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1 **Secondary sexual characteristics in codfishes (*Gadidae*) in relation to sound**

2 **production, habitat use, and social behaviour**

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11 **Running head;** Secondary sexual characteristics in codfishes (Gadidae)
12

Abstract

Little is known about the reproductive biology of the codfishes (Gadidae). Lacking direct observations, the study of secondary sexual characteristics can provide cues to their reproductive biology and behaviour. We reviewed here published accounts on sexual dimorphisms in 25 gadids in light of their general lifestyle, i.e. pelagic or demersal, and social behaviour. In addition, complementary data on fin lengths and drumming muscle size in haddock (*Melanogrammus aeglefinus*), saithe (*Pollachius virens*), blue whiting (*Micromesistius poutassou*) and cod (*Gadus morhua*) are presented. Capacity for sound production occurred in almost half of the studied species, but was most prevalent in demersal species, where it is probably used in resource contests and to attract mates. For semi-pelagic gadids, we postulate that sound production may be linked to the formation of male-biased spawning shoals and the attraction of females towards such shoals; we identify candidate species to further test this hypothesis. Though rarely studied, sexual fin dimorphisms occur in several gadids. Cod, saithe and blue whiting males have longer pelvic fins than females, whereas no such dimorphism was observed in haddock. In cod and haddock, males use pelvic fins during courtship of females and agonistic encounters with other males. Pelvic fins probably have a similar function also in other gadids. The hitherto available information on sexually dimorphic traits and/or courtship behaviour in 7 gadid species suggests that complex mating systems and non-random mate choice occurs frequently in this important group of exploited fishes.

Key words; Codfishes, sexual selection, mating systems, fin dimorphisms, sound production

Introduction

Sexual selection, typically through female choice of certain male traits, can lead to the emergence of secondary sexual characteristics or sexual dimorphisms, provided there is a genetic component to the variation in said trait (Ryan 1997). Such traits are thought to give females either a direct, e.g. more offspring produced, or indirect, e.g. higher quality offspring, benefit. Sexual selection can result in sexual dimorphism in size, body structure or colour (e.g. Kodric-Brown 1990, Hendry & Berg 1999, Gardner 2010). Teleost examples abound and include the genus *Xiphophorus* where males develop 'swordtails' or elongated caudal fins (Basolo 1990a) and females show preference for males with longer swords (Basolo 1990b), whereas dominant black goby *Gobius niger* (Linnaeus, 1758) males have a distinct dark nuptial colouration (Mazzoldi & Razzotto 2002). Given that sexual dimorphisms are commonly closely linked to reproductive behaviour, they may therefore provide important insights into the mating systems of species that are poorly understood.

The codfishes (family Gadidae) comprise numerous species of which many are of significant commercial and cultural importance and have been harvested for thousands of years (Cohen et al. 1990). Despite this, little is known about their mating behaviour and reproductive systems, because most spawn in the ocean at depths where direct observations of spawning behaviour are difficult. Only Atlantic cod (*Gadus morhua* Linnaeus, 1758) and haddock (*Melanogrammus aeglefinus* Linnaeus, 1758) have been subject to close scientific scrutiny.

Laboratory studies have demonstrated that during the reproductive period, male cod and haddock court females and there is pronounced aggression between males (Brawn 1961a, b; Hutchings et al. 1999; Hawkins & Amorim 2000). In cod, these behaviours appear to be energetically costly (Skjæraasen & Hutchings 2010; Skjæraasen et al. 2010a) and linked to individual male reproductive success (Rowe et al. 2008), suggesting the presence of female

3

61 choice (Rowe et al. 2008; Skjæraasen et al. 2010b). Concurrent with these displays male cod

62 and haddock also produce sound (Brawn 1961a; Hawkins & Amorim 2000). In the field, male

63 cod are observed to form dense sex-biased shoals (Morgan & Trippel 1996; Nordeide 1998),

64 which females appear to visit at the time of mating (Robichaud & Rose 2001; Meager et al.

65 2009, 2010). The cod mating system has therefore been suggested to resemble a lek

66 (Hutchings et al. 1999; Nordeide & Folstad 2000; Windle & Rose 2007; Meager et al. 2010).

67   Cod and haddock vocalise during reproductive displays with 'drumming muscles',

68 large pairs of striated muscles attached to the swim bladder (Brawn 1961c; Hawkins &

69 Amorim 2000; Nordeide et al. 2008). These muscles are larger in cod and haddock males than

70 females during the reproductive period (Hawkins 1993; Engen & Folstad 1999). Hawkins and

71 Rasmussen (1978) examined sound production and drumming muscles in nine gadid species

72 and found that they were present in all sound producing species, but not in 'silent' species.

