

Sexual dimorphism in pelvic fin length of Atlantic cod

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Abstract: Behavioural differences between females and males may result in sexual dimorphism among morphological traits associated with these behaviours. In the broadcast-spawning Atlantic cod (*Gadus morhua* L., 1758), 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. Males also display the pelvic fins during agonistic encounters with other males. Based on data obtained from four Atlantic cod populations off Canada and Norway, we find clear evidence of sexual dimorphism in pelvic fin size, the fins being significantly larger in males than in females. Pelvic fin size was, however, not more variable than other morphological traits and was not correlated with body condition or drumming muscles mass (hypothesized to be a secondary sexual characteristic in this species). To our knowledge, this is the first study to demonstrate sexual dimorphism in any external morphological trait in a gadoid fish. Although the observed differences in pelvic fin size may be a product of sexual selection, we identify future work to test this hypothesis and to explore more fully the causes and fitness consequences of this sexual bias in Atlantic cod.

Résumé : Les différences comportementales entre les femelles et les mâles peuvent entraîner un dimorphisme sexuel dans les caractéristiques morphologiques associées à ces comportements. Chez la morue franche (*Gadus morhua* L., 1758), qui fraye à la volée, la libération des gamètes se fait au cours d’une « saillie ventrale » durant laquelle le mâle se place directement sous la femelle, tout en l’êtreignant de ses nageoires pelviennes. Les mâles exposent aussi leurs nageoires pelviennes lors des rencontres agonistes avec d’autres mâles. D’après des données provenant de quatre populations de morues au large du Canada et de la Norvège, il existe des indications nettes de l’existence d’un dimorphisme sexuel de la taille des nageoires pelviennes qui est significativement plus grande chez les mâles que chez les femelles. Néanmoins, la taille des nageoires pelviennes n’est pas plus variable que les autres caractéristiques morphologiques et n’est pas en corrélation avec la condition corporelle, ni avec la masse des muscles de tambourinage (que l’on croit être un caractère sexuel secondaire chez cette espèce). À notre connaissance, notre étude est la première à démontrer l’existence de dimorphisme sexuel dans une caractéristique morphologique externe chez un poisson gadoïde. Puisque les différences observées dans la taille des nageoires pelviennes pourraient être le résultat de la sélection sexuelle, nous précisons les études futures nécessaires pour vérifier cette hypothèse; nous examinons plus en profondeur les causes de cette différence sexuelle chez la morue franche et ses conséquences sur la fitness.

[Traduit par la Rédaction]

Introduction

Among broadcast-spawning marine fishes, particularly those not inhabiting coral reefs, females and males often appear very similar with respect to external body morphology. The apparent infrequency of sexual dimorphism might be attributed to a lack of visually conspicuous weapons or other ornament-like characteristics in these fishes relative to other groups such as birds and mammals. It might also be predicated by the hypothesis that the mating system of broadcast-spawning fishes lacks the behavioural complexity

necessary to generate sexual selection and, as a consequence, sexually dimorphic traits, resulting from factors such as mate competition and mate choice (reviewed by Nordeide and Folstad 2000).

The mating system of at least one broadcast-spawning marine fish appears to be considerably more complex than previously thought (Rowe and Hutchings 2003), raising the possibility that subtle sexually dimorphic characteristics may be evident in this species and in others for which gametes are released directly into the oceanic environment and for which no parental care is provided. The Atlantic cod (*Gadus morhua* L., 1758) has been the subject of an increasing number of studies of mating behaviour (Brawn 1961a; Hutchings et al. 1999; Rowe and Hutchings 2006). In this species, release of gametes occurs during a “ventral mount” in which the male positions himself directly beneath the female while apparently grasping her with his pelvic fins and matching her swimming speed (Brawn 1961a; Rowe and Hutchings 2003). This use of the pelvic fins is characteristic of spawning males, but not of spawning females, and appears to represent a behaviour expressed in a consistent and repeatable manner by males during the spawning period. The observation that males undertake a behaviour, appa-

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rently integral to spawning, that is not undertaken by females raises the possibility that pelvic fin morphology might differ between the sexes.

