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A cost of reproduction in male Atlantic cod (*Gadus morhua*)

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Abstract: In many species, females are thought to base their choice of mate on quality, which males signal through displays and body ornamentation. One important question is whether these signals represent an honest reflection of quality so that they carry an intrinsic cost to the male. A considerable body of evidence has revealed complex mating behaviours in gadoid fish, such as Atlantic cod (*Gadus morhua* L., 1758), for which male reproductive success may be related to some form of female choice. However, if present, the cost of male signalling is not clear. To test the hypothesis that male behavioural displays are energetically costly, we quantified the number of displays initiated by males during spawning, and their corresponding mass loss, in two separate experiments. The number of displays was positively associated with mass loss in both experiments, suggesting that reproductive displays are costly to males; they also may be regarded as an honest signal of quality upon which females could base their choice of mate. To our knowledge, this is the first study to demonstrate a cost of male reproductive behaviour in a broadcast-spawning fish.

Résumé : On pense que, chez plusieurs espèces, les femelles fondent leur choix de partenaire sur la qualité des mâles, que ceux-ci signalent par leurs déploiements comportementaux et l'ornementation de leur corps. Une question importante est de savoir si ces signaux constituent une représentation honnête de la qualité au point de présenter un coût intrinsèque pour le mâle. Un ensemble important de données indique que les comportements d'accouplement chez les poissons gadoïdes, par exemple chez la morue franche (*Gadus morhua* L., 1758), sont complexes, dans lesquels le succès reproductif du mâle est relié à une forme de choix de la femelle. Cependant, si la signalisation existe chez le mâle, son coût reste imprécis. Afin de tester l'hypothèse selon laquelle les signalisations comportementales des mâles comportent un coût énergétique, nous avons mesuré, dans deux expériences différentes, le nombre de déploiements entrepris par les mâles durant la fraie et leur perte correspondante de masse. Le nombre de déploiements est en association positive avec la perte de masse dans les deux expériences, ce qui indique que les déploiements reproductifs entraînent un coût pour les mâles; ils peuvent aussi être considérés comme des signaux honnêtes de la qualité sur lesquels les femelles peuvent baser leur choix de partenaire. À notre connaissance, la nôtre est la première étude à démontrer le coût du comportement reproductif du mâle chez un poisson qui fraie à la volée.

[Traduit par la Rédaction]

Introduction

For many mating systems, it is frequently assumed that females choose mates based on certain male attributes, such as ornamentation or reproductive behaviour (Andersson 1994). This is thought to arise because, compared with males, females invest heavily in gamete production (Trivers 1972). Because of their differential investment, females are predicted to reproduce with high-quality males to enhance offspring survival and, by extension, maternal fitness (e.g., Hasselquist et al. 1996). Males, by contrast, signal their quality to females. One prerequisite of such reproductive be-

haviour is that it represents an honest signal of quality and, hence, carries a cost (e.g., Zahavi 1975; Grafen 1990).

Male reproductive behaviour, which in its broadest sense involves both male–male aggression, courtship of females, and parental care, can be expected to incur costs; male–male aggression can, in extreme cases, lead to injury or even death (Hutchings and Myers 1987; Bean and Cook 2001). Perhaps more common is the cost associated with the energy demanded of reproductive behaviour in itself. For example, chorus tenure in male American Bullfrogs (*Lithobates catesbeianus* (Shaw, 1802)) is positively correlated with male condition (Judge and Brooks 2001), claw size in male Atlantic sand fiddler crabs (*Uca pugilator* (Bosc, 1802)) is positively associated with energetic expenditure (Allen and Levinton 2007), and male bird song and displays can also be energetically costly (e.g., Vehrencamp et al. 1989; Hasselquist and Bensch 2008). Among teleost fishes, both the fanning of fertilized eggs in sand gobies (*Pomatoschistus minutus* (Pallas, 1770)) (Lissaker et al. 2003) and parental care in smallmouth bass (*Micropterus*

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dolomieu Lacepède, 1802) (Gillooly and Baylis 1999) increase male mass loss. In the marine environment, many fish are termed broadcast spawners, meaning that eggs are spawned pelagically with no subsequent parental care. To our knowledge, no study to date has quantified the cost of male displays in a broadcast-spawning fish.

