Spawning behavior in Atlantic cod: analysis by use of data storage tags

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ABSTRACT: Electronic data storage tags (DSTs) were implanted into Atlantic cod captured in Icelandic waters from 2002 to 2007 and the depth profiles recovered from these tags (females: n = 31, males: n = 27) were used to identify patterns consistent with published descriptions of cod courtship and spawning behavior. The individual periods of time that males spent exhibiting behavior consistent with being present in a spawning aggregation — i.e. periods consisting of a clear tidal signature in the DST depth profile associated with an individual remaining on or near the substrate — were longer than those of females. Over the course of a spawning season, male cod spent approximately twice the amount of time in spawning aggregations than females, but female cod visited more aggregations per unit time. On average, males participated in approximately 57% more putative spawning events, i.e. vertical ascents potentially corresponding to gamete release, than did females. However, males <85 cm total length participated in the same number of putative spawning events as females of comparable size. In both sexes, larger individuals and/or individuals that spent a longer period of time within an aggregation participated in a larger number of putative spawning events. Although further validation and refinement is necessary, particularly in the identification of spawning events, the ability offered by DSTs to quantify cod spawning behavior may aid in the development of management and conservation plans.

KEY WORDS: *Gadus morhua* · Electronic data storage tags · Leks · Mating system · Reproductive behavior

INTRODUCTION

The majority of marine teleost fishes are broadcast spawners that release their gametes directly into the water column (Breder & Rosen 1966, Balon 1975). It is generally thought that this manner of reproduction is strongly tied to a promiscuous mating system, as little evidence has been presented demonstrating mate choice or intrasexual competition (Breder & Rosen 1966, Balon 1975, Berglund 1997). This perception has persisted in spite of studies reporting complex mating systems in diverse taxa of broadcast spawning fishes, such as synodontid lizardfishes (Donald-

son 1990), labrid wrasses (Warner & Robertson 1978, Moyer &Yogo 1982, Donaldson 1995), and serranid seabass and groupers (Fischer & Petersen 1987, Brule et al. 1999). The obstacle to assessing the mating system of most marine fishes is that they are very 'discreet' regarding their sex lives; spawning at depths or times of the year that render direct observation difficult, expensive, and at times even dangerous.

Atlantic cod *Gadus morhua* is one such species for which the lack of detailed knowledge of its mating system was a critical concern due to dramatically reduced population sizes throughout much of its range (Hutchings et al. 1999, Rowe & Hutchings

2003, Rowe et al. 2004). Throughout the 1900s, surprisingly little was known about cod reproductive behavior in the wild despite the economic importance of this species. The lack of direct observations (Nordeide & Folstad 2000) coupled with an apparent lack of mate selection led to the conclusion that cod employed a promiscuous mating system (Berglund 1997, Nordeide & Folstad 2000). However, analysis of trawl and gillnet catches, laboratory studies, and a few telemetry studies suggest that Atlantic cod employ a more complex, lekking mating system (reviewed in Nordeide & Folstad 2000). A lek is a polygamous mating system in which males spend the majority of the reproductive period aggregated for the purpose of displaying to females (Emlen & Oring 1977, Höglund & Alatalo 1995). Females tend to be highly asynchronous in their receptivity, resulting in a highly skewed operational sex ratio in the aggregation as receptive females enter the lek for the sole purpose of assessing males (Emlen & Oring 1977, Höglund & Alatalo 1995). Females are not influenced in their decision by the resources controlled by the male, but instead base their assessment on some inherent trait of male quality (Höglund & Alatalo 1995). This results in relatively small numbers of fit males receiving a disproportionate share of mating opportunities (Mackenzie et al. 1995).

While there may be considerable variability in cod spawning behavior among various stocks or stock components (Brander 2005), the general pattern seems to be as follows. Atlantic cod form large aggregations of individuals during the spawning season at depths of 20 to 400 m (Marteinsdóttir et al. 2000, Brander 2005,). These aggregations consist mostly of male fish (Morgan & Trippel 1996, Lawson & Rose 2000, Windle & Rose 2007) with non-spawning females located peripherally to these aggregations (Windle & Rose 2007, Meager et al. 2010). Males are generally present in these areas for longer periods of time than females (Robichaud & Rose 2003, Windle & Rose 2007). Within the aggregation, male cod seem to remain in close association with the substrate, presumably establishing a dominance hierarchy and courting receptive females that enter the aggregation (Brawn 1961a,b, Hutchings et al. 1999, Meager et al. 2009). These courtship displays are thought to consist mostly of a 'song and dance' (Brawn 1961b, Engen & Folstad 1999, Hutchings et al. 1999, Nordeide & Folstad 2000) involving the display of traits, such as fin area and acoustic signaling abilities, that may be correlated to reproductive fitness (Engen & Folstad 1999, Rowe et al. 2008). Upon successful courtship, a male–female pair is believed to rise off

the substrate to release gametes into the water column (Hutchings et al. 1999, Rowe & Hutchings 2003). It is unclear how far from the bottom a spawning pair travels before releasing gametes, with estimates ranging from ≤1 m (Hutchings et al. 1999) to 10 m or more (Rose 1993, Fudge & Rose 2009, Grabowski et al. 2012). In laboratory studies, multiple males may trail the spawning pair while releasing gametes (Hutchings et al. 1999, Rowe & Hutchings 2003) and this behavior may account for the 'spawning columns,' i.e. small groups of individuals that seem to rise above main aggregation, observed in hydroacoustic surveys of cod spawning aggregations (Rose 1993, Fudge & Rose 2009, Grabowski et al. 2012).