73 Similarly, the pelvic fins of male cod are also used in both courtship and aggressive

74 behaviours (Brawn 1961a,b) and are larger in males than females (Skjæraasen et al. 2006).

75 Examination of secondary sexual dimorphisms in combination with insights into shoaling

76 dynamics and lifestyle thus represents a useful tool for making inferences about the

77 reproductive behaviour and thereby sexual selection of species difficult to observe in the field.

78   Here we review the literature on the presence of sound production and sexual

79 dimorphisms in gadids in the light of their general lifestyle, i.e. pelagic or demersal, and,

80 where such information was available, shoaling behaviour during reproduction (Table 1). In

81 addition we present new data on fin lengths and drumming muscle size in four common North

82 Atlantic gadids; haddock, saithe (*Pollachius virens* Linnaeus, 1758), blue whiting

83 (*Micromesistius poutassou* Risso, 1826) and cod.

84

Material and Methods

86 All fish sampled for the purpose of the present study were sourced from the Institute of

87 Marine Research surveys conducted between February and April 2007. Northeast Arctic

88 (NEA) haddock and saithe (~ N 70° 38, E 20° 50) were caught in the Barents Sea. Cod were

89 sourced from catches at the main spawning grounds for NEA cod in Lofoten (67° 38, E 1°

90 30). Blue whiting were caught in the Faroe-Shetland Channel (~ N 59° 48, W 07° 43). See

91 Table 2 for further information on sample sizes. All fish were frozen to – 30° C immediately

92 upon capture, and subsequently transported to a freezer room (– 30° C) at the University of

93 Bergen until they were measured in June–July 2008.

94

Laboratory measurements of fin lengths and drumming muscle size

96 Fish were first thawed for approximately 16–20 hours before total length (± 1 cm) and body

97 weight (± 1 g) was measured. We then measured the length of the longest pelvic and pectoral

98 fin ray from the base of the fin to the tip of the ray with callipers (± 1 mm). For the three

99 dorsal and two anal fins we followed the procedure of Engen & Folstad (1999) and measured

100 the length of the third fin ray along the length of the spine, counting in a head-to-tail

101 direction. This is usually the longest fin ray. The only exception to this procedure was the first

102 dorsal fin of haddock where we measured the length of the first fin ray, which is the longest

103 fin ray for haddock. Only whole, undamaged fin rays were measured.

104　　　Fish were then gutted and sexed based on macroscopic examination of the gonads. All

105 drumming muscles were subsequently removed using forceps. These were placed in

106 numbered aluminium trays and dried at 60º C and weighed daily (± 0.0001 g) until the weight

107 remained stable and no more weight loss occurred to obtain muscle protein weight and

108 exclude water. We took the utmost care to remove and only weigh the drumming muscle itself

109 and not any connective fibres or swimbladder tissue.

110

Data analyses

In addition to the results of the present study, we examined published research on gadids for

records of sexual dimorphisms, drumming muscles, sound production, reproductive

behaviour, spawning shoaling dynamics, and habitat association.

For the new data, we tested for sexual dimorphisms by comparing pelvic-fin length or

drumming-muscle mass between sexes using ANCOVAs. We controlled for the effect of

body size by including total length as the covariate for analyses involving fin length as the

response variable, and total weight in analyses where drumming muscle mass was the

response variable. The initial models also contained an interaction term between the

categorical variable sex and slope. If this parameter was not significant, i.e. slopes were

homogenous, a standard ANCOVA analysis was applied. All mass and length data, i.e. both

the response and covariate variables, were $\log_e$-transformed to meet the assumption of

normality and to linearise allometric relationships. We also investigated the variability in

pelvic-fin length and drumming-muscle mass by comparing the coefficient of variance (CV)

for each trait, because theory suggests that sexually selected characters exhibit large

individual variation (Andersson 1994).

We then used partial correlation to measure correlation between pelvic-fin length and

drumming muscle mass while correcting for total body length. This test determined if there

was a trade-off between pelvic-fin length and drumming-muscle size, i.e. do males with large

pelvic fins have small drumming muscles after controlling for fish size (e.g. Engen & Folstad

1999). All three variables were $\log_e$-transformed to linearise relationships.

132

Sexual dimorphism in morphological characters

Drumming muscles

Sound production has now been described in more than 800 teleosts world wide (Kaatz 2002). Sound can be produced by various means such as extruding gas through the cloaca (Wilson et al. 2004) or rubbing fins together (Fine et al. 1996), but the most common mechanism of making sound in teleosts is contracting muscles attached to the swimbladder wall, i.e. the 'drumming muscles' (Ladich & Fine 2006).