One mating system in which such costs might be realised is that of leks, wherein males compete vigorously for access to females (e.g., Höglund and Alatalo 1995). Several authors have suggested that broadcast-spawning Atlantic cod (*Gadus morhua* L., 1758) possess a lek-like mating system (Morgan and Trippel 1996; Hutchings et al. 1999; Nordeide and Folstad 2000). During the spawning period, males initiate aggressive interactions towards other males and court females, using acoustic and behavioural displays (Brawn 1961; Hutchings et al. 1999). These reproductive behaviours are associated with substantial movement and activity, e.g., burst swimming of males towards other males during agonistic interactions and multiple attempts by males to court and mate with females (Brawn 1961; Hutchings et al. 1999). No parental care is provided to the broadcasted eggs and, hence, there are no postcopulatory energetic costs associated with spawning.

Reproductive behaviour appears to be associated with reproductive success in male Atlantic cod (Rowe et al. 2008) and the former has been proposed to provide an opportunity for female choice (Hutchings et al. 1999; Rowe et al. 2008). Indeed, similar reproductive behaviour also has been described for another gadoid fish, the haddock (*Melanogrammus aeglefinus* (L., 1758)) (Hawkins and Amorim 2000). However, it is unknown whether such behaviour is energetically costly to male gadoids. If evidence to this effect was forthcoming, it would be consistent with the hypothesis that some elements of reproductive behaviour may be regarded as an honest signal of male quality. To address this question, we examined data from two laboratory studies on reproductive interactions among cod to test the null hypothesis that there is no correlation between male reproductive behaviour and male mass loss, a correlate of energy use, during spawning.

Materials and methods

We analysed data obtained from separate spawning experiments conducted in Canada and Norway, both of which were conducted in large tanks and used a combination of wild-caught cod and cod reared in captivity. The husbandry of all animals and the experimental protocols followed the guidelines of and were approved by the Canadian Council on Animal Care and Norwegian Council for Animal Research.

Canadian study

The reared cod were first-generation offspring of wild-caught cod from the NAFO (Northwest Atlantic Fishery Organization) subdivision 4X (41°N, 64°W) off southwestern Nova Scotia, Canada. Eggs were collected from the parental stock, which had been allowed to breed undisturbed in the 15 m diameter pool tank (684 m³) in the Aquatron Facility at Dalhousie University from February to March 2001. After collection, eggs were kept in incubators until hatching in

mid-April. Larvae were fed a diet of natural zooplankton until mid-June when they were fed dry pellets. Larvae and juveniles experienced a simulated natural photoperiod that followed the natural cycle for Halifax (44°40'N, 63°36'W). In February 2002, the reared cod were transferred to the 10 m deep, circular tower tank (117 m³) at the Aquatron. At the beginning of the experimental period in 2003, individuals were selected at random from a pool of approximately 150 reared cod.

Wild cod were caught from subdivision 4X by a commercial vessel, transported to Dalhousie University, and placed in the pool tank in January 2003.

The experiment

On 21 February 2003, all cod were sedated with Metacaine (0.5 g·L⁻¹), sexed by ultrasound (Karlsen and Holm 1994), weighed and measured for total length. Based on the ultrasound examination, 10 reared (5 males and 5 females) and 10 wild-origin (5 males and 5 females) cod were chosen for the study and introduced into the experimental tank. All males expressed sperm following the application of mild pressure to their ventral sides. Similarly, the ultrasound images were used to select females thought to have a high probability of spawning in the near future. These experimental fish were then tagged individually, using a two-tag system that permitted unambiguous visual identification, following Hutchings et al. (1999).