The available data suggest that cod do employ a complex mating system, but it remains difficult to relate laboratory-based findings to reproduction in the wild. The habitat used by spawning cod and the depth at which spawning occurs means it is difficult, if not impossible, to monitor large numbers of individuals at single locations or over a wide geographic area for the duration of the spawning season using direct observation or telemetry. However, electronic data storage tags (DSTs) are making it possible to monitor the behavior of individuals across a wide area at high temporal resolutions for extended periods of time (Hunter et al. 2003, Solmundsson et al. 2003, Hobson et al. 2007) including during the spawning season (Grabowski et al. 2011, Nielsen et al. 2013). Several studies have used DSTs to characterize spawning habitat depth and temperature and to document spawning migrations and residency on spawning grounds for Atlantic cod (Grabowski et al. 2011, Thorsteinsson et al. 2012, Nielsen et al. 2013), plaice *Pleuronectes platessa* (Solmundsson et al. 2003), Pacific halibut *Hippoglossus stenolepis* (Seitz et al. 2005, Loher & Seitz 2008), and small spotted catshark *Scyliorhinus canicula* (Wearmouth et al. 2013).

The objective of this study was to determine whether information related to spawning behavior could be extracted from the data collected by DSTs implanted in Atlantic cod in Icelandic waters and specific behaviors quantified, such as time spent within a spawning aggregation or number of spawning events participated in.

MATERIALS AND METHODS

Data storage tag implantation and recovery

Data storage tags (DST Centi and DST Milli: Star Oddi Marine Device Manufacturing) capable of

recording temperature in the range of −2.0 to 40.0°C (±0.1°C) and depth range of 0 to 800 m (±0.6%) were used for this study. The DSTs recorded temperature and depth at 10 min intervals throughout the spawning season (March to June), and at either 10 min or 6 h intervals for the remainder of the year, depending on the model and programming of the tag. The DSTs weighed 12.0 g in air and did not exceed the recommended 2.0% of body weight for any of the individuals in which they were implanted (Winter 1996).

Spawning Atlantic cod were captured from spring spawning aggregations around Iceland from 2002 through 2007 by commercial fishermen using gill nets and Danish seines. Individuals were placed in on-board observation tanks and those displaying no indication of barotrauma or external injury were selected for tagging. A DST was surgically implanted into each individual's abdominal cavity following the procedure described in Thorsteinsson & Marteinsdóttir (1998). Briefly, an individual was removed from the holding/observation tank and measured to the nearest cm total length (TL). The fish was placed on its back in a surgical cradle with its head covered to induce tonic immobility. A constant flow of seawater was maintained across its gills during the procedure. A small (10 to 20 mm) incision was made into the abdominal cavity just off the ventral midline and a DST was inserted. Each DST was anchored in place using a conventional tag attached to the DST and inserted through a small secondary opening in the body wall posterior to the main incision using a shielded needle (Ross & Kleiner 1982). The sex of the individual was determined through a visual examination of the gonads before closing the main incision using 3 interrupted 3-0 coated absorbable sutures. A 100 mg kg^{-1} dose of the antibiotic oxytetracycline (Engemycin, Intervet International) and 1.0 ml kg^{-1} dose of a vitamin solution (Becoplex, Boehringer) were injected into each fish prior to release to minimize the risk of post-surgical infections. The entire procedure took less than 5 min and all fish were returned to the sea immediately. All surgeries were deemed successful based on the criteria that tagged cod were alive and swam out of sight under their own power upon release. Tagged fish were later recovered by commercial fishermen who returned the DST, sagittal otoliths for age determination, information regarding location of capture, and TL. From 2002 to 2007, 1188 DSTs were implanted into Atlantic cod in the waters around Iceland. A total of 449 (37.8%), were recovered by commercial fishermen generating a database of over 25 million paired temperature–depth measurements.

Data interpretation

Depth data from the DSTs were used to identify behaviors in Atlantic cod consistent with those described for participation in spawning aggregations in laboratory studies by Brawn (1961a,b) and Hutchings et al. (1999), field studies using sonar by Rose (1993) and Fudge & Rose (2009), and field studies using high-resolution acoustic telemetry by Meager et al. (2009, 2010). These studies, as well as visual and hydroacoustic observations of shallow water cod spawning aggregations around Iceland (Grabowski et al. 2012, G. Marteinsdóttir unpubl. data), suggest that the majority of cod courtship and male–male interactions take place on or near the bottom. Individuals spending extended periods of time on the bottom with little vertical movement produce a depth profile with a clear tidal signature (Righton et al. 2001, Grabowski et al. 2011).