In accordance with the results of Hawkins & Rasmussen (1978), drumming muscles were present in cod and haddock, but not in saithe and blue whiting (Table 1). For haddock, there was a strong, significant difference in drumming muscle size between males and females with males having bigger muscles ($F_{(1,75)}$=251, p<0.0001, Fig.1). Overall, the slopes of the drumming muscle size-body size relationships did not differ between sexes (p>0.05), but this result was strongly influenced by a single point: a male with a very small drumming muscle (Fig. 1A). If this male was excluded from the analysis, the difference in drumming muscle mass between the sexes increased with size ($F_{(2,73)}$=251, p<0.0001, Fig. 1A). For a given body weight male haddock also had larger drumming muscles than male cod ($F_{(1,95)}$=80.5, p<0.0001, Fig 1AB, Table 2). The partial correlation coefficients did not indicate that males with bigger drumming muscles had shorter pelvic fins for either cod (*r*=0.108, p=0.47) or haddock (*r*=0.096, p=0.53).

Cod mating sounds consist of calls of short duration, i.e. grunts and hums (Brawn 1961c; Finstad & Nordeide 2004), whereas haddock can produce long pulses lasting for several seconds with a number of 'knocks' (Hawkins & Amorim 2000). The larger drumming muscle size of male haddock compared to similarly-sized cod (Table 2, Hawkins 1993) thus concurs with their larger vocal repertoire. The observed sexual dimorphism in haddock drumming muscle was also noted by Hawkins (1993). Sound production may vary between

158   populations (Mann & Lobel 1998; Parmentier et al. 2005; Amorim et al. 2010) and

159   individuals (Amorim et al. 2011); for cod, such differences in the frequency of vocalisations

160   are positively associated with drumming muscle mass (Rowe & Hutchings 2006).

161   The presence of drumming muscles has, to our knowledge, been examined in 25

162   different gadids (family Gadidae) to date (Table 1). Eleven species possess well developed

163   drumming muscles in the adult stage; eight of these have a predominantly demersal lifestyle.

164   The only clear exceptions were the bentho-pelagic Atlantic cod, walleye pollock (*Theragra*

165   *chalcogramma* (Pallas, 1811)) and the pelagic/bentho-pelagic pollack (*Pollachius pollachius*

166   (Linnaeus, 1758)) (Table 1). It seems further likely that sound production during reproduction

167   is not only found in the Gadidae family, but instead could be more widespread in the order

168   Gadiformes. Indeed, drumming muscles have been reported for European hake (*Merluccius*

169   *merluccius* (Linnaeus, 1758)) (Groison et al. 2011). Many gadiforms are demersal, a lifestyle

170   that appears to favour sound production (Table 1).

171

172   *Fin lengths*

173   Sexual fin dimorphisms are found in many teleosts (e.g. Ostrand et al. 2001; Park et al. 2001)

174   and may take on very elaborate forms (e.g. Kottelat et al. 2006; Britz & Conway 2009).

175   Notably, we found only the pelvic fin to be sexually dimorphic in the gadids examined. There

176   was no sexual dimorphism in dorsal, anal or pectoral fins for haddock, saithe or blue whiting

177   ($p > 0.05$ for all cases). In contrast, pelvic fins were sexually dimorphic with males having

178   longer fins than females for saithe ($F_{(1,108)}=9.09$, $p<0.01$, Fig. 2) and blue whiting

179   ($F_{(1,29)}=17.9$, $p<0.001$, Fig. 2), but not for haddock ($F_{(1,72)}=0.798$, $p=0.38$). The slopes of the

180   fin length-body length relationships did not differ between sexes for either species ($p>0.05$).

181   Fin lengths were not compared between sexes for Northeast Arctic cod, because only 2 out of

182   the 50 sampled fish were females (Table 2), but cod have previously been shown to possess

183   sexually dimorphic pelvic fins (Skjæraasen et al. 2006). Fish were generally well above the

184   size at which maturation is expected to occur (Table 2).

185   Our results concur with the results of Andersen & Jakupsstova (1978) who detected

186   sexual dimorphism only in the pelvic fins of blue whiting and Engen & Folstad (1999) who

187   examined the ventral and dorsal fins of Norwegian coastal cod and found them not to be

188   dimorphic. Sexual dimorphism in the pelvic fins is not restricted to gadids, but has also been

189   reported for various other families (e.g. Schenck & Whiteside 1977; Barbieri et al. 1992;

190   Oliveira, & Almada 1995; Kottelat et al. 2006; Britz & Conway 2009; Arbour et al. 2010).

191   Yamanoue et al. (2010) proposed that the pelvic fin may be more readily modified by sexual

192   selection than other fins given their limited use for propulsion during swimming.