The volume of the experimental arena was 33 m³. The photoperiod in the tank was controlled by two separate timers, set to approximately 0800–1600. Temperature was approximately 4 °C in the tank during the experimental period. The cod were offered minute amounts of pellets, i.e., 400–500 g·week⁻¹ in total, during the experiment. On 20 April, the experiment was terminated and the cod sacrificed by an overdose of anaesthetic. All cod were then again weighed.

Behavioural observations

Three CCTV cameras were used to record spawning behaviour on videocassette recorders (VCR). One was mounted 2.5 m above the water surface in the centre of the tank, and additional cameras were mounted on side windows at depths of 1 and 2 m. Recordings were made continuously between 0800 and 1600 daily, from 26 February to 17 April, with the exceptions of 12 and 17 March because of a VCR malfunction.

The behavioural interactions examined in both experiments (Table 1) represent a compilation of behaviours described by Brawn (1961) and Hutchings et al. (1999). In Canada, each recording was first examined at 8× natural speed. If any reproductive behaviour by any individual was observed, the individuals involved were manually scored using Observer version 3.0 (Noldus 1991). Behaviours were primarily scored from recordings taken from the camera mounted above; the side-mounted cameras were used to assist in fish identification when necessary.

Norwegian study

Local coastal cod were captured from the Herdla-Øygarden area of western Norway: 51 fish were caught at 60°29'N and 4°53'E, and 24 fish were caught at 60°34'N

Table 1. The behavioural interactions considered during spawning of Atlantic cod (*Gadus morhua*).

Interaction	Name	Description	Reference
Courtship	Paired swim	Two fish are in motion following each other's movements closely, resulting in a circling pattern either near to the bottom or in the water column	Brawn 1961*
	Mount	Male mounts another cod ventrally, starting on top of the fish and "clasping" it with the pelvic fins. Thereafter, sliding down and ending up underneath the other fish, stomach-to-stomach, and with genital apertures close together. Associated with spawning, also frequently observed at other times	Brawn 1961
	Lateral display	A cod approaches another fish and freezes in mid-water, flexing its pectoral and pelvic fins	Hawkins and Amorim 2000
	Circling	One or more males circle around a female who lies motionless on the bottom	Hutchings et al. 1999
Aggression	Chase	Burst swimming towards a swimming fish	Hutchings et al. 1999
	Approach	Swimming towards a stationary fish	Hutchings et al. 1999
	Prod	Contact between a fish's snout and another fish's body	Hutchings et al. 1999
	Nip or bite	One fish biting or attempting to bite another	Hutchings et al. 1999

Note: Courtships are initiated by males towards both sexes, whereas aggressions are initiated by males almost exclusively against other males.

*The circling pattern was a part of the "flaunting display" described by Brawn, but other elements in the display she described were not observed.

and 4°56'E. The former were caught between November and December 2005 and held in a large 800 m³ sea pen (13 m diameter, 6 m depth) for 1–2 months after capture; the latter were caught in early January 2006 and held in submerged cages (1 m length, 60 cm width, 1 m depth) for 2 weeks. Prior to the experiment the wild fish were fed a mixture of fish, shrimp, and pellets. Fish were then transferred to the Institute of Marine Research (IMR) facility at Austevoll (60°05'N, 5°15'E) and placed in a 28 m³ holding tank. Farmed cod were obtained from a population maintained under standard commercial conditions at IMR, Austevoll. These cod were either repeat spawners hatched in spring 2003 or recruit spawners hatched in spring 2004, and were the progeny of local wild cod caught west of the Øygarden area (60°37'N, 4°48'E) (further details are given by Skjæraasen et al. 2008).