Prior to mounting attempts, agonistic interactions, often in the form of fast approaches and threat displays, are typically seen among males and are believed to influence access to females (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).

Like many fishes, cod can produce and detect sound (Hawkins 1993). The calls of Atlantic cod are produced using three pairs of drumming muscles exterior to the swim-bladder wall (Brawn 1961b; Rowe and Hutchings 2004). Although both sexes can produce sounds, only males seem to do so during the spawning season (Brawn 1961b). Sound production may reinforce threat displays directed towards other males (Brawn 1961b; Rowe and Hutchings 2006) and has been predicted to be a sexually selected character upon which females base an active choice of spawning partner (Engen and Folstad 1999; Hutchings et al. 1999; Rowe and Hutchings 2006). Drumming muscle mass is sexually dimorphic and may reflect male size, condition, and fertilization potential (Engen and Folstad 1999; Rowe and Hutchings 2004).

The primary objective of this paper is to test the hypothesis that size of the pelvic fin differs between female and male Atlantic cod. A secondary objective is to explore the degree to which any differences between the sexes in this trait might be a consequence of sexual selection. To undertake the second objective, we first examined whether male pelvic fin size co-varied with drumming muscle mass and (or) reflected body condition. Based on the observation that traits favoured by sexual selection often exhibit comparatively large variation relative to those under other forms of natural selection (Alatalo et al. 1988; Evans and Barnard 1995; Jones et al. 2000; Rowe and Hutchings 2004), we then examined whether variability in pelvic fin size differed between sexes, or in relation to the variability expressed in drumming muscles mass or other morphological traits.

Materials and methods

Study populations

To quantify variation in pelvic fin size, we examined cod from three spatially distinct areas off eastern Canada and from one area off western Norway. The regions from which cod were sampled from the Northwest Atlantic included the Western Scotian Shelf, Southern Gulf of St. Lawrence, and Eastern Scotian Shelf, identified by the Northwest Atlantic Fishery Organization (NAFO) as divisions 4X, 4T, and 4W, respectively. Individuals from each NAFO area were captured approximately 2–3 weeks prior to their annual spawning periods and transported to the 684 m³ pool tank at Dalhousie University where, as part of a separate behavioural study, they were allowed to spawn undisturbed. During the behavioural studies, cod experienced water temperatures of approximately 8 °C, ambient photoperiods, and were fed

Shurgain[®] 8 mm fish feed daily. Norwegian coastal cod were captured off Bergen (60°25'N, 5°20'E) during November and December 2005 by local fishermen. These Norwegian cod were held in a large outdoor sea-pen and fed small rations of Atlantic herring (*Clupea harengus* L., 1758) until mid-January 2006, whereafter they were transported to the Austevoll Research facility near Bergen, placed in a 30 m³ tank, fed rations of dry pellets, and allowed to spawn undisturbed. Spawning periods for each population were as follows — Western Scotian Shelf: December 2000–March 2001; Southern Gulf of St. Lawrence: May–July 2001; Eastern Scotian Shelf: November–December 2002; and coastal Norway: February–March 2006.

At the termination of spawning, fish were sacrificed so that they could be sexed and measured. For each individual examined, we recorded total body length to the nearest millimetre, as well as total body mass and gonad mass to the nearest 0.5 g. Somatic mass was calculated as total body mass less the gonad mass. We determined sex 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, for Eastern Scotian Shelf fish, we measured the width of the pelvic fin at its base. All aspects of fin size were measured to the nearest millimetre using a caliper. The three pairs of drumming muscles were extracted by forceps from the surrounding tissue (Rowe and Hutchings 2004) and their combined dry mass was measured to the nearest 0.0001 g for each fish.

Data analyses

We used an analysis of covariance (ANCOVA) with body length (a metric of body size) as the covariate to test for differences in pelvic fin size in relation to sex for each population, based on preliminary regressions which revealed that body length explained more of the variation in pelvic fin size than body mass. For our analyses of drumming muscle mass, we followed the protocol of Rowe and Hutchings (2004), which also used an ANCOVA but with somatic mass as the covariate. The assumption of slope homogeneity was not met in three of our tests for sexual differences (pelvic fin length in 4T and 4W cod, and drumming muscle mass for 4W cod), necessitating the application of a separate-slopes model for these analyses.

