The function of sound production by Atlantic cod as inferred from patterns of variation in drumming muscle mass

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Abstract: We quantified variation in the mass of drumming muscles (the sound-producing musculature) among individual Atlantic cod (*Gadus morhua* L., 1758) for comparison with other evidence on the role of sexual selection in the evolution of sound production by this species. Based on 913 cod sampled from the Western Scotian Shelf in 2001–2002, we found that males had drumming muscles that were larger than those of females and that increased in mass prior to spawning and declined thereafter. Drumming muscle mass was highly variable, particularly among males, and generally more variable than other morphological traits (somatic mass and body length). This pattern of drumming muscle variation is consistent with the hypothesis that drumming muscles are influenced by sexual selection and suggests that sound production by males during the spawning season has fitness benefits, perhaps through a role in mate competition. Drumming muscle mass of spawning males was also positively associated with body size, condition, and fertilization potential, suggesting that sound production may be an indicator of the size of the signaler and may reveal information about individual quality. In conjunction with previous studies of sound production by Atlantic cod, our study underscores the potential importance of sound production to cod spawning behaviour.

Résumé : Nous avons mesuré quantitativement la variation individuelle de la masse des muscles de tambourinage (la musculature qui sert à produire des sons) chez la morue franche (*Gadus morhua* L., 1758) pour la comparer aux autres indications du rôle de la sélection sexuelle dans l'évolution de la production de sons chez cette espèce. À l'examen de 913 échantillons de morues provenant de la région occidentale de la plate-forme néo-écossaise en 2001–2002, nous trouvons que les mâles possèdent des muscles de tambourinage plus importants que ceux des femelles et que ces muscles s'accroissent en masse avant la fraye et perdent ensuite de la masse. La masse des muscles de tambourinage est très variable, particulièrement chez les mâles, et elle est en général plus variable que celle des autres caractères morphologiques (masse et longueur du corps). Ce pattern de variation des muscles de tambourinage s'accorde bien avec l'hypothèse qui veut que le tambourinage soit influencé par la sélection sexuelle et il indique que la production de sons par les mâles durant la période de fraye apporte des bénéfices de fitness, peut-être en jouant un rôle dans la compétition entre les partenaires. La masse des muscles de tambourinage chez les mâles en train de frayer est en corrélation positive avec la taille du corps, la condition physique et le potentiel de fertilisation; cela indique que la production de sons peut être un indicateur de la taille du poisson qui émet les sons et qu'elle peut fournir des informations sur sa qualité individuelle. À l'instar d'études antérieures sur la production de sons chez la morue franche, notre étude met en évidence l'importance potentielle de la production de sons dans le comportement de fraye des morues.

[Traduit par la Rédaction]

Introduction

Conspicuous song and other acoustic displays produced by animals during the breeding season may vary between females and males, across size or age classes, and among individuals in ways that reveal much about their function. In many species, including a neotropical frog (*Physalaemus pustulosus* (Cope, 1864)) and the bicolor damselfish (*Stegastes partitus* (Poey, 1868)), experimental evidence has demonstrated that song and other acoustic displays by males may be favoured by sexual selection because females prefer to mate with males that have the most exaggerated features, such as the largest song repertoire or the loudest, longest, or lowest pitch acoustic displays (Ryan 1983; Myrberg et al. 1986; Andersson 1994). Song and other acoustic displays may also be favoured by sexual selection through their role in intrasexual contests for access to mates. For instance, possession of a good territory is crucial for male mating success in many animals (Andersson 1994), and song or other acoustic displays may aid in territory defense, as demonstrated in red-winged blackbirds (*Agelaius phoeniceus* (L., 1766); Peek 1972; Smith 1976, 1979). Such differences in the force

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of sexual selection on males versus females often make sexual dimorphism an important aspect of display trait variation.

Several studies have also documented high levels of variation in sexually selected display traits relative to morphological traits thought to be favoured by other forms of natural selection (Alatalo et al. 1988; Jones and Montgomerie 1992; Evans and Barnard 1995; Jones et al. 2000). Wide variation in display traits has been hypothesized to result from a lack of stabilizing selection (Alatalo et al. 1988) and the tendency for their expression to be costly and thus correlated with individual health or condition (Grafen 1990; Iwasa et al. 1991), or alternatively in some cases because certain display traits are inexpensive to produce and maintain and are subject to weak mating preferences (Jones et al. 2000).

Most studies of song and other acoustic displays have focused on birds, insects, and frogs (Andersson 1994). Fishes also perform acoustic displays that may be critical to mating success (Hawkins 1993) but these have received comparatively little attention.