193   In our complementary data analysis we tested whether sexually dimorphic traits had a

194   larger CV in males than females. The coefficient of variation (CV) was generally lower for fin

195   lengths than for body weight or drumming muscle mass, but we found no indication that

196   males had a larger CV than females in the sexually dimorphic traits (Table 2). These findings

197   match the results of Skjæraasen et al. (2006); potential explanations for why this occurs are

198   outlined there and therefore not reiterated here.

199

200   **Sexual dimorphisms in relation to habitat use, sound production and social**

201   **behaviour**

202   Sexual dimorphisms can give insights into mating systems. For example, in *Paedocypris*

203   *progenetica* (Kottelat, Britz, Tan & Witte, 2006) the males possess modified pelvic fins with

204   hypertrophied muscles and a keratinized pad in front of the pelvic girdle (Kottelat et al. 2006).

205   This is thought to function as a clasping or holding device used during reproduction to either

206   facilitate internal fertilization, secure the male's position on a spawning site, or give males the

207   possibility to manipulate eggs.

208   Compiling the limited drumming muscle data and general life-history information of

209   the different gadid species, some patterns emerge. Firstly, drumming muscles, and

210   presumably sound production appear common, but occur predominantly in demersal species

211   (Table 1). As in other teleosts, gadids use sound production for social communication (Ladich

212   & Fine 2006). The main contexts in which sound production occurs are male mating calls and

213   aggressive vocal displays towards other males during the reproductive period and in food and

214   territorial contests (Hawkins 1993). The latter may thus involve both juveniles and adults

215   throughout the year. Arguably, territorial contests are more likely to occur at the seafloor

216   where potential landmarks may make resources defendable (Brawn 1961c). Tentatively

217   supporting this, some of the world's most highly vocal fish are both demersal and highly

218   territorial such as Lusitanian toadfish *Halobatrachus didactylus* (Bloch & Schneider, 1801)

219   and plainfin midshipman *Porichthys notatus* (Girard, 1854) (e.g. Bass et al. 2008; Amorim et

220   al. 2010). Saithe are interesting as they possess drumming muscles as juveniles when

221   occupying the demersal, benthic habitat, but lack these muscles in the adults that are pelagic

222   (Hawkins & Rasmussen 1978). For saithe, the primary function of sound production may thus

223   be to support interference competition for food or shelter or social aggregation formation

224   during the juvenile phase.

225   Drumming muscles are absent in most pelagic/semi-pelagic gadids examined to date

226   (Table 1). The only exceptions were the bentho-pelagic cod and walleye pollock and the

227   pelagic/bentho-pelagic pollack. Interestingly, the pelagic whiting (*Merlangius merlangus*

228   (Linnaeus, 1758) exhibit similar reproductive behaviour to cod and haddock, but drumming

229   muscles are absent and no sounds are produced during reproduction (Hawkins & Rasmussen

230   1978). Hence, although sound production is associated with courtship and aggression in cod

231   and haddock, it is not an obligatory feature of gadid reproductive behaviour.

232   It has been suggested that sound production in male haddock may be important in

233   attracting distant females to male-biased spawning aggregations (Hawkins and Amorim

234   2000). This is known as acoustic chorusing, and has been well studied in other taxa such as

235   insects and lekking anurans (e.g. Ryan et al 1981; Castellano et al 2009). Fishing targeted at

236   northeast Atlantic haddock spawning shoals produce catches dominated by males, clearly

237   indicating that haddock do indeed form such sex-biased shoals (Knut Korsbrekke, Institute of

238   Marine Research, Bergen, Norway, *pers. comm.*).

239   Male cod aggregate in reproductive shoals that resemble leks and produce a loud

240   chorus that can be detected several kilometers away (Nordeide & Kjellsby 1999; Nordeide &

241   Folstad 2000). Formation of similar sex-biased shoals has also been noted for walleye pollock

242   (Baird & Olla 1991 and references therein), but has hitherto not been examined in the sound-

243   producing bentho-pelagic/pelagic pollack. Interestingly, the bentho-pelagic gadoid European

244   hake possess drumming muscles (Groison et al. 2011), and the closely related Argentinean

245   hake (*Merluccius hubbsi* Marini, 1933) form sex-biased shoals off the Patagonian coast

246   (Martin Ehrlich, INIDEP, Buenos Aires, Argentina, *pers. comm.*). Previously it has been

247   suggested that sound production in gadids may be linked to fish size in relation to predation

248   pressure, i.e. larger gadids are safer from predators and have much lower risk when producing

249   sound (Hawkins & Rasmussen 1978), and, secondly, that it is mostly absent in schooling fish

250   (Hawkins 1993). Whilst our comparative analysis does not dismiss such explanations (Table

251   1), we suggest that there is clearly merit in examining whether sound production is also linked

252   to the formation of sex-biased spawning shoals whenever present in semi-pelagic gadids.