To determine whether male pelvic fin size was related to either body condition or drumming muscle investment, we undertook partial correlation analyses following Freckleton (2002), using pelvic fin length/width as the dependent variable and body length as the independent variable. To test whether pelvic fin size reflected body condition, we selected somatic mass as the covariate in our analysis because it excluded the mass of the gonad, 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, somatic mass may be considered a good reflection of condition (Lambert and Dutil 1997). Similarly, to test whether male pelvic fin size co-varied with drumming muscle investment, we used drumming muscle mass as the covariate.

For both the ANCOVA and partial correlation analyses,

mass and length data were ln-transformed to meet the assumption of normality and to linearize allometric relationships otherwise described by a power function.

We also examined whether variability in pelvic fin size differed between sexes or differed from the variability expressed by other morphological traits. Direct statistical comparisons of the variance in each trait were complicated by the observation that the mean values of the traits often differed from one another. Despite this limitation, the questions of whether pelvic fin variability differed between sexes or was greater than that expressed for other traits could be adequately addressed by simple inspection of the coefficients of variation (CVs) for each trait. Nonetheless, in addition to these inspections, we did compare the variance in residuals of pelvic fin length and pelvic fin width with that for drumming muscle mass, the one trait hypothesized to be a secondary sexual characteristic in Atlantic cod (Engen and Folstad 1999; Rowe and Hutchings 2004). This was done by using a Student's *t* test to compare the variance in residuals for pelvic fin length and width, after controlling for body length, with the variance in residuals for drumming muscle mass, after controlling for differences in somatic mass.

Results

The size of the pelvic fin increased with body size and differed between sexes, the length of the fin being greater among males than among females within each of the study populations ($p < 0.05$ for all populations; Fig. 1). Pelvic fin width, for which data were available for only one population (4W cod), was also positively correlated with body length ($F_{[1,87]} = 147.7$, $p < 0.0001$) and was wider among males than among females ($F_{[1,87]} = 10.8$, $p < 0.01$; Fig. 2). For comparative purposes, the difference in pelvic fin length between a male and female cod of 60 cm, based on the results of simple regressions for each population with sexes considered separately, ranged from 0.41 cm (4T) to 0.79 cm (4W).

Drumming muscle mass differed significantly between sexes within 3 of the 4 study populations (Fig. 1). The drumming muscles were significantly heavier among males than females sampled from the 4X, 4W, and Bergen populations ($p < 0.05$). Males also possessed heavier drumming muscles than females among cod sampled from the 4T population, although the difference was not statistically significant ($p = 0.08$).

There was little evidence that pelvic fin size was associated with either drumming muscle mass or condition, based on the results of the partial correlation analyses. After controlling for the effects of body size on each variable, there was no significant relationship between pelvic fin length and drumming muscle mass within any of the study populations ($p > 0.05$). Similarly, pelvic fin length was independent of condition in 3 of the 4 populations ($p > 0.05$). Although pelvic fin length was significantly associated with condition among 4W cod (partial correlation coefficient = -0.39 , $df = 13$, $p < 0.05$), the variation in pelvic fin length explained by condition was very small (adjusted $r^2 = 0.13$). Among cod sampled from the 4W population, pelvic fin width was not associated with either drumming muscle mass or condition ($p > 0.05$).

Although pelvic fin length was greater among males than

among females (Fig. 1), there was no consistent sexual bias in the CVs for this trait among the study populations and there was no evidence that the CVs for pelvic fin size were greater than those of other traits (Table 1). Based on simple inspection of the estimates presented in Table 1, variability in pelvic fin length and pelvic fin width was either considerably less than (somatic mass, drumming muscle mass), or comparable with (body length), variability in other morphological traits.