Atlantic cod (*Gadus morhua* L., 1758) is a broadcast-spawning marine demersal fish found on both sides of the North Atlantic that reproduces at water depths ranging from tens to hundreds of metres (Brander 1994; Morgan et al. 1997; Smedbol and Wroblewski 1997). Like many fishes, cod are capable of producing and detecting sound (Hawkins 1993). The calls of Atlantic cod are produced by three pairs of drumming muscles exterior to the swim bladder wall (Brawn 1961*a*) and consist of short "grunts" with peak sound amplitudes at frequencies ranging between about 50 and 500 Hz (Brawn 1961*a*; Hawkins and Rasmussen 1978; Midling et al. 2002; Finstad and Nordeide 2004). Recent studies have shown that successful reproduction in Atlantic cod involves complex behaviour within and between sexes and it has been hypothesized that acoustic displays are used in mate competition (Brawn 1961*a*, 1961*b*; 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. Prior to mounting attempts, males exhibit aggression towards other fish, typically in the form of fast approaches and threat displays that are often accompanied by grunting sounds (Brawn 1961*a*, 1961*b*; Hutchings et al. 1999). Agonistic interactions are believed to reflect competition among males for mates and influence male access to females (Brawn 1961*b*; Hutchings et al. 1999). Interactions between sexes are consistent with the hypothesis that females, and possibly males, exercise mate choice (Hutchings et al. 1999). One prominent behaviour observed in large tanks is the "flaunting" display exhibited by males as they circle around individual females with median fins fully erect (Brawn 1961*b*; Hutchings et al. 1999). Brawn (1961*a*, 1961*b*) reported that while flaunting before the female during courtship, the male also makes grunting sounds that have been hypothesized to form the basis of female choice of mate (Hutchings et al. 1999).

Preliminary observation has suggested that Atlantic cod produce sound most frequently during the spawning period and although both sexes are capable of producing sounds throughout the year, only males seem to do so during the spawning season (Brawn 1961*a*). This pattern of sound production strongly suggests a sexually selected function, but sporadic observations at variable times of day and examination of only a small group of captive individuals that varied in number and sex composition limits the conclusions that can be drawn from observations to date (Brawn 1961*a*, 1961*b*). Furthermore, there has been no attempt to quantitatively relate characteristics of the sounds produced to seasonal or individual variation.

To understand the function of a trait, it is essential to understand its patterns of variation. However, measuring variation in acoustic displays among individual fish has proven challenging. Because sounds propagate rapidly and effectively in water, it is often difficult to identify which individual emitted a particular sound when fish occur in groups. Furthermore, fish rarely produce acoustic displays when alone (Bremner et al. 2002). Nonetheless, mass of the drumming muscles, the acoustic display structure, may have a large influence on the characteristics of sound produced (Connaughton et al. 1997, 2000) and could be used as a metric of acoustic display trait expression. For instance, male weakfish (*Cynoscion regalis* (Bloch and Schneider, 1801)) also produce sounds using drumming muscles exterior to the swim bladder wall. In weakfish, the mass of these muscles is as seasonal as their use, with the muscles hypertrophying early in the spring spawning season and atrophying markedly late in the summer in response to changes in blood androgen levels (Connaughton and Taylor 1994, 1995). Sound amplitude mirrors this pattern, becoming more intense when the muscle is hypertrophied and decreasing in amplitude coincident with muscle atrophy (Connaughton et al. 1997).

In the present study, we sampled Atlantic cod captured in the commercial fishery to quantify variation among individuals in the size of the drumming muscles (the acoustic display structure) for comparison with other evidence on the role of sexual selection in the evolution of sound production (acoustic display trait expression) by cod. Specifically, our objectives were to (*i*) evaluate potential differences in drumming muscle mass in relation to sex, spawning status, and body size; (*ii*) quantify the amount of variation expressed in drumming muscles by each sex and the relative amount of variation expressed in drumming muscles versus other morphological traits; and (*iii*) test whether drumming muscle mass reflected body condition or fertilization potential of spawning males.

Materials and methods

To quantify variation in drumming muscle mass, we examined random samples of Atlantic cod caught on the Western Scotian Shelf (Northwest Atlantic Fisheries Organization Division 4X; 42°25′–44°20′N, 65°57′–67°30′W). Samples of 60–139 individuals were collected on nine occasions between 21 March 2001 and 25 February 2002 (Table 1). Fishing trips typically lasted 3–5 days. Fish were captured using an otter trawl and placed on ice until arrival in port, where they were measured and processed. For each individual examined, we recorded total body length to the nearest centimetre and total body mass and gonad mass to the nearest gram. Somatic mass was calculated as total body mass minus the gonad mass. We also determined sex and maturity

Table 1. Summary of Atlantic cod (*Gadus morhua*) sampled from the Western Scotian Shelf, 2001–2002.