253   Obvious candidates for a comparative study are the sound-producing bentho-pelagic/pelagic

254   pollack and the 'silent' pelagic saithe (Table 1).

255

256 The male pelvic fin likely has a special significance during reproduction in gadids. It has been

257 shown to be used prominently in both courtships towards females and during antagonistic

258 interactions between males for cod and haddock (Brawn 1961a, b; Hawkins & Amorim

259 2000). Similar reproductive behaviour has also been observed for walleye pollock (Baird &

260 Olla 1991; Park et al. 1994) and whiting (Hawkins & Rasmussen 1978), which thus might be

261 expected to also show the same fin dimorphisms. Given the observed dimorphism in blue

262 whiting and saithe (Fig. 2), similar courtship and antagonistic displays may be present in these

263 species as well. It is curious that the pelvic fins were not sexually dimorphic in haddock,

264 despite their documented use in haddock reproductive behaviour (Hawkins & Amorim 2000)

265 and in contrast to the dimorphisms exhibited by our other study species. We can only

266 hypothesize as to the causes, but it may be that their large investment in drumming muscle

267 size (Fig. 1) and the associated, complex (Hawkins & Amorim 2000), energetically costly

268 sound production (e.g. Amorim et al. 2002) has hindered the development of sexually

269 dimorphic pelvic fins.

270

271 **Concluding remarks**

272 Our review of previously published accounts indicates that drumming muscles, and as a

273 consequence, sound production, is common in gadids, and seems to be associated primarily

274 with the benthic habitat. Close to the bottom, sound production probably has a function during

275 both contests for food and territories, and for mate attraction and agonistic encounters

276 between males, mainly during the reproductive season. For pelagic/bentho-pelagic gadids, the

277 presence of drumming muscles may be linked to the formation of sex-biased spawning shoals

278 during spawning, but more research is needed to further investigate this assumed function.

279 The sexually dimorphic pelvic fins are likely to play an important role during reproduction in

280 some North Atlantic gadids, potentially in support of male courtship and aggressive displays.

281 Sexually dimorphic traits and/or courtship behaviour have been studied only in few gadid

282 species so far. Complex mating systems and non-random mate choice may be widespread and

283 hence we encourage morphological studies to shed light into the reproductive biology of this

284 important group of partially heavily exploited fishes. Such studies should preferably also be

285 designed in a way that makes it possible to further disentangle inter-, intrasexual, and natural

286 selection and their differential influences on dimorphic characters (e.g. Lailvaux & Irschick

287 2006, Bonduriansky 2007, Clutton-Brock 2009).