A depth profile consisting primarily of a tidal signature lasting at least 12.5 h was interpreted as presence in a spawning aggregation. The minimum length of periods of potential residency was limited to 12.5 h due to the semi-diurnal tidal pattern around Iceland and the limitations of our approach. Periods of potential residency within a spawning aggregation were visually identified from the DST depth profiles occurring between migratory events, i.e. in-migration to and out-migration from the spawning grounds, using SeaStar v. 3.7.9.4 (Star Oddi Marine Device Manufacturing). Migratory events consisted of a directed change in the depth occupied by an individual (Grabowski et al. 2011, Thorsteinsson et al. 2012; Fig. 1A), indicated by a shift in the mean daily depth from deep water to the shallower waters occupied during spawning (Thorsteinsson et al. 2012). Typically in-migration started in late winter or early spring and out-migration started in late spring to midsummer, bookending the Atlantic cod spawning season in Icelandic waters of mid-March to early June (Thorsteinsson & Marteinsdóttir 1998, Marteinsdóttir et al. 2000). The tidal signatures of the periods of potential residency within a spawning aggregation were of varying quality with varying levels of noise in the data, depending upon sea surface conditions and vertical movements of individuals. Therefore, we used trigonometric regression to fit a tidal period of 12 h 12.5 min, consistent with the semidiurnal tidal pattern of the Icelandic continental shelf (Cartwright et al. 1980, Gjevik & Straume 1989, Anonymous 1993), and amplitude equal to the difference between the mean depth recorded during a period of potential

residency and the measured depth at each observation to the depth profiles of each candidate period. The presence of a tidal signature was considered confirmed when the trigonometric regression model was significant at α ≤ 0.10.

The return of a more variable depth profile suggestive of a moving or feeding cod (Godø & Michalsen 2000, Righton et al. 2001, Pálsson & Thorsteinsson 2003, Grabowski et al. 2011) coupled
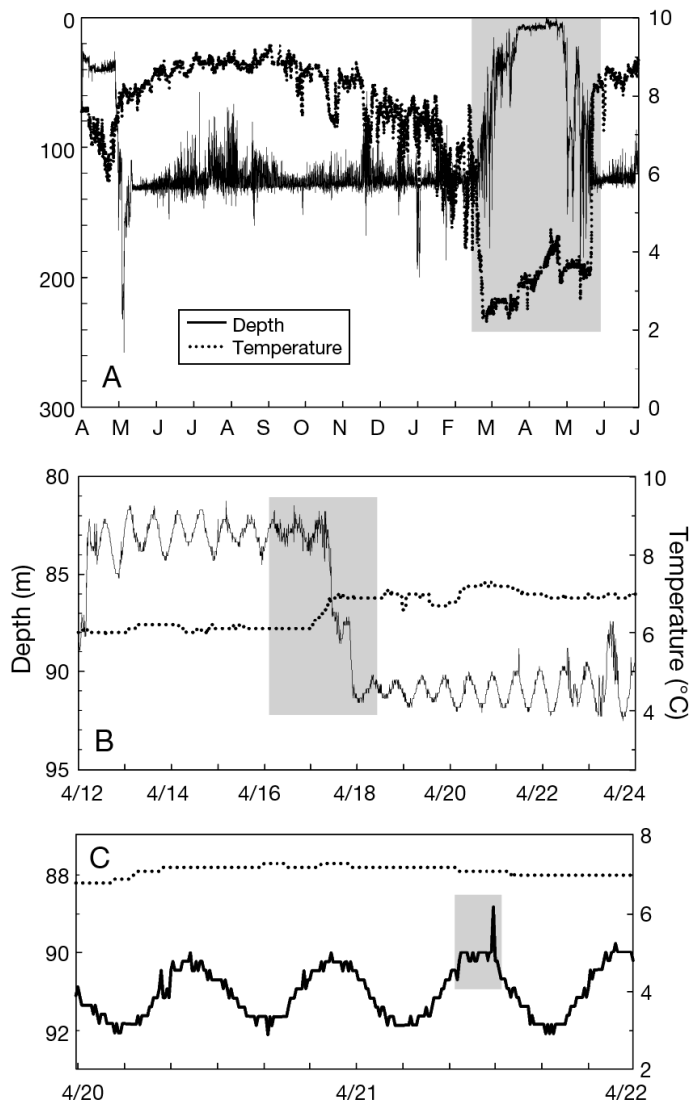

Fig. 1. Temperature and depth profiles from electronic data storage tags recovered from Atlantic cod in Icelandic waters from 2002 to 2007 showing (A) the change in depth associated with migratory and spawning behavior, (B) the tidal signature associated with participation in a spawning aggregation and the change in depth range interpreted as movement between aggregations, and (C) an example of a putative spawning event highlighted in gray boxes. Panels are excerpts from different individuals

with the loss of a clear tidal signature was interpreted as the departure of an individual from a spawning aggregation. If a clear tidal signature was subsequently identified from the depth profile, the fish was interpreted as having resumed residency within a spawning aggregation. We considered a fish to have entered a different spawning aggregation if the depth range of the 2 periods of residency did not overlap (Fig. 1B), whereas the fish was considered to have returned to the same aggregation if the depth ranges of the 2 tidal signatures overlapped.

The depth profile data were also used to identify patterns consistent with spawning events. In laboratory studies, male and female cod rise off the bottom after a period of courtship, in a behavior termed a ventral mount, during which they release their gametes before returning to the bottom (Brawn 1961b, Rose 1993, Hutchings et al. 1999). Individuals that are presumably spawning travel into the water column, as much as 150 m from the bottom, and can form large columns above the aggregation (Rose 1993, Fudge & Rose 2009). However, vertical movements of 5 to 10 m may be more common (Grabowski et al. 2012). Events consistent with spawning activity were identified from the DST data in a 3-part process that occurred within a period identified as occupation of a spawning aggregation (Fig. 1C). The first step required the individual to occupy an initial depth of ±0.25 m for 3 consecutive observations to limit the possibility of identifying noise from rough sea conditions as a putative spawning event. During the next 10 min interval, the fish had to be recorded at a depth at least 1.5 m above that occupied during the previous 3 observations. On the next time step, the fish must have returned to its initial depth ±0.25 m. The resulting counts of spawning events are subject to error from both false positives and false negatives, i.e. missed events. For example, spawning events are likely underestimated due to the low probability of recording a spawning event because of its short duration relative to the DST sampling interval. The ventral mount behavior of cod under captive conditions lasts 9.9 ± 2.8 s on average (Hutchings et al. 1999), while the ascent rate of cod has been estimated to be no more than 1 to 3 m min^{-1} during routine activity (Arnold & Greer Walker 1992, Godø & Michalsen 2000) and 12 to 15 m min^{-1} during spawning (Grabowski et al. 2012). At the same time, spawning activity could be overestimated, as short duration vertical movements could be due to a number of factors unrelated to spawning.