Date	Sample size		Percentage spawning	
	Females	Males	Females	Males
21 March 2001	39	41	2.56	2.44
4 May 2001	68	67	0.00	0.00
18 June 2001	34	29	0.00	0.00
27 July 2001	52	52	0.00	0.00
20 September 2001	31	29	0.00	6.90
27 November 2001	69	55	21.74	65.45
17 December 2001	37	49	97.30	100.00
14 January 2002	76	46	11.84	19.57
25 February 2002	92	47	6.52	31.91
Total	498	415	13.45	26.99

(immature, ripening, ripe/spawning, and spent) of each individual by observation of gross morphology of the gonad (Morrison 1990). We found that it was sometimes difficult to distinguish between the immature and spent maturity stages and between the ripening and ripe/spawning maturity stages (Morrison 1990). Therefore, for the purpose of our analyses, we considered individuals to be "spawning" if they were initially scored as ripening or ripe/spawning and "nonspawning" if they were initially scored as immature or spent. Saggital otoliths were collected and ages later determined by experienced staff at Fisheries and Oceans Canada in Dartmouth, Nova Scotia, and St. Andrews, New Brunswick, through a process of sectioning the otoliths and counting annuli. The three pairs of drumming muscles cover the second, third, and fourth lobes of the swim bladder and are attached dorsally to the adjacent vertebral parapophyses and ventrally to the swim bladder wall (Brawn 1961*a*; Fig. 1). They are easily separated from the surrounding tissue using forceps. After extraction, the combined dry mass of these three pairs of muscles was measured to the nearest 0.0001 g.

We used ANCOVA with somatic mass (a metric of body size) as the covariate to test for differences in drumming muscle mass in relation to sex and spawning status. Initial models included all interaction terms, but nonsignificant interaction terms were removed from subsequent models.

Controlling for fish age, we used sign tests to assess whether there was sexual dimorphism in the coefficients of variation of drumming muscle mass and other morphological traits (somatic mass and body length). In addition, controlling for fish sex and age, we used sign tests to compare the coefficients of variation of drumming muscle mass with those of other morphological traits. For all sign tests, only age classes in which at least 10 individuals were sampled were included in the analysis.

To test whether drumming muscle mass reflected body condition of spawning males, we regressed the residuals of the regression of drumming muscle mass on somatic mass against the residuals of the regression of somatic mass on body length. We selected somatic mass for use in this analysis because it excluded the mass of the gonad, which can vary significantly and independently of fish condition between seasons and within stocks. In addition, because available energy reserves will be located in somatic tissues as opposed to germ cells, somatic mass may be considered a