The experiment

Cod selected for the experiment, on 20 and 22 February 2006, were first sedated with Metacaine (0.5 g·L⁻¹) and then examined with ultrasound to determine the sex of each fish (Karlsen and Holm 1994). All males selected for the experiment were running with sperm upon application of gentle pressure to their ventral side and all females were either running with eggs or, based on the ultrasound image, predicted to be spawning in the near future. Fish were then measured for total length and whole body mass and tagged according to the protocol developed by Hutchings et al. (1999). Twenty-four cod (12 farmed, 12 wild) were released at equal sex ratios into a 27.5 m³ tank. Fish were allowed 1–2 days to recover prior to commencement of the study on 23 February. Cod were maintained under a normal photoperiod for Bergen (60°23'N, 5°20'E) and temperature in the tanks was approximately 8 °C throughout the experiment. Final sampling of fish, effected by an overdose of anaesthetic, occurred on 26 March after 31 days of behavioural observations, when individuals were again measured for total mass. No food was offered to the cod during the experiment.

Behavioural observations

Behavioural observations were filmed continuously from 1030 to 1830 daily, using a CCTV camera mounted 3 m above the water surface and connected to a VCR recorder. This camera covered approximately 90% of the tank volume and reliable identification was possible for all individuals. Fifteen minutes of every recorded hour were analysed and the frequency of all reproductive behaviours and identity of the individuals involved (see Table 1) were scored.

Data analyses

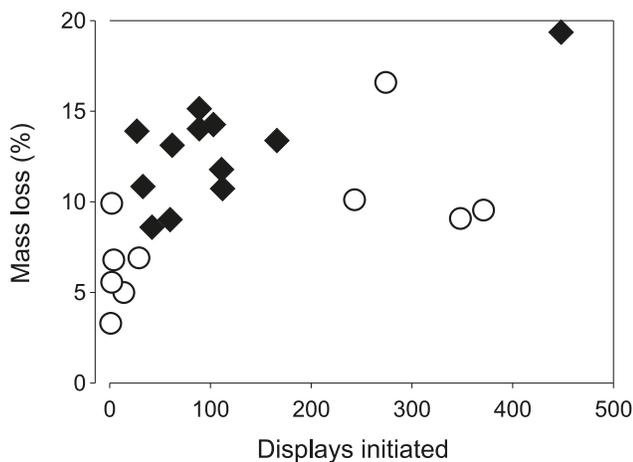
In both studies, least-squares linear regression was used to determine the relationship between the number of male displays (sum of all different behaviours; Table 1) and relative mass loss of males, i.e., $(\text{mass}_{\text{start}} - \text{mass}_{\text{end}}) / \text{mass}_{\text{start}}$. Both the dependent (relative mass loss) and explanatory variables (number of male displays) were log-transformed to linearize the relationship. We initially included separate intercepts and slope values for farmed and wild fish. We then used the Bayesian information criterion (BIC) to arrive at the final model (Venables and Ripley 2002). Graphical regression diagnostics (residual and Q–Q plots in R version 2.9.1; R Development Core Team 2009) and robust regressions (MM estimation, Library MASS of R version 2.9.1) were used to check the final models for homogeneous variance and the possible influence of outliers (Venables and Ripley 2002). We also tested the alternative hypotheses that male mass loss was related to (i) fish body size, by a simple regression between $\text{mass}_{\text{start}}$ and relative mass loss, both ln-transformed, and (ii) sperm expenditure, by a simple regression between relative gonad size, i.e., $\text{GSI} = \text{gonad mass} / \text{total mass}$, against relative mass loss. In the latter regression, both variables were arcsine-transformed before applying the model. Because of the size difference between reared and wild males, the regression between initial male mass and male mass loss was done separately for each male type in the Canadian study.

Table 2. Data from individual Atlantic cod (*Gadus morhua*).