Data analysis

For each individual, we counted the number of putative spawning events and the length of time an individual was interpreted as resident in a spawning aggregation. We also noted the potential number of aggregations visited based on overlap in depth ranges. We summed the spawning events and time spent in each aggregation within a season for each individual to get the seasonal totals. All data were evaluated for adherence to parametric assumption of normality and independence, and the appropriate transformations were made when necessary. We used mixed-model analysis of covariance (ANCOVA) to assess seasonal and per aggregation differences between the sexes in time spent within spawning aggregations, putative spawning events, and number of aggregations visited (assessed seasonally only). In the per-aggregation and seasonal models assessing differences in time at aggregations, TL was used as a covariate. In the remaining models assessing number of putative spawning events and number of aggregations visited, both TL and time were used as covariates. We used individuals as a random effect in the models. If the assumption of equal slopes was violated, we used a nested mixed-model ANCOVA and assessed differences across values of total length and residence time common to both sexes (Neter et al. 1996). Individual ID was used as a random effect in both models. All analyses were performed using SAS (SAS v. 9.2; Statistical Analysis Software). Data reported are mean ± SE, unless otherwise noted; a significance level of $\alpha = 0.05$ was used for all statistical tests.

RESULTS

Only 58 of the 449 recovered Atlantic cod (females: n = 31, males: n = 27) were at liberty for at least one complete spawning season (1 season: n = 31, 2 seasons: n = 23, 3 seasons: n = 3, 4 seasons: n = 1). The majority of individuals were recaptured during their first year at liberty, and most of these were caught during the spawning season. We counted 151 discrete periods potentially corresponding to residency within spawning aggregations; in total there were 822 events recorded that met our criteria for putative spawning events (see Fig. 2 for examples). While changes in depth exceeding 10 m were recorded during 4.7 % of the events, rises of 2 to 5 m were more typical, accounting for approximately 51.8 % of the events, and rises of < 2 m were observed in about 32.1 % of the events (Fig. 3). There was no difference

between males and females in the frequency distributions of the changes in depth during putative spawning events ($\chi^2 = 4.20$, df = 9, p = 0.90). However, males tended to exhibit a shorter interval between events than did females (Table 1).

Male and female Atlantic cod showed different patterns at spawning aggregations. The mean duration of periods where clear tidal signatures were recorded during the spawning season was shorter in females (ANCOVA: $F_{2,93} = 14.57$, p < 0.0002; Fig. 4A). Time individuals spent within a spawning aggregation, i.e. the duration of each period where a clear tidal signature was exhibited, was unrelated to the TL of the fish (ANCOVA: $F_{1,93} = 1.07$, p = 0.30). The duration of a tidal signature was independent of whether it was the first or last one in the depth profile (ANCOVA: $F_{1,93} = 0.01$, p = 0.92). Similarly, the mean total duration of periods with clear tidal signatures per season was greater in males than in females (ANCOVA: $F_{2,32} = 6.58$, p = 0.004; Fig. 5B) and did not depend upon TL (ANCOVA: $F_{1,32} = 0.03$, p = 0.87).

Despite spending less time per season in spawning aggregations than males, female cod exhibited more shifts in depth ranges between periods of clear tidal signatures, which we interpreted as movement between aggregations. Females exhibited depth profiles suggesting that they visited up to 4 aggregations per season with 24 % of individuals visiting 3 or more aggregations. Males participated in up to 5 aggregations but only about 33 % of individuals visited 2 or more aggregations compared to 50 % of females. Female depth profiles exhibited approximately double the number of shifts in depth ranges per hour spent in spawning aggregations than did males (ANCOVA: $F_{2,31} = 27.47$, p < 0.0001; Fig. 5C). Individuals that spent more time in spawning aggregations also exhibited a greater number of shifts in depth between these periods (ANCOVA: $F_{1,31} = 56.33$, p = 0.0001). There was no relationship between TL and the number of aggregations visited per season (ANCOVA: $F_{1,31} = 1.41$, p = 0.24).