Fig. 1. Atlantic cod (*Gadus morhua*) of unknown sex and spawning status with viscera and peritoneum removed to show drumming muscles (contained within boxes). Panels (*a–c*) represent photos of the same individual at increasing magnification.
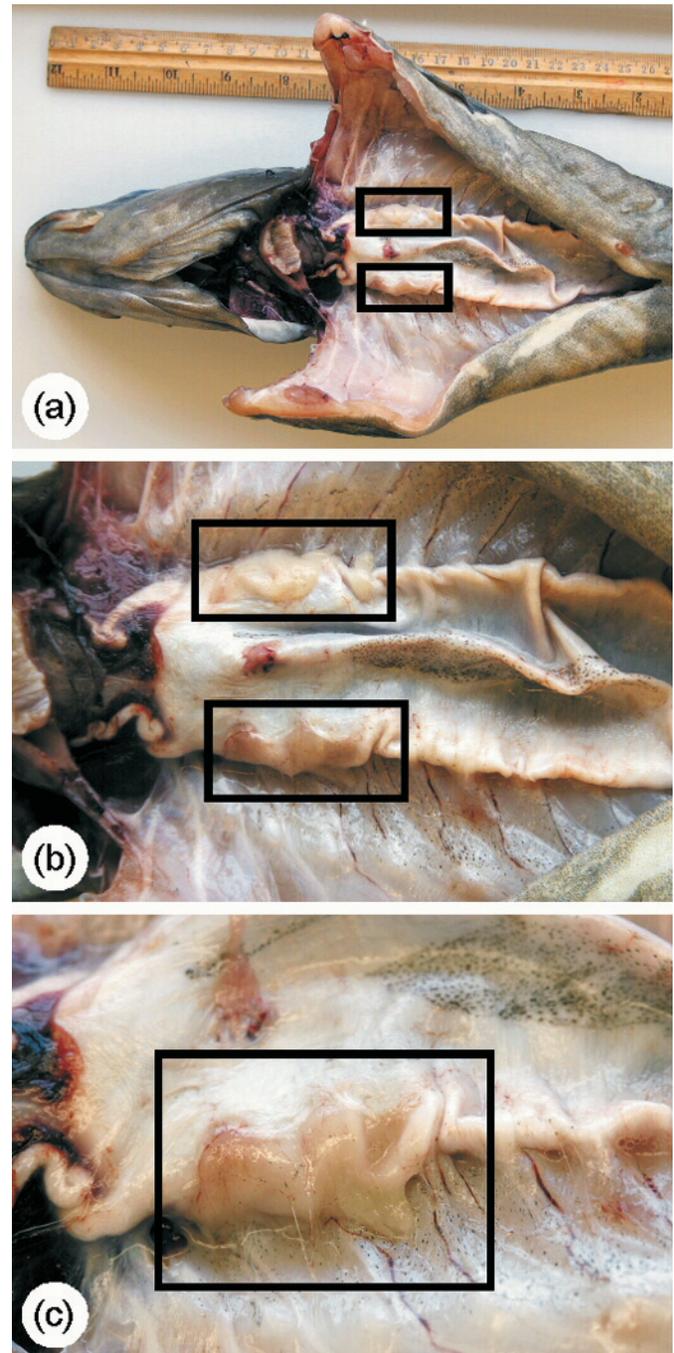
good reflection of condition (Lambert and Dutil 1997). Our technique produced a standard metric of condition on the *x* axis, and by using the residuals of the regression of drumming muscle mass on somatic mass on the *y* axis, we removed the possibility that any association with condition was a spurious consequence of drumming muscle mass being associated with somatic mass. Similarly, to test whether drumming muscle mass reflected fertilization potential of spawning males, we examined whether there was any asso-

Fig. 2. Variation in drumming muscle mass in relation to somatic mass for (*a*) non-spawning female, (*b*) non-spawning male, (*c*) spawning female, and (*d*) spawning male Atlantic cod from the Western Scotian Shelf.
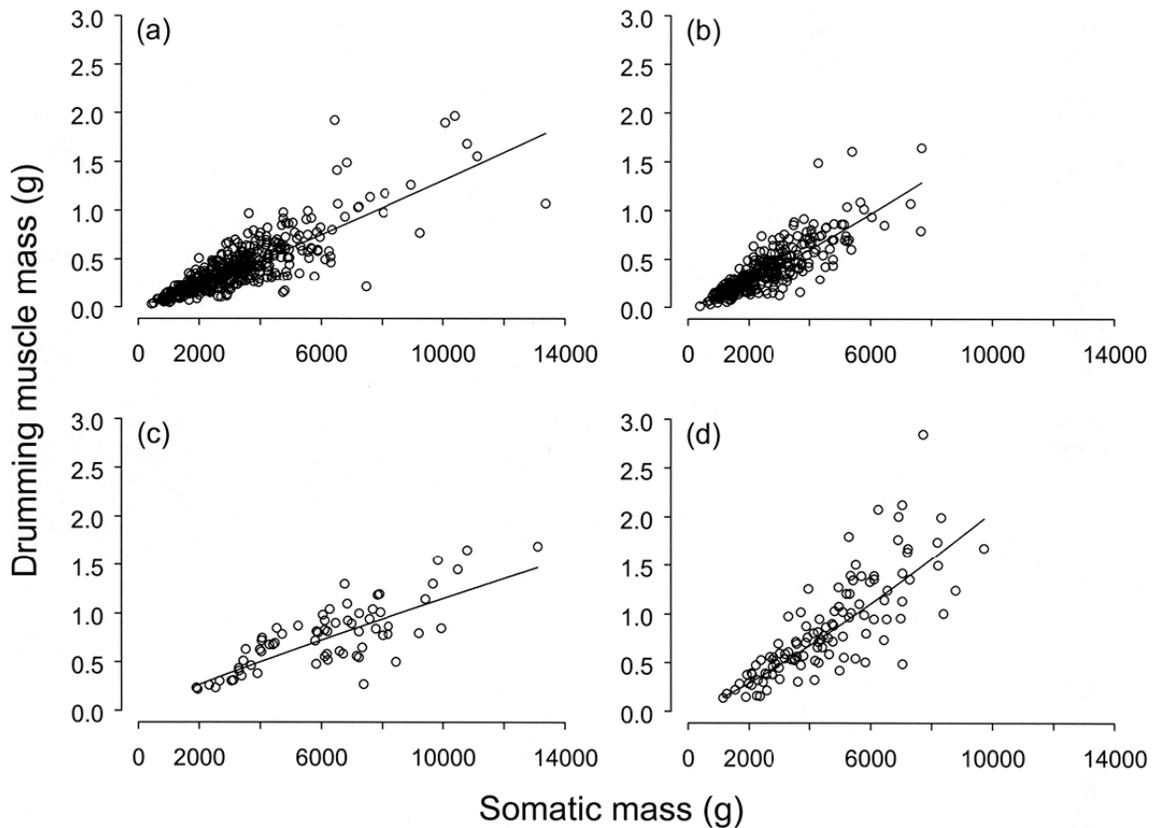