288

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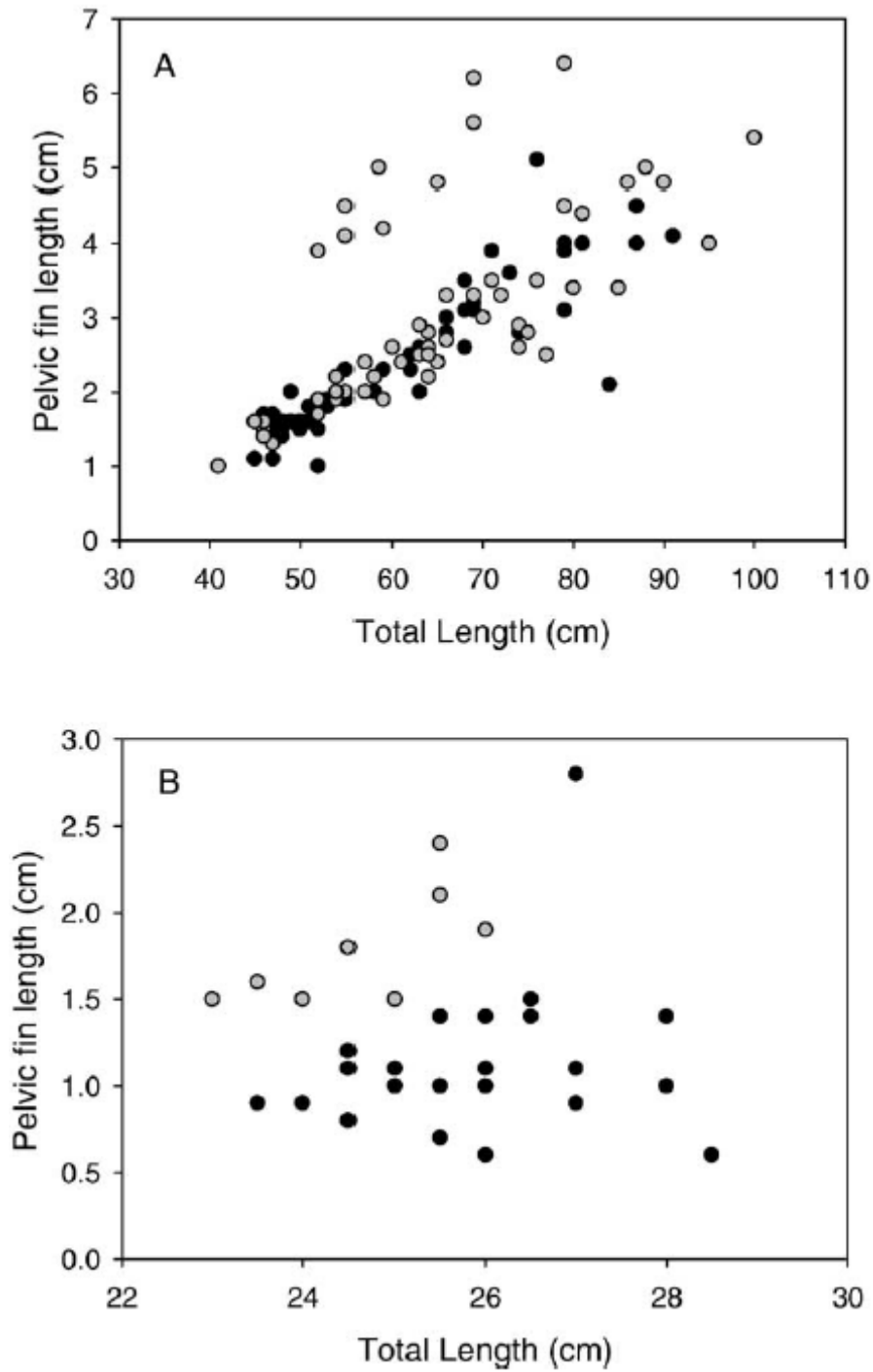443   and evolution. Journal of Fish Biology 77:1173-1208.

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Figure Legends
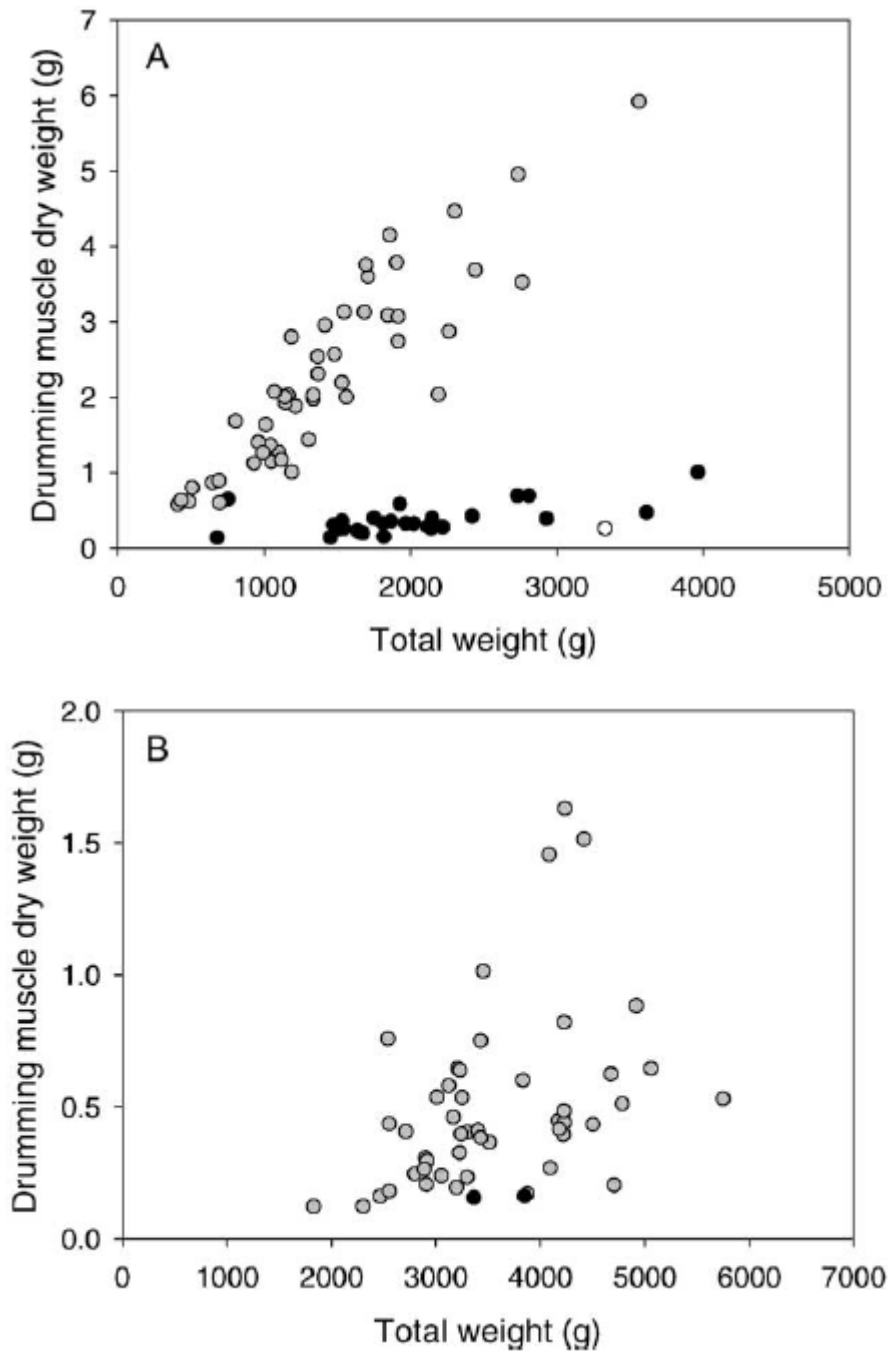
447 Figure 1. Drumming muscle mass of male (grey) and female (black) (A) haddock