Depth profiles from males contained 57 % more putative spawning events per aggregation visited than females (ANCOVA: $F_{2,86} = 5.72$, p = 0.005; Fig. 5A). The number of events participated in covaried with the length of time an individual was resident in a spawning aggregation by sex (ANCOVA: $F_{2,86} = 32.80$, p < 0.0001), but did not exhibit a strong relationship with TL by sex (ANCOVA: $F_{1,86} = 0.93$, p = 0.40; Fig. 6). There was no difference between the sexes in the mean number events participated in per unit time (mean ± SE: males = 0.20 ± 0.01 events h^{-1}, females = 0.20 ± 0.01 events h^{-1}). However, males
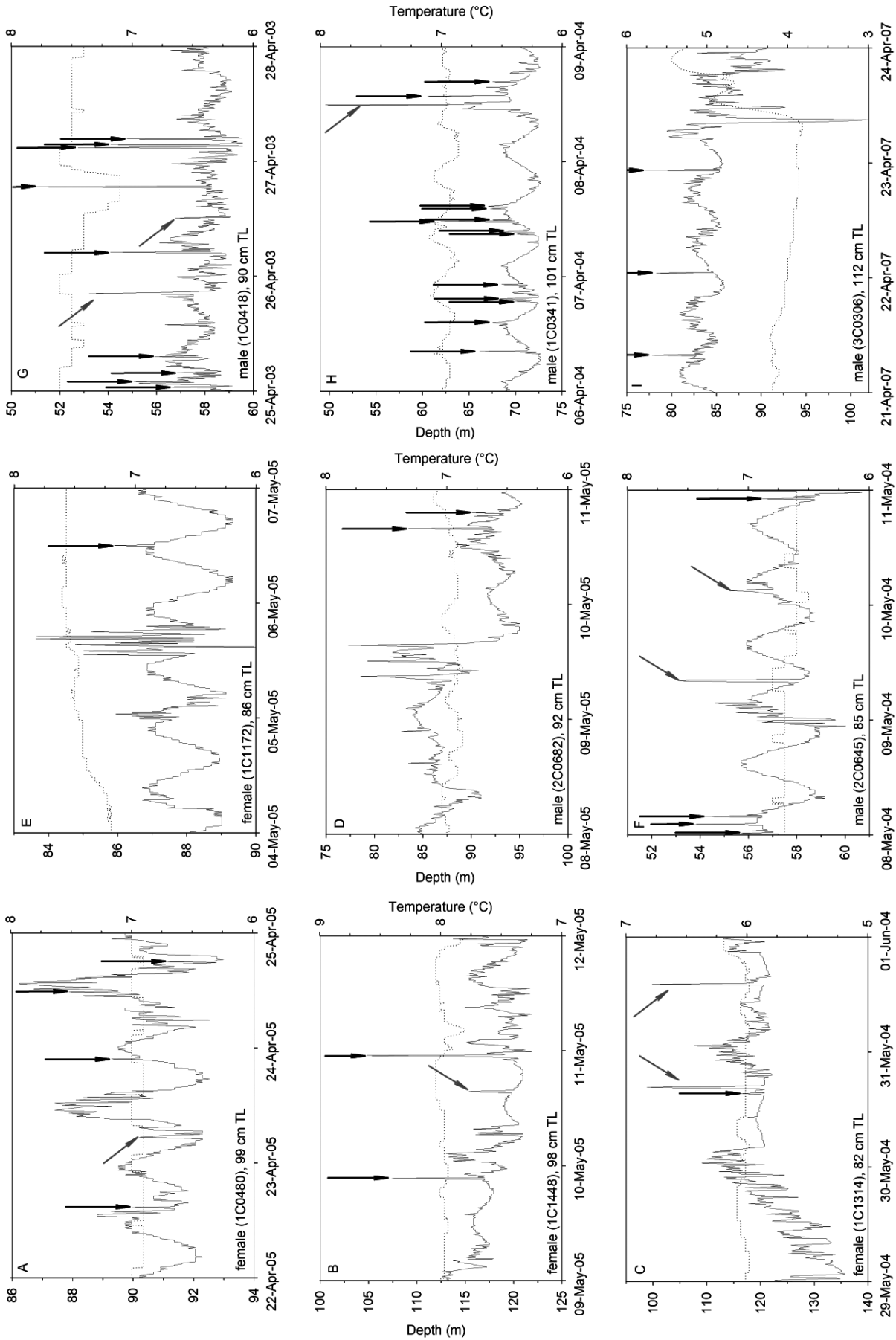
Fig. 2. Temperature and depth profiles from electronic data storage tags recovered from (A–D) 4 female and (E–I) 5 male Atlantic cod in Icelandic waters. Putative spawning events are indicated by black arrows. Note that while the x-axis always represents a 72 h period, the scale of the y-axes is not consistent among panels
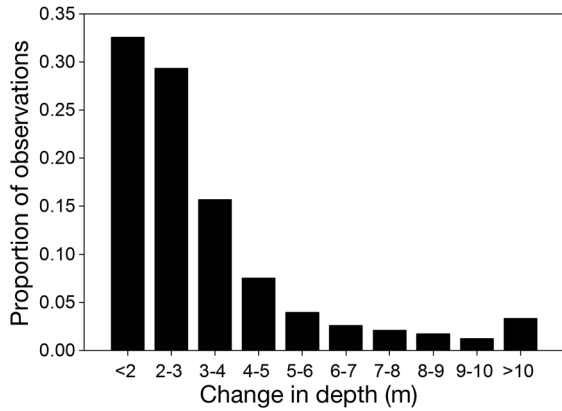
Fig 3. Frequency distribution of the change in depth during putative spawning events (n = 822) interpreted from the depth profiles of Atlantic cod (n = 58)
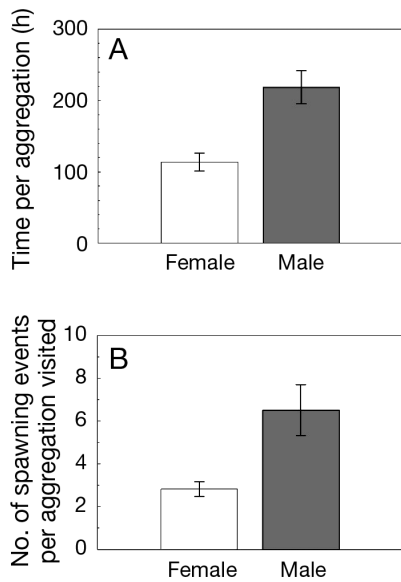

Fig. 4. (A) Mean length of time per aggregation visited and (B) putative spawning events participated in by male and female Atlantic cod (mean ±SE)

>85 cm TL tended to exhibit a greater number of spawning events per aggregation visited then females of the same size when controlling for the duration of the period of clear tidal signature (Dunnett's Multiple Comparison test: p ≤ 0.045). Males <85 cm TL exhibited the same number of events as females of comparable size.