Table 2. Regression equations describing drumming muscle mass (*y*) as a function of somatic mass (*x*) for female and male Western Scotian Shelf Atlantic cod in non-spawning and spawning condition.

	Regression equation	Sample size	r^2	P
Non-spawning females	$y = 1.08x - 4.22$	431	0.74	<0.0001
Non-spawning males	$y = 1.17x - 4.45$	303	0.73	<0.0001
Spawning females	$y = 0.91x - 3.56$	67	0.64	<0.0001
Spawning males	$y = 1.21x - 4.54$	112	0.72	<0.0001

Note: Both variables were log transformed.

ciation between residuals of the regression of drumming muscle mass on somatic mass and residuals of the regression of gonad mass on somatic mass.

For both ANCOVA and residual analyses, mass and length data were log transformed to meet the assumptions of normality and to linearize allometric relationships otherwise described by a power function.

Results

Data were collected for 913 Atlantic cod from the Western Scotian Shelf. Individuals sampled in this study ranged from small, 2-year-old juveniles to large adults that were 9 years of age. Drumming muscle mass increased as a power function of somatic mass for both females and males in non-spawning and spawning condition (Fig. 2, Table 2). Using ANCOVA with somatic mass as the covariate to test for dif-

ferences in drumming muscle mass in relation to sex and spawning status, we found a significant interaction between sex and somatic mass (ANCOVA; $F_{[1,908]} = 13.93$, $P = 0.0002$). Specifically, when we controlled for body size, males generally displayed larger drumming muscles than females; the magnitude of this difference tended to increase with increasing body size. Further ANCOVA involving only males revealed a significant change in drumming muscle mass with changes in spawning status (ANCOVA; $F_{[1,412]} = 6.61$, $P = 0.01$). However, when only females were included, there was no change in drumming muscle mass with changes in spawning status (ANCOVA; $F_{[1,495]} = 0.07$, $P = 0.79$). In other words, it seems that after Atlantic cod reach maturity, drumming muscle mass increases more rapidly in males than in females and drumming muscles of mature males appear to undergo an annual cycle of hypertrophy during the spawning period, followed by postspawning atrophy.

Table 3. Variation in drumming muscles and other morphological traits of Western Scotian Shelf Atlantic cod in relation to gender.

| | Sample size | | Coefficient of variation | | | | | |
| | | | Drumming muscle mass (g) | | Somatic mass (g) | | Body length (cm) | |
Age (years)	Females	Males	Females	Males	Females	Males	Females	Males
2	20	18	0.50	0.63	0.45	0.43	0.14	0.14
3	162	138	0.61	0.61	0.45	0.40	0.14	0.13
4	150	128	0.57	0.66	0.49	0.49	0.17	0.16
5	106	79	0.64	0.75	0.49	0.51	0.17	0.18
6	32	23	0.73	0.62	0.50	0.42	0.17	0.13
7	12	13	0.31	0.55	0.39	0.41	0.11	0.17
8	11	6	0.58	0.58	0.48	0.28	0.19	0.08
9	3	3	0.82	0.64	0.60	0.72	0.23	0.24

