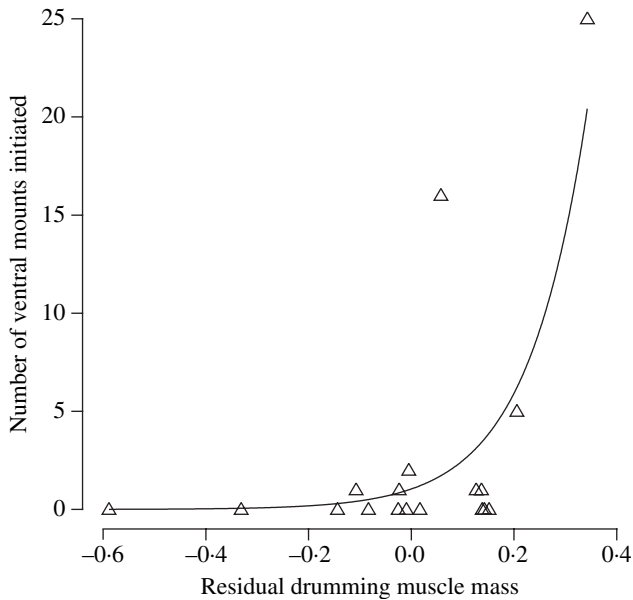


FIG. 2. Number of ventral mounts initiated on females in relation to residual drumming muscle mass after controlling for somatic mass of male Atlantic cod from the southern Gulf of St Lawrence, Canada. The line indicating values predicted by the minimal adequate model was fitted by $y = 1.04e^{8.68x}$.

The present study underscores the value of examining multiple traits in studies of mate competition and mate choice in fishes. In addition to examining phenotypic and behavioural characters described as influencing Atlantic cod mating and reproductive success in previous studies (Brawn, 1961a; Hutchings *et al.*, 1999; Rakitin *et al.*, 2001; Bekkevold *et al.*, 2002), the present study incorporated characters hypothesized to be used in visual and acoustic communication, including fins and drumming muscles (Brawn, 1961a, b; Engen & Folstad, 1999; Rowe & Hutchings, 2004, 2006; Skjæraasen *et al.*, 2006). Upon examination of this suite of characters, the mass of the sound producing musculature (corrected for body size) was found to be the only trait to explain a significant amount of the variability in male mating success.

Given that the sole known function of drumming muscles is to produce sound and that drumming muscle mass significantly influences the characteristics of sounds produced (Rowe & Hutchings, 2004; Amorim, 2006), the significant positive association between size of the drumming muscles and mating success documented here suggests that acoustic communication is fundamentally important to reproduction in Atlantic cod. Important as sound production may be to successful reproduction, it is unclear whether the correlation between drumming muscle mass and mating success is a product of mate choice or mate competition. The sound of a male's call might relay information about his quality (*e.g.* physical, gametic and genetic), allowing females to use acoustic communication as a means of selecting the male with whom she will mate (Brawn, 1961a, b; Hutchings *et al.*, 1999; Rowe & Hutchings, 2006). By contrast, a male's success in achieving a ventral mount with a female could

be an indirect consequence of his having attained a relatively high position in a dominance hierarchy. Although agonistic interactions were not associated with mating success in the present study, male sound production might influence position in a dominance hierarchy (Brawn, 1961a, b; Hutchings *et al.*, 1999; Rowe & Hutchings, 2006), under which circumstances a male's call might communicate information to others about his competitive ability. Accordingly, drumming muscle mass of spawning males has been reported to be positively associated with body size, condition and fertilization potential (Rowe & Hutchings, 2004), suggesting that sound production may be an indicator of the size of the signaller and may reveal information about individual quality. Although it is conceivable that Atlantic cod could visually assess characteristics of conspecifics, most spawning occurs at night (Brawn, 1961a; Rowe & Hutchings, 2006) when visual signals are less effective (Anthony, 1981).