The same difference in the number of putative spawning events between the sexes was evident over the course of a full spawning season (ANCOVA: $F_{2,27}$ = 8.27, p = 0.002; Fig. 5C). The number of events an individual participated in dur-

Table 1. Spawning behavior in Atlantic cod based on interpretation of depth profiles from electronic data storage tags and laboratory and field-based studies. For the interval between putative spawning events/egg batches, numbers for present study reflect number of putative spawning events participated in as inferred from DST data. In other studies, this number reflects egg batches or egg releases

	n	Mean	SD	Range	Source
Total length of individuals (cm)					
Females	31	89	10	69–110	This study
	3	65	10	56–75	1[a]
	10	57	6	46–68	2
	5	–	–	42–67	3
	27	–	–	64–87	4
	12	65	10	–	5
Males	27	91	11	72–112	This study
	21	–	–	67–88	4
	12	66	7	–	5
Putative spawning events participated in/egg batches produced per season					
Females	–	5.8	3.9	1–20	This study
	–	18.0	1.0	17–19	1[a]
	–	7.0	2.5	4–11	2
	–	15.8	4.9	10–21	3
Males	–	13.0	10.9	1–67	This study
Interval between putative spawning events/egg batches (h)					
Females	–	39.4	38.4	0.7–901.0	This study
	–	75.1	5.2	23–280	1[a]
	–	134.4	156.2	72–216	2
Males	–	19.9	15.1	0.7–975.0	This study
Residence time in spawning aggregations per year (d)					
Females	–	7.5	4.5	0–31.3	This study
	–	18.6	–	–	4[c]
	–	17.8	13.5	–	5[d]
Males	–	13.2	8.3	0–40.9	This study
	–	9.5	–	–	4[c]
	–	22.0	12.4	–	5[d]
Date of entrance into a spawning aggregation					
Both	–	12 Mar	22 d	17 Feb–11 Apr[b]	This study
Both	–	mid-Mar	–	–	6,7,8
Date last fish exited a spawning aggregation					
Both	–	5 Jun	11 d	24 May–12 Jun	This study
Both	–	mid-Jun	–	–	7,8

[a]Reports number of batches of eggs released and interval between batches as assessed from daily sampling from tanks. Actual spawning events not enumerated. Only 3 fish were allowed to complete their spawning season
[b]Most fish were tagged during the first week of April 2003
[c]Results of telemetry study with sufficient resolutions to determine presence/absence on known spawning grounds, but not to evaluate participation in an aggregation
[d]Excludes fish present for <3 d

Sources: (1) Kjesbu (1989); (2) Chambers & Waiwood (1996); (3) Kjesbu et al. (1996); (4) Robichaud & Rose (2003); (5) Meager et al. (2009); (6) Jónsson (1982); (7) Marteinsdóttir et al. (2000); (8) Brander (2005)

ing a spawning season was related to the total time it spent in spawning aggregations per season (ANCOVA: $F_{1,27}$ = 37.28, p < 0.0001) and there was no difference between males (mean ± SE: 0.20 ±
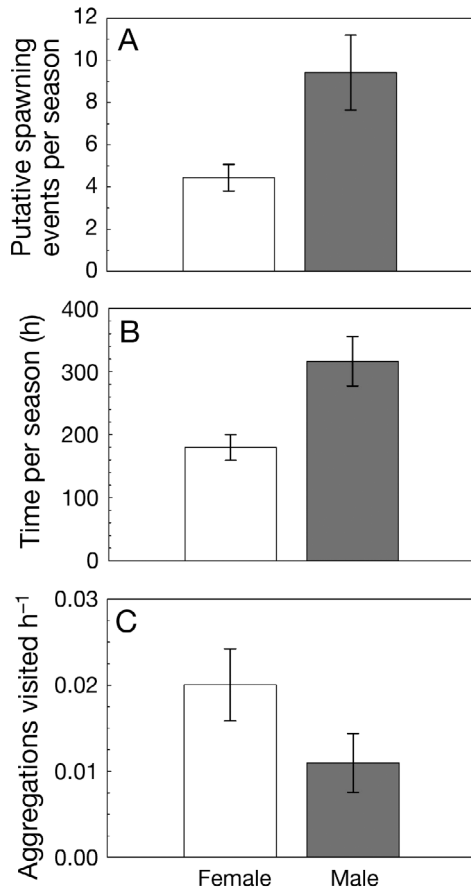
Fig. 5. (A) Putative spawning events participated in, (B) mean length of time spent in spawning aggregations, and (C) mean number of aggregations visited per hour spent in aggregations during a full spawning season by male and female Atlantic cod (mean ± SE)

0.02 events h^{-1}) and females (0.20 ± 0.01 events h^{-1}). There were indications of larger individuals participating in a greater number of events over the course of a full spawning season compared smaller individuals, regardless of sex (ANCOVA: $F_{1,27}$ = 3.62, p = 0.07; Fig. 6).