Fig. 3. Association between residual drumming muscle mass after controlling for somatic mass and residual somatic mass after controlling for body length in spawning male Atlantic cod from the Western Scotian Shelf: (*a*) ages 3–9, (*b*) age 3, (*c*) age 4, and (*d*) age 5.
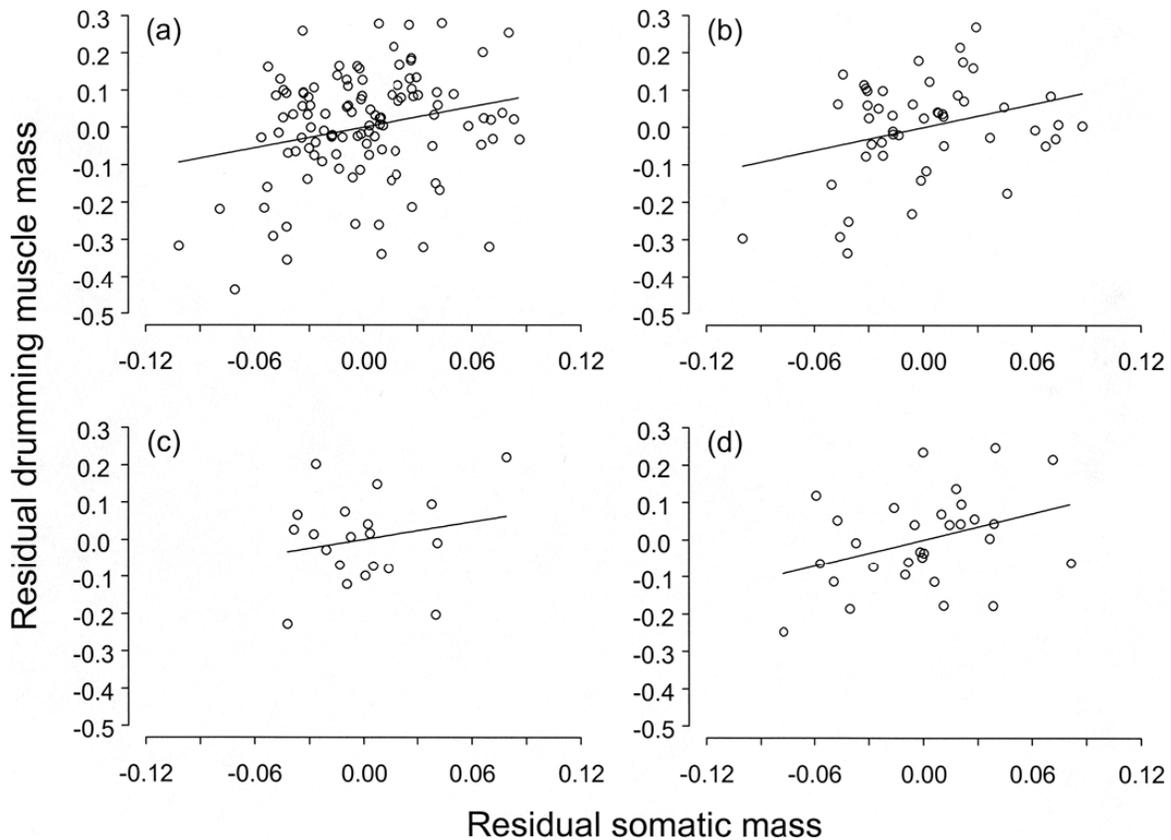
Sign tests provided no evidence for sexual dimorphism in the coefficients of variation for drumming muscle mass ($P = 0.38$), somatic mass ($P = 1.00$), or body length ($P = 1.00$; Table 3). This may be attributable to small sample sizes, particularly in the case of drumming muscle mass, where differences in the coefficient of variation between females and males within age classes were large. Generally, drumming muscles exhibited more variation than other morphological traits examined (Table 3). The coefficients of variation for drumming muscle mass were greater than those for body length for both females ($P = 0.02$) and males ($P = 0.03$). We also found greater coefficients of variation for drumming muscle mass than for somatic mass among males ($P = 0.03$), but there was no such difference among females ($P = 0.13$).

Residual analyses revealed that among spawning males, drumming muscle mass was weakly but significantly associated with both our metric of body condition ($F_{[1,110]} = 6.61$, $P = 0.01$, $r^2 = 0.06$; Fig. 3a) and fertilization potential ($F_{[1,110]} = 5.24$, $P = 0.02$, $r^2 = 0.05$; Fig. 4). When we controlled for differences in age and, to some degree, differences in lifetime breeding events, associations between drumming muscle mass and body condition were positive for spawning male cod 3, 4, and 5 years of age (Figs. 3b–3d) and statistically significant for all but the 4-year-old spawning males (spawning males aged 3 years, $F_{[1,47]} = 4.83$, $P = 0.03$, $r^2 = 0.09$; spawning males aged 4 years, $F_{[1,18]} = 0.80$, $P = 0.38$, $r^2 = 0.04$; spawning males aged 5 years, $F_{[1,28]} = 4.22$, $P = 0.05$, $r^2 = 0.13$).