The present work is not inconsistent with previous studies insofar as there also appeared to be positive associations between mating success and male condition, median fin size and aggression although the amount of additional variability explained by these factors was not significant. Contrary to the observations of Brawn (1961a) and Hutchings *et al.* (1999), however, there was no evidence for a positive association between mating success and male body size in the present study. This may have, in part, been due to low variability in body size among males (Bekkevold, 2006) or the female-biased sex ratio in the present experimental group. A considerable amount of variation remained unexplained by the minimal adequate model, suggesting that additional unidentified factors also may be of import to Atlantic cod mating success.

Broadcast spawning provides an opportunity for intense sperm competition (Stockley *et al.*, 1997) and may promote a variety of male reproductive strategies (Taborsky, 1998) such that mating success may not reflect reproductive success (*i.e.* some males may adopt strategies to achieve reproductive success without courting females). Unfertilized Atlantic cod eggs and sperm remain viable for >1 h in sea water (Kjørsvik & Lønning, 1983; Trippel & Morgan, 1994), potentially enabling sperm to compete for fertilization during a long period following ejaculation. Ejaculating sperm, even when not engaged in a ventral mount with a spawning female, may enable some males to acquire some reproductive success. Behavioural and genetic data are consistent with the hypothesis that alternative mating tactics exist among male Atlantic cod. Upon extrusion of the female's batch of eggs, the spawning couple may be joined by 'satellite males', which swim among the eggs and also release sperm (Hutchings *et al.*, 1999). Indeed, genetic data indicate that eggs from single reproductive bouts can be fertilized by more than one male (Hutchings *et al.*, 1999; Rakitin *et al.*, 2001; Bekkevold *et al.*, 2002). The ability of some males to sire offspring without courting females or aggressively interacting with other males may partially explain weak relationships apparent between reproductive success and morphological traits examined in previous studies (Rakitin *et al.*, 2001; Bekkevold *et al.*, 2002). Further studies of Atlantic cod spawning behaviour that consider both sexes while exploring linkages between mating and reproductive success (*i.e.* parentage) are warranted. It would be particularly interesting to examine how individual variability in mating and reproductive success might change with varying sex ratio or size structure.

Although anthropogenic noise has increased dramatically in the ocean (McDonald *et al.*, 2006), its impact on sound producing fishes is unknown. The results of the present study, showing an association between mass of the sound producing musculature and mating success in Atlantic cod, heighten concern regarding the potential for noise to interfere with acoustic communication in fishes, particularly during spawning. For example, the highest catch rates in many commercial fisheries, including those for Atlantic cod, are achieved by mobile fleets that target spawning aggregations (Hutchings, 1996). Noise produced during fishing activity (*e.g.* from engines, trawl doors, gear contact with substrata and trawl cables) overlaps the frequencies of sounds produced by Atlantic cod (Brawn, 1961*b*; Hawkins & Rasmussen, 1978; Midling *et al.*, 2002; Finstad & Nordeide, 2004; Rowe & Hutchings, 2006) and may interfere with their acoustic communication. Disruption of acoustic signalling associated with mating may prolong intervals between egg batch releases because of increased time required by males to aggressively compete for females and 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 & Lønning, 1983; Kjørsvik *et al.*, 1990).

Sound is integral to the mating system of many species (*e.g.* birds, insects and frogs), allowing individuals to communicate information related to their quality as a mate, a competitor for mates, or both (Andersson, 1994). Sound production is phylogenetically widespread in fishes (>800 species, 109 families) and often associated with spawning (Amorim, 2006; Rountree *et al.*, 2006), yet its functional significance is largely unknown. The present study suggests a link between sound producing musculature and a metric of fitness (*i.e.* mating success). In conjunction with previous work, this study highlights the potential importance of sound production to Atlantic cod spawning behaviour, indicating that acoustic displays may play a critical role in mate choice and intrasexual competition, thus leading to high variability in male mating success. Playback experiments are required to elucidate the precise role of acoustic signals in the reproductive behaviour of Atlantic cod. The present work underscores the urgent need for research on the effects of anthropogenic noise in the marine environment, particularly to address the potentially negative consequences to reproductive behaviour and population dynamics of sound producing marine fishes.

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