DISCUSSION

Male and female cod were found to exhibit different patterns of behavior consistent with those described in other studies (Table 1). Both males and females remained at relatively constant depths for extended periods during the spawning season, presumably on or near the substrate, with occasional excursions into the water column (cf. Brawn 1961a,b, Rose 1993, Hutchings et al. 1999, Fudge & Rose 2009, Meager et al. 2009, 2010).

Residency in spawning aggregations

Consistent with previous studies, males seemed to spend more time within spawning aggregations than did females. Telemetry studies of relatively small numbers of individuals in cod spawning aggregations indicated that males do spend a greater proportion of time in the spawning aggregation (Windle & Rose 2007) or associated with a focal area delineated as a spawning arena (Meager et al. 2009, 2010). Furthermore, other studies have described highly skewed sex ratios in the catches of Atlantic cod on their spawning grounds (see Nordeide & Folstad 2000 for review). This is attributed to the tendency of males to remain in the spawning aggregation or arena on or near the substrate while females take up residence in areas located peripherally to the males and join them only when ready to spawn (Morgan & Trippel 1996, Windle & Rose 2007, Meager et al. 2009, 2010).

Females exhibited shifts in depth ranges suggestive of relocating to different spawning aggregations more frequently than males. If interpreted correctly, the DST profiles suggest that most female cod do not linger in a spawning aggregation during this period between putative spawning events. Females instead displayed a depth profile more similar to that of a foraging or moving fish (Godø & Michalsen 2000, Righton et al. 2001, Pálsson & Thorsteinsson 2003, Grabowski et al. 2011) during these interludes between tidal signatures. There has not been direct observation of this phenomenon in the field. However, it is consistent with both descriptions of the reproductive biology and the presumed lekking mating system of Atlantic cod (Nordeide & Folstad 2000) and a lekking mating system generally (Höglund & Alatalo 1995). Female Atlantic cod are batch spawners, releasing several batches of eggs over the course of a spawning season. The time elapsed between the release of a batch of eggs and the ovulation of the next is variable (approx. 2 to 6 d; Kjesbu 1989, Kjesbu et al. 1996) and there is little reason to believe that females would have to remain within a spawning aggregation during this period. Furthermore, in many lekking species, there is evidence that females may assess numerous leks prior to making a selection (Schroeder 1991, Widemo & Owens 1995, Durães et al. 2009) and this may be the case for female Atlantic cod. However, additional investigation of this phenomenon with other methodologies is necessary before a definitive interpretation can be made.
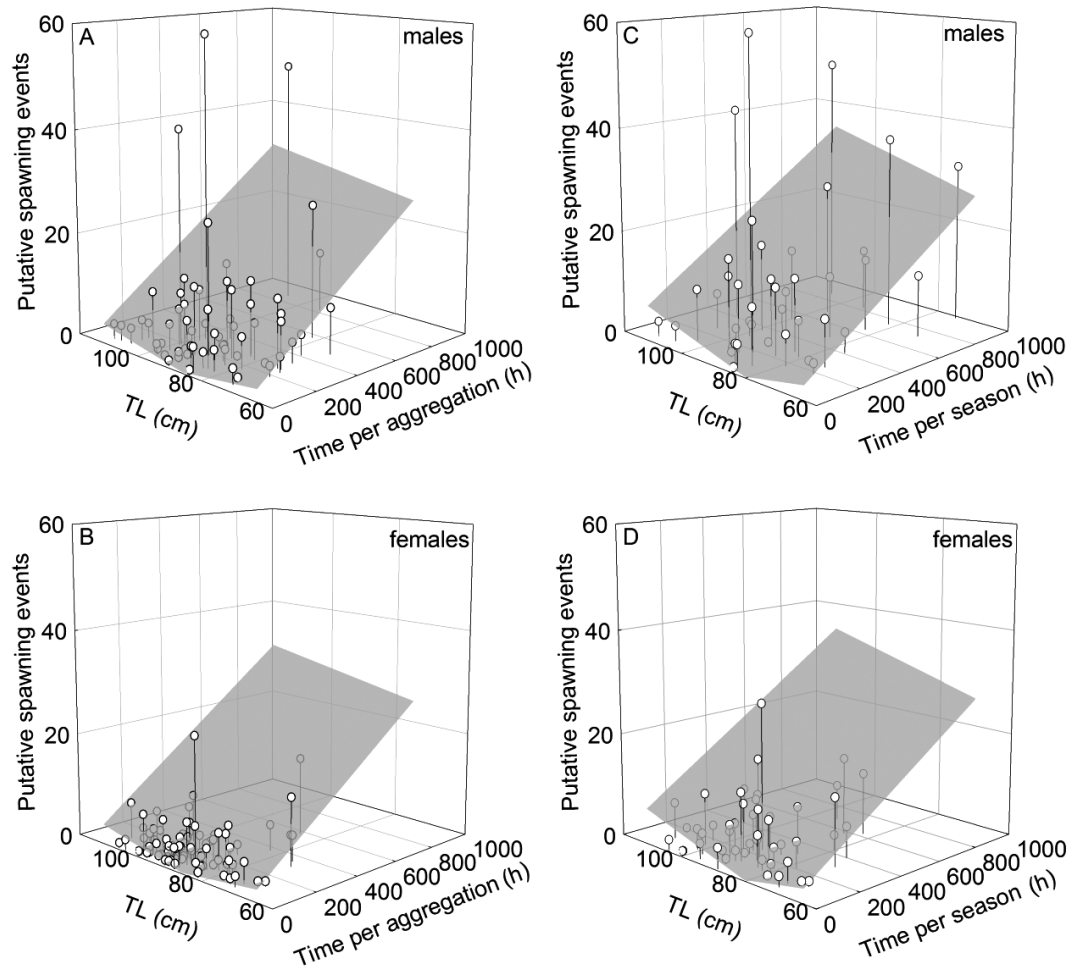
Fig. 6. Relationship between total length (TL) and (A,B) time per aggregation or (C,D) season and number of putative spawning events participated in by (A,C) male and (B,D) female Atlantic cod in Icelandic waters