Fig. 4. Association between residual drumming muscle mass and residual gonad mass after controlling for somatic mass in spawning male Atlantic cod from the Western Scotian Shelf.
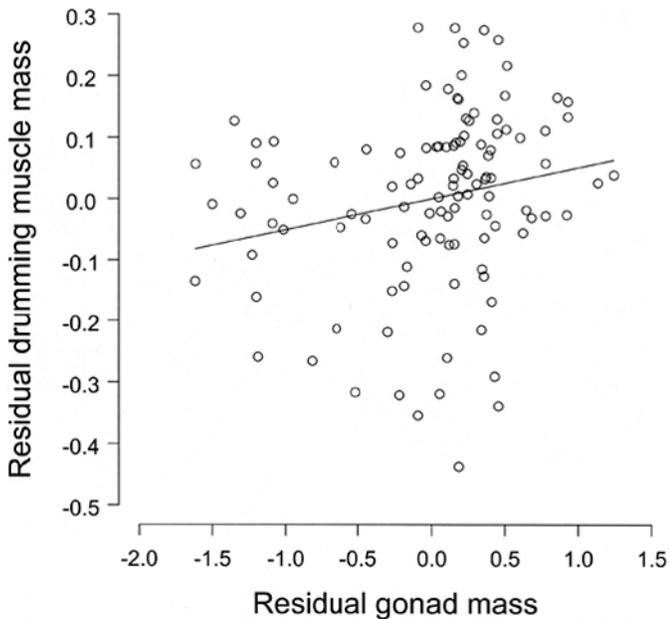
Discussion

To assess the function of sound production by Atlantic cod, we examined patterns of seasonal and individual variation in the mass of the sound-producing musculature. Although there are no data confirming that the mass of drumming muscles determines the loudness or other characteristics of sounds produced by Atlantic cod, we believe drumming muscle mass to be an appropriate metric for potential sound production by individuals. First, it seems logical that the muscles powering cod sound production should directly determine the nature of the sound. One would predict, for example, that larger muscles should produce greater sound energy; evidence for this has been forthcoming in weakfish, where sound pressure increases with increasing sonic muscle mass (Connaughton et al. 1997). Second, individual drumming muscle mass should be more consistent over time than the characteristics of the sounds they produce, thus making it a more reliable indicator of individual sound-producing ability. For example, sound characteristics, including sound pressure and frequency, have been shown to vary in relation to environmental conditions, particularly water temperature, on a day-to-day basis, making an individual's sounds difficult to measure and compare over time (Fine 1978; Brantley and Bass 1994; Connaughton et al. 2000; Midling et al. 2002).

Controlling for the influence of body size, we found that male Atlantic cod have larger drumming muscles than females and that among males, drumming muscles increase in mass before spawning and decline thereafter. Sexual dimorphism and seasonal variation in sound-producing musculature have been documented for several other fishes, including haddock (*Melanogrammus aeglefinus* (L., 1758);

Templeman and Hodder 1958), weakfish (Connaughton and Taylor 1994), and plainfin midshipman (*Porichthys notatus* Girard, 1854; T.P. Mommsen and K. Nickolichuck, unpublished observations in Walsh et al. 1995). In haddock, for instance, males have drumming muscles that are larger than those of females and that increase to nearly twice their normal size during the prespawning and spawning periods (Templeman and Hodder 1958). This pattern of drumming muscle variation matches the pattern of display trait variation of numerous other animals including insects, amphibians, reptiles, birds, and mammals that relates to the primary use of these traits in intrasexual contests and courtship during the breeding season (Andersson 1994). In addition, the coefficients of variation observed for Atlantic cod drumming muscles indicate that they are generally more variable than other morphological traits, a pattern consistent with a widespread pattern in animals whereby traits believed to be influenced by sexual selection are more variable than other traits (Andersson 1994).

Why should male cod have larger drumming muscles than females and invest in their development during the breeding season? An accumulating variety of circumstantial evidence suggests that it is because acoustic displays by males during the spawning season may have fitness benefits, perhaps by reinforcing threat displays directed primarily towards other males and by attracting and communicating spawning readiness to females (Brawn 1961a, 1961b; S. Rowe and J.A. Hutchings[2]).