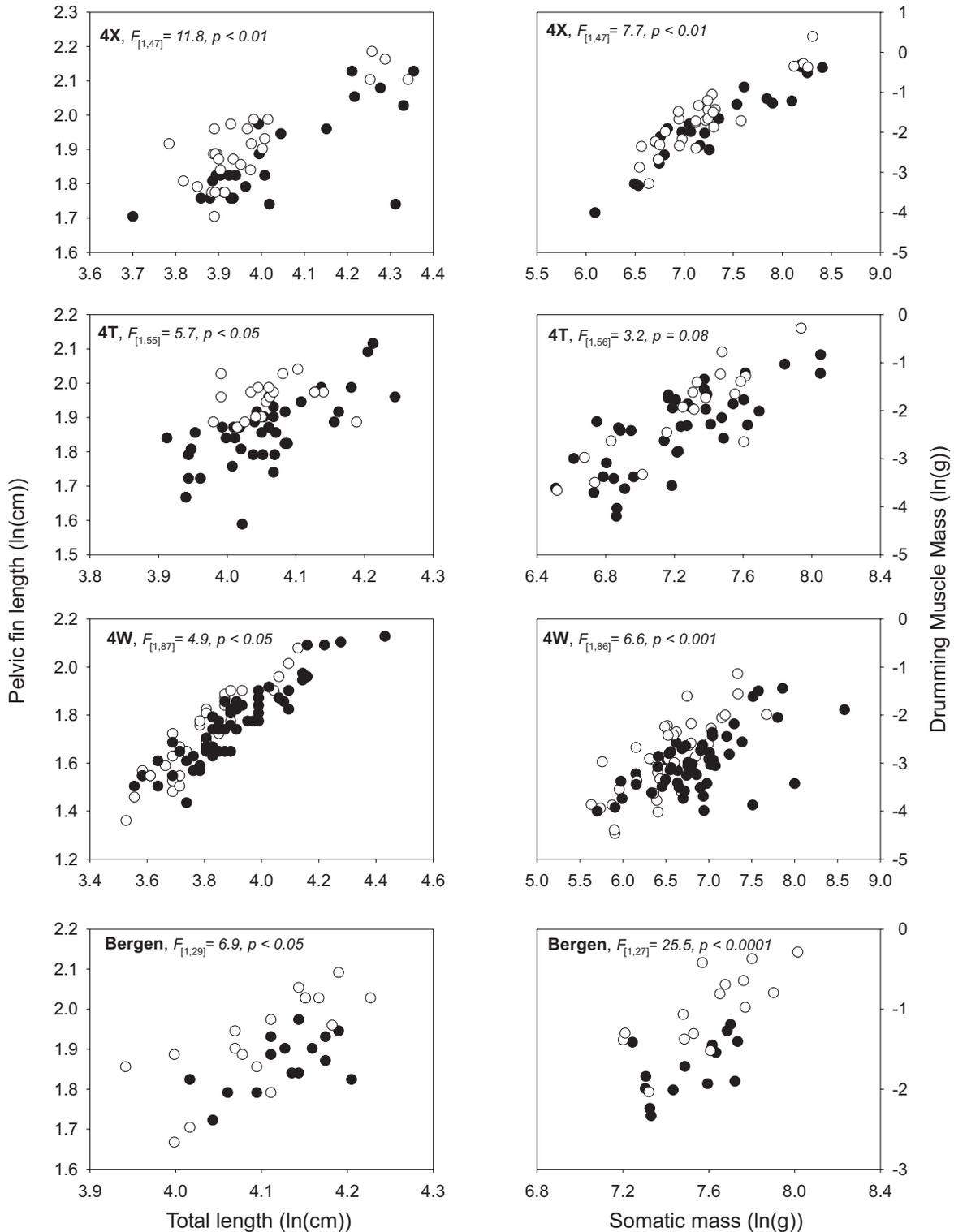
Our statistical comparison between the residuals in pelvic fin size and drumming muscle mass indicated that the variance in the latter trait was significantly greater than the variance in either pelvic fin length or pelvic fin width ($p < 0.05$). In addition, the variance in pelvic fin width exceeded that in pelvic fin length ($p < 0.05$). There was no evidence that the variance in pelvic fin length, pelvic fin width, or drumming muscle mass differed between sexes ($p > 0.14$ for all comparisons).