Fish No.	Prespawn		Postspawn		Reproductive behaviour		ΔM (%)
	Mass (g)	Length (cm)	Mass (g)	Gonad mass (g)	No. of aggressions initiated	No. of courtships initiated	
Canadian study							
MR_10	1048	47	948	16.5	76	295	-9.5
MR_11	621	40	590	26	7	7	-5.0
MR_15	605	38	544.5	11.5	1	1	-10.0
MR_19	839	41	781.5	34	3	1	-6.9
MR_4	668	37	645.5	11.5	1	0	-3.4
MW_18	2960	68	2469	42.5	141	133	-16.6
MW_2	3216	69	2924	8	113	235	-9.1
MW_5	2670	67	2400	16	56	187	-10.1
MW_6	2708	66	2521	19.5	4	25	-6.9
MW_8	2286	66	2159	2	0	2	-5.6
Norwegian study							
2MW1	3418	68	3124	99	11	31	-8.6
2MW2	2798	64	2399	50	2	101	-14.3
2MW3	2650	62	2411	44	1	59	-9.0
2MW4	3400	66	2923	221	17	66	-14
2MW5	2604	63	2242	84	2	25	-13.9
2MW6	2826	66	2493	49	1	110	-11.8
2MF1	3170	62	2830	255	9	103	-10.7
2MF2	3170	65	2754	159	33	29	-13.1
2MF3	3208	63	2587	59	110	338	-19.4
2MF4	3466	67	3090	238	3	30	-10.9
2MF5	2630	59	2278	155	79	87	-13.4
2MF6	3402	67	2887	70	1	88	-15.1

Note: W, R, and F indicate wild, reared, and farmed males, respectively. Mass is the total mass of each fish, whereas gonad mass is the gonad mass at sacrifice. Reproductive behaviour is divided into the number of aggressions and courtships initiated by different males following the definitions given in Table 1. ΔM is the relative change in mass from the start to the end of the experiment.

Fig. 1. Scatterplot of displays initiated against mass loss for male Atlantic cod (*Gadus morhua*) in the Canadian study (○) and the Norwegian study (◆). Note that data from Canada and Norway were not pooled in our statistical analyses.



Results

There were large differences between individual male display intensity in both studies with values ranging from 1 to 371 displays in the Canadian study and from 27 to 416 in the Norwegian study (Table 2), but no difference in overall mass loss or display intensity between wild and reared cod

in the Canadian study or the farmed and wild cod in the Norwegian study (two-tailed Student's *t* tests, all *p* values > 0.21). Overall, mean mass loss by males was higher (two-sample Student's *t* test, *df* = 20, *p* < 0.01) for the cod in the Norwegian study, but mass loss was not associated with initial mass in either study. Relative gonad size at sacrifice was not associated with mass loss in the Canadian study (*p* > 0.05), whereas we found a significant interaction between GSI at sacrifice and mass loss between male types in the Norwegian study. This was caused by a nonsignificant tendency for wild cod to have a positive association between mass loss and gonad size (Student's *t* test, $t_{[5]} = 0.83$, *p* = 0.45), whereas it was negatively associated with mass for farmed males (Student's *t* test, $t_{[5]} = -4.29$, *p* < 0.05). Mass loss during the spawning period increased significantly with the number of reproductive displays initiated by males (Fig. 1). For the Canadian study, the number of initiated displays explained 49% (Fig. 1; $R^2 = 0.49$, $\beta = 0.13$, $t_{[8]} = 2.73$, *p* < 0.05) of the variation in male mass loss (Table 2). Males lost between 3% and 16% of mass over the experimental period (Fig. 1, Table 2). In the Norwegian study, male mass loss ranged between 8% and 19% (Table 2, Fig. 1), and the number of displays initiated explained 35% of male mass loss during spawning (Fig. 1; $R^2 = 0.35$, $\beta = 0.18$, $t_{[10]} = 2.34$, *p* = 0.042). Male type affected neither the slope nor the intercept of the regression lines in the Norwegian and Canadian studies (*p* values from 0.67 to 0.86) and in both

studies the final model selected by the BIC criterion included only the number of displays initiated as an independent variable. The regression parameters estimated by robust models were very similar to the least-squares regressions for both studies (Canada: $\beta = 0.13$; Norway: $\beta = 0.18$), indicating that the relationships were not strongly influenced by outliers.