448 (*Melanogrammus aeglefinus*) and (B) cod (*Gadus morhua*). The white point (A) indicates the

449 'outlier' male mentioned in the results. Note the different scales on the y-axes of both graphs.

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451

452   Figure 2. Pelvic - fin versus total length of male (grey circles) and female (black circles) (A)

453   saithe (*Pollachius virens)* and (B) blue whiting (*Micromesistius poutassou*).

454 **Table 1.** Summary table of information on adult habitat, social behaviour and sexual dimorphism in codfishes (Gadidae); maximum size (total length, cm); reproductive
455 behaviour (RB); presence of, and sexual dimorphism in drumming muscles (D, drumming muscle present, SD, sexually dimorphic drumming muscle), and the presence of
456 sexual pelvic-fin length dimorphism (PFD) sorted according to habitat. Under 'Habitat', D denotes demersal, P denotes pelagic, and BeP denotes bentho-pelagic. Under 'RB',
457 A denotes the presence of aggressive behaviour and C courtship behaviour during reproduction. Under D/SD the first Y denotes the presence of drumming muscles and *
458 indicates that actual sound production of the species has been recorded. The second Y indicates that the drumming muscle have been shown to be sexually dimorphic. ** -
459 juvenile, but not adult saithe possess a drumming muscle. N denotes the absence of a drumming muscle/ pelvic - fin dimorphism. '–' Indicates that the species in question has
460 not been examined for this particular trait. Data on habitat and maximum size (cm) were obtained from the FAO species catalogue (Cohen et al. 1990).