Participation in putative spawning events

Both size and sex seemed to be related to the number of putative spawning events participated in. In laboratory studies, size is a good predictor of male reproductive success either directly through fertilization rate (Bekkevold et al. 2002, Rowe et al. 2004, 2007, Bekkevold 2006) or indirectly through other traits correlated with size, such as muscle mass associated with sound production (Engen & Folstad 1999, Rowe et al. 2008) or fin area (Rowe et al. 2008). The greater mean number of putative spawning events participated in by males relative to females may simply reflect the lack of an inter-batch period between gamete releases or may support laboratory studies finding, i.e. that a spawning pair of Atlantic cod may attract additional males who trail the spawning pair into the water column while releasing gametes (Hutchings et al. 1999, Rowe & Hutchings 2003). These trailing males may account for a sizeable proportion

of successful fertilizations from any given spawning event (Bekkevold et al. 2002) and they also may potentially account for the observed difference between the sexes in the number of putative spawning events recorded by the DSTs. However it is important to note, the data collected by DSTs cannot definitively demonstrate that the events identified as participation in a spawning event represent an interaction between 2 individuals of the opposite sex or whether gametes were released.

The uncertainty surrounding the interpretation of the depth profiles from the DSTs highlights some of the limitations of the data collected by DSTs. The results are conservative estimates of spawning behavior. The relatively low sampling rate of the DSTs compared to the potential duration of a spawning event and the criteria we imposed to accept a pattern as a spawning event likely resulted in an underestimate of the number of spawning events tagged individuals actually participated in. For example, our

estimates for the number of putative spawning events participated in by females over the course of a season are lower than that reported by Kjesbu (1989) and Kjesbu et al. (1996) from direct observations of captive females (Table 1). The interval between female putative spawning events observed in the DST profiles seems to match that observed in laboratory studies (Kjesbu 1989, Chambers & Waiwood 1996, Kjesbu et al. 1996; Table 1). However, the low minimum time interval between putative spawning events observed in females may represent an example of a false positive in the dataset or variation in spawning behavior among individuals, e.g. incomplete release of eggs or interruption of a previous spawning event.

Conclusions

Overall, DSTs are capable of producing results that are consistent with previous accounts of Atlantic cod reproductive behavior (Table 1) and add insights otherwise unobtainable by other methodologies. However, there are some issues requiring further analysis before this approach can be widely applied to other species: in particular, the conservative nature of the estimates of behavior, the assumptions made to generate these data, and the need for pre-existing descriptions of spawning behavior to enable interpretation. There are also 2 important assumptions that require validation: (1) confirming that residence in a spawning aggregation and participation in a spawning event produce depth profiles similar to those associated with these behaviors in this study, and (2) that the tagged individual is not acting in isolation. Advances in DST technology will produce tags capable of monitoring egg releases or detecting and recording the presence of nearby tagged individuals (Metcalfe et al. 2009), but likely at the expense of sample size. However, our ability to interpret the data collected by DSTs is due in large part to the large body of information derived from other methodologies. This lack of context may limit the usefulness of this approach to a complementary role in behavioral research of less intensively studied marine fishes until such time that the necessary information is available.

The ability to examine the complex mating system and reproductive behavior of Atlantic cod and other broadcast spawning fishes has the potential to aid in the development of fisheries management and conservation plans. The reproductive behaviors of these fishes may produce unexpected consequences in heavily exploited populations. For example, in many cod stocks, the spawning aggregations are actively targeted (Rowe & Hutchings 2003, Brander 2005). During the spawning season, males would be more vulnerable to most of the fishing gears employed, and the larger males that are involved in a large number of spawning events may be particularly susceptible to capture (Rowe & Hutchings 2003, Rowe et al. 2004). This may ultimately result in reduced reproductive output as a chain of events stemming from females preferring larger males is set in motion by the removal of these individuals from the aggregations (Rowe & Hutchings 2003, Rowe et al. 2004, Gascoigne et al. 2009). There is also evidence that the deployment of active fishing gears, such as bottom trawls, is a substantial disruption to the spawning behavior of individuals who manage to avoid capture (Morgan et al. 1997), potentially due to the need to reestablish the spatial and social structure required by a complex mating system, and results in stress that can affect the survival of offspring (Morgan et al. 1999). It is likely that Atlantic cod are not an isolated example, and that other broadcast-spawning marine fishes may possess similarly complex mating systems and behaviors (Rowe & Hutchings 2003, Solmundsson et al. 2003). This love and lust at 50 fathoms, i.e. fish reproductive behavior, may have important ramifications to the management and conservation of marine fishes, particularly at reduced population densities. Though additional refinement and validation is necessary, our results suggest that DSTs offer the potential to monitor a complex