Discussion

Our study may be the first to document an association between number of mating displays and subsequent mass loss, i.e., a cost of reproduction, in a broadcast-spawning fish. Males that were the most active behaviourally experienced a relative mass loss 2–3 times higher than that experienced by the least behaviourally active males. The higher mass loss among cod in the Norwegian study may be attributable to elevated (*i*) basal metabolic rates and (*ii*) increased costs of behavioural activity associated with a higher water temperature.

The energetic costs of reproduction documented here may have particular relevance to animals that mate in leks, as has been hypothesized for Atlantic cod (e.g., Nordeide and Folstad 2000). It seems highly probable that these costs will contribute significantly to individual variability in reproductive success because of the energy demanded by the territorial behaviour, mating displays, and aggression associated with leks. Energetic costs may be exacerbated by a strong reduction, or cessation, of feeding during the spawning period (Fordham and Trippel 1999; Skjæraasen et al. 2004; Michalsen et al. 2008). The minimal amounts of food received by cod in our Canadian study would, if anything, result in a conservative estimate of male mass losses during spawning. Cod are also known to experience increased mortality if their body condition becomes too low (Dutil and Lambert 2000). Thus, a doubling or even tripling of mass loss resulting from reproductive behaviour, such as that documented here, could negatively influence the reproductive success of low-condition males.

It might be argued that the positive association between male mass loss and male activity was caused by an increased expenditure of sperm by active males, rather than the cost of displays per se, given the observation that reproductive behaviour is associated with reproductive success in cod (Rowe et al. 2008). Although we cannot entirely discount such an influence, we do feel that this cannot fully explain our results. If displaying males were the only ones to release sperm, then it would be difficult to separate between the energetic cost of display behaviour and the mass of sperm as the primary reason for male mass loss. However, the extrusion of sperm is not limited to dominant males; satellite males also release sperm and compete with the primary male during egg release by the female (Hutchings et al. 1999; Rowe et al. 2007). This point to behavioural displays as the most parsimonious explanation for male mass loss. Relative gonad size at sacrifice also showed no general pattern in regard to male mass loss. The higher mass loss experienced by cod in the Norwegian study also suggests that differential sperm release is not the main cause of the observed variation in male mass loss, given that this arguably would not be expected to be greatly influenced by ambient temperature. Even so, differential sperm release by the satellite males may still account for some of the unexplained

variation in our regressions. Cod also are known to be behaviourally most active during the night (Finstad and Nordeide 2004). Although our significant correlations indicate that males active during the day were also active during the night, this could potentially also account for some of the unexplained variation in our data.

We have not distinguished between courtship and aggression behaviours in our analyses, given that our objective was to estimate the total reproductive effort of each male and its potential cost. It is also difficult to partition mass losses according to aggressions and courtships given the different swimming speeds and durations at which they occur. However, aggression may, in addition to courtship, be regarded as a form of honest signalling. We suggest two reasons for this hypothesis. Females may base their choice of mate on the outcome of male–male contests, i.e., by eavesdropping (e.g., Doutrelant and McGregor 2000). Secondly, the quantity and quality of aggressive interactions are likely to be important determinants of the dominance position of a male within a lek (e.g., Young et al. 2009).

In sum, male reproductive behaviour in Atlantic cod appears to be energetically costly, a conclusion consistent with numerous studies on other vertebrates (e.g., Vehrencamp et al. 1989; Allen and Levinton 2007; Sullivan and Kwiatkowski 2007). We also hypothesize that reproductive behaviour provides an opportunity for the expression of an honest signal of quality of male cod upon which females can base their choice of mate (reviewed in Andersson 1994).

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