Species	Habitat	Size	RB	D/SD	PFD	References
Melanogrammus aeglefinus (Linnaeus, 1758)	D	100	AC	Y*/Y	N	Hawkins & Rasmussen 1978; Hawkins & Amorim 2000; this study
Raniceps raninus (Linnaeus, 1758)	D	30	-	Y*/-	-	Hawkins & Rasmussen 1978
Gadus ogac (Richardson, 1836)	D	70	-	Y/-	-	Hawkins & Rasmussen 1978
Boreogadus saida (Lepechin, 1774)	D	40	-	Y/-	-	Hawkins & Rasmussen 1978
Molva molva (Linnaeus, 1758)	D	200	-	Y/-	-	Hawkins & Rasmussen 1978
Molva dypterygia (Pennant, 1784)	D	155	-	Y*/-	-	Hawkins & Rasmussen 1978 – only examined in males
Brosme brosme (Ascanius, 1772)	D	110	-	Y/-	-	Hawkins & Rasmussen 1978
Gaidropsarus mediterraneus (Linnaeus, 1758)	D	50	-	Y*/-	-	Almada et al. 1996
Gaidropsarus vulgaris (Yarrell, 1836)	D	60	-	N	-	Hawkins & Rasmussen 1978
Ciliata mustela (Linnaeus, 1758)	D	25	-	N	-	Hawkins & Rasmussen 1978
Enchelyopus cimbrius (Linnaeus, 1776)	D	41	-	N	-	Hawkins & Rasmussen 1978
Microgadus proximus (Girard, 1854)	D	30	-	N	-	Hawkins & Rasmussen 1978
Eleginus navaga (Pallas, 1811)	D	42	-	N	-	Hawkins & Rasmussen 1978
Eleginus gracilis (Tilesius, 1810)	D	55	-	N	-	Hawkins & Rasmussen 1978
Pollachius virens (Linnaeus, 1758)	P	130	-	N**	Y	Hawkins & Rasmussen 1978, this study
Gadiculus argentus (Guichenot, 1850)	P	15	-	N	-	Hawkins & Rasmussen 1978
Micromesistius poutassou (Risso, 1826)	P/BeP	50	-	N	Y	Andersen and Jákupsstova 1978; Hawkins and Rasmussen 1978; this study
Pollachius pollachius (Linnaeus, 1758)	P/BeP	75	-	Y*/-	-	J. Nilsson, Institute of Marine Research, Bergen, Norway, *pers. comm*
Trisopterus esmarkii (Nilsson, 1855)	P/BeP	20	-	N	-	Hawkins & Rasmussen 1978
Trisopterus minutus (Linnaeus, 1758)	BeP	40	-	N	-	Hawkins & Rasmussen 1978
Trisopterus luscus (Linnaeus, 1758)	BeP	45	-	N	-	Hawkins & Rasmussen 1978
Gadus morhua (Linnaeus, 1758)	BeP	200	AC	Y*/Y	Y	Brawn 1961 ab; Morgan & Trippel 1996; Engen & Folstad 1999; Skjæraasen et al. 2006
Merlangius merlangus (Linnaeus, 1758)	BeP	70	AC	N	-	Hawkins & Rasmussen 1978
Theragra chalcogramma (Pallas, 1811)	BeP	80	C	Y/-	-	Hawkins & Rasmussen 1978; Baird & Olla 1991; Onuki & Somiya 2006
Gadus macrocephalus (Tilesius, 1810)	BeP	100	N	N	-	Sakuri & Hattori 1996

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462 **Table 2.** Summary of morphological measurements. Mean (M) and coefficient of variance

463 (CV) of total length (TL, cm), total weight (TW, g), drumming-muscle dry weight (DR, g)

464 and lengths (cm) of the first (D1), second –(D2), and third dorsal - (D3) fin, pectoral (PF),

465 pelvic (PL), pectoral (PF), and first (A1) and second (A2) anal fin (all lengths are given in

466 cm). Numbers in parentheses indicate sample size. Not all fin measurements were conducted

467 on each sample.

| | Blue whiting | | | | Haddock | | | | Saithe | | | | Cod | | | |
| | ♂ (10) | | ♀ (25) | | ♂ (50) | | ♀ (27) | | ♂ (56) | | ♀ (57) | | ♂ (48) | | ♀ (2) | |
	M	CV	M	CV	M	CV	M	CV	M	CV	M	CV	M	CV	M	CV
TL	24.9	0.06	25.8	0.05	49.8	0.16	53.1	0.13	65.0	0.21	60.6	0.21	70.9	0.09	68	-
TW	99	0.27	103	0.17	1450	0.48	2010	0.36	2806	0.67	2393	0.68	3570	0.23	3613	-
DR	-	-	-	-	2.2	0.57	0.37	0.55	-	-	-	-	0.50	0.68	0.16	
D1	2.4	0.09	2.4	0.17	6.3	0.17	6.7	0.18	4.0	0.27	3.7	0.28	5.5	0.17	5.8	-
D2	2.1	0.14	2.4	0.14	3.4	0.35	3.5	0.16	3.2	0.29	2.9	0.29	4.4	0.22	4.6	-
D3	1.6	0.10	1.5	0.22	2.5	0.31	2.6	0.20	2.0	0.48	1.6	0.42	4.6	0.16	4.6	-
PF	3.0	0.14	3.1	0.10	5.2	0.26	5.7	0.16	5.3	0.22	4.9	0.25	6.6	0.11	6.5	-
PL	1.8	0.19	1.1	0.39	3.4	0.20	3.5	0.14	3.1	0.41	2.4	0.41	5.6	0.10	5.1	-
A1	1.8	0.15	1.9	0.14	3.7	0.22	4.1	0.18	3.8	0.27	3.5	0.30	4.9	0.25	4.9	-
A2	1.6	0.06	1.5	0.15	2.6	0.30	2.83	0.20	2.1	0.51	1.6	0.45	4.8	0.12	4.8	-

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