Discussion

Our results reveal clear sexual dimorphism in pelvic fin size in Atlantic cod. Males possess significantly larger fins than females, a sex bias documented within four spatially disparate populations across the North Atlantic and after controlling for individual differences in body size. This observation raises the question as to why males should have larger pelvic fins than females. Although pelvic fins are used during food search (Harvey and Batty 2002) and fine-scale maneuvering, there is no reason to believe that natural selection under these circumstances would act differentially between sexes.

We suggest that this morphological difference between females and males may be attributable to a sex bias in the functional importance of the pelvic fins during spawning. Given the observation that males use their pelvic fins to grasp females during the ventral mount that accompanies egg release (Brawn 1961a; Rowe and Hutchings 2003), it could be argued that larger fins enhance the ability of a male to maintain his physical proximity to the female, potentially increasing the probability of egg fertilization as a consequence (Rakitin et al. 2001). By contrast, it is also possible that the functional significance of the pelvic fins lies in their association with mating success. The pelvic fins are a prominent feature of agonistic interactions between males; during threat displays, they are completely extended and held in such a way that their maximum area can be seen by other males and, presumably, by females (Brawn 1961c). As a consequence, pelvic fins displayed during agonistic interactions might reveal information about either sex or some aspect of individual quality not measured in this study (e.g., immunocompetence). However, should it occur, we suggest that such individual assessment is almost certainly based on multiple cues which include morphological traits, behavioural activity (Brawn 1961a; Hutchings et al. 1999), and acoustic communication (Engen and Folstad 1999; Rowe and Hutchings 2004, 2006). Thus, rather than, or in addition to, increasing the probability of fertilization success, pelvic fin size might also influence mating success because of information communicated to members of the same (mate competition) or opposite (mate choice) sex.

Fig. 1. Associations between pelvic fin length and body length, and between drumming muscle mass and somatic mass, for Atlantic cod (*Gadus morhua*) from three Northwest Atlantic populations (represented by NAFO divisions 4X, 4T, and 4W) and from coastal cod sampled near Bergen, Norway (○, males; ●, females). The F and p values reported in each panel are the product of the ANCOVAs that tested for differences in pelvic fin length and drumming muscle mass in relation to sex.



Viewed in this context, increased pelvic fin size in male Atlantic cod might be hypothesized to be a result of sexual selection. Under these circumstances, however, theory would predict that the variability in pelvic fin size would ex-

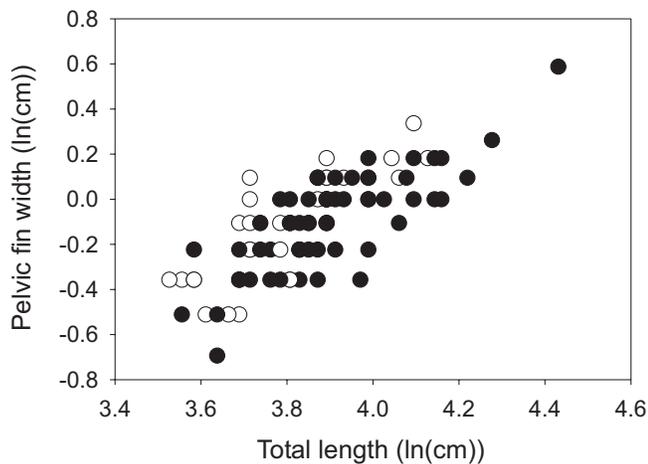
ceed that of traits, such as body length, presumed to be favoured by other forms of natural selection (Alatalo et al. 1988; Grafen 1990; Iwasa et al. 1991; Jones et al. 2000). In contrast, we found that pelvic fin size was either less varia-

Table 1. Coefficients of variation for several morphological traits for Atlantic cod (*Gadus morhua*) from three Northwest Atlantic populations (represented by NAFO divisions 4X, 4T, and 4W) and from coastal cod sampled near Bergen, Norway, in relation to gender.