We found that drumming muscle mass showed a strong positive relationship with body size, indicating that sound production is potentially a reliable indicator of size of the signaler. This can be seen in weakfish, where there is also a strong positive relationship between the mass of the sound-producing musculature and overall body size, which results in increased sound pressure and decreased dominant frequency with increasing fish size (Connaughton et al. 2000). Atlantic cod are broadcast spawners that release eggs and sperm during a ventral mount, and there is evidence to suggest that size complementarity between spawning partners might be important to ensure that the urogenital openings of both fish are aligned opposite one another and that high fertilization success is achieved (Rakitin et al. 2001). Consequently, assessment of male sound characteristics may provide information to females regarding size and hence suitability of potential mates. Although it is conceivable that cod could visually assess the size of conspecifics, most spawning occurs at night (Brawn 1961b; S. Rowe, personal observation), when visual signals are less effective (Anthony 1981).

Elaborate animal displays are often thought to convey not only size information but also details about the condition or quality of the signaler to potential mates (Andersson 1994, but see Bonduriansky and Day 2003). We found a weak but statistically significant positive relationship between relative drumming muscle mass and an index of body condition. Given that male Atlantic cod provide neither parental care nor physical resources to females, the possible benefits to female fitness associated with mate preferences are limited. Males in good condition may be less likely to be affected by

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parasites and diseases that could be acquired by the female during reproduction. In addition, there is recent evidence to suggest that male condition is a potentially critical factor determining sperm fertilization potency in Atlantic cod (Rakitin et al. 1999). We also found evidence that males with relatively large drumming muscles have larger gonads, even after controlling for body size, thus potentially allowing them to produce large amounts of sperm. In broadcast spawners such as Atlantic cod, it is seldom that all eggs are fertilized, and sperm limitation may be a significant issue (Rowe et al. 2004). Thus, females would be expected to benefit directly by mating with males that possess large quantities of sperm. The only possible longer term benefits to females would arise if males differ in their genetic quality, which would be reflected in the genotypes provided by their gametes. These kinds of genetic qualities might also be reflected by male condition. This suggests that by assessing characteristics of sound production by males, females might also be able to gather information relating to the ability of the individual to provide "good genes" and consequent benefits to offspring viability. In our study, as in many others (e.g., Jones et al. 2000; Veit and Jones 2003), the relationship between display trait expression and condition or fertilization potential was quite weak, suggesting that sound production may be only a weak reflection of individual quality and that other processes may contribute to mate selection in Atlantic cod. Furthermore, the relationships among sexually selected traits and other traits are likely to be complex and difficult to interpret (Bonduriansky and Day 2003).

An important study by Engen and Folstad (1999) also examined whether male Atlantic cod drumming muscles could provide information to females about male quality. They found no association between drumming muscle mass and parasite intensity or leukocyte density when controlling for body mass. However, they did find a negative correlation between spermatocrit (i.e., the percentage of the total volume of milt composed of sperm cells) and residual mass of drumming muscles after controlling for fish body size, which they inferred to be the result of attractive males having frequent ejaculations.

In addition to its potential use as a short-range signal related to agonistic and courtship behaviour (Brawn 1961a, 1961b; S. Rowe and J.A. Hutchings[2]), sound production by male Atlantic cod may serve as a long-range signal to attract females to the spawning area (Nordeide and Kjellsby 1999). It has been suggested that during the spawning season, mature male Atlantic cod aggregate near the bottom of spawning grounds, where they actively defend small mating "territories", and females enter male aggregations for only a brief period when ready to spawn a batch of eggs (Brawn 1961b; Morgan and Trippel 1996; Nordeide 1998; Hutchings et al. 1999). Nordeide and Kjellsby (1999) estimated that the chorus of sound produced by a large aggregation of male Atlantic cod may be heard by females up to several kilometres away and hypothesized that it may draw females to the spawning area.

Together with previous studies of sound production by Atlantic cod, our study underscores the potential importance of sound production to cod spawning behaviour, suggesting that acoustic displays act as a sexually selected indicator of male size, condition, and fertilization potential. Experiments should be undertaken to assess the proximate mechanism of seasonal and sex-related variation in Atlantic cod drumming muscles (e.g., the role of blood androgens) and to quantify the relationship between drumming muscle mass and sound characteristics. Further studies of cod sound production in which individual females and males are identifiable are required to elucidate the precise role of acoustic signals in reproductive behaviour. Specifically, we need to determine whether there are temporal patterns of variation in sound production, identify the behavioural contexts in which sounds are produced, and quantify the extent to which cod populations differ in drumming muscle investment and in the characteristics of sounds they produce.

Acknowledgements

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