	Coefficients of variation							
	4X		4T		4W		Bergen	
	♀ (25)	♂ (27)	♀ (41)	♂ (18)	♀ (55)	♂ (37)	♀ (16)	♂ (16)
Pelvic fin length	0.14	0.13	0.10	0.05	0.16	0.17	0.08	0.12
Pelvic fin width	—	—	—	—	0.23	0.28	—	—
Drumming muscle mass	0.92	1.10	0.78	0.93	0.78	0.85	0.34	0.46
Somatic mass	0.66	0.63	0.40	0.35	0.72	0.52	0.17	0.34
Body length	0.18	0.16	0.08	0.06	0.18	0.16	0.05	0.08

Note: Sample sizes are indicated in parentheses. Data on drumming muscle mass were available for 54 of 55 females from the 4W population and for 15 of 16 females from the Bergen population; somatic mass data for Bergen males were available for 15 of 16 fish.

Fig. 2. Association between pelvic fin width and body length for Atlantic cod from NAFO division 4W. ○, males; ●, females.



ble (compared with the CVs in body mass and drumming muscle mass) or as variable (compared with the CVs in body length) as other morphological characteristics. Furthermore, male pelvic fin size was not correlated with either drumming muscle mass (hypothesized to be a secondary sexual characteristic for cod; Engen and Folstad 1999; Rowe and Hutchings 2004) or body condition, which can be significantly associated with drumming muscle mass (Rowe and Hutchings 2004).

We suggest three reasons for the incongruence of our results with those that might have been anticipated. Firstly, being a product of osteological and cartilaginous development, the size of the pelvic fins might not be expected to vary, relative to body length, seasonally (i.e., pelvic fins being relatively larger during the breeding season and smaller otherwise) as do the display traits of numerous other animals that relate to their primary use in intrasexual contests and courtship during the breeding season (Andersson 1994). As such, this might contribute to a reduction in variability among individuals and a lack of correlation with secondary sex traits that do undergo seasonal variation (such as drumming muscles; Rowe and Hutchings 2004) or with body condition (Schwalme and Chouinard 1999). Secondly, if pelvic fin size constitutes a primary sex trait (sensu Darwin 1871) so that its function is directly connected to reproduction (the prime example being a copulatory organ), it

might also be expected to be comparatively invariant relative to secondary sex traits that are related to mate attraction or mate competition (Andersson 1994). Thirdly, the lack of association between pelvic fin size and drumming muscle mass or body condition might be attributable to potentially weak links between these latter two variables and mating/reproductive success in our study populations. Furthermore, it would have been desirable to have quantified these aspects of morphology and body condition at the time that individuals were first investing resources into reproduction. It is also possible that the feeding of cod during our experimental studies may have confounded our estimates of these variables, particularly body condition.

Given that ventral mounts are not an uncommon feature of the spawning behaviour of gadoid fishes (Hawkins et al. 1967), pelvic fin size might also be sexually dimorphic in other species. The hypothesis that other fins might also be sexually dimorphic is not supported by the available, albeit exceedingly limited, data. Based on the results of a principal component analysis, Engen and Folstad (1999) concluded that there was no difference between sexes in the size of the unpaired, median fins in Atlantic cod. Although Rudolfson et al. (2005) found no association between offspring survival (19 days post fertilization) and either pelvic fin length or pelvic fin muscle mass in Atlantic cod, their results may have been confounded by the exclusion of mating behaviour in their *in vitro* fertilization experiments.

To further examine the causes of sexual dimorphism in pelvic fin size and its fitness consequences in Atlantic cod, we suggest two types of studies that would be beneficial in this regard. The first would be a study of seasonal variability in pelvic fin length within individuals to determine whether the size of this trait changes prior to or during the breeding period, as is often observed for secondary sex traits thought to be favoured by sexual selection (Andersson 1994). The second type of study would allow for the expression of mate competition and mate choice among large numbers of breeding individuals, and would test the hypothesis that male pelvic fin size is correlated to either mating or reproductive success in Atlantic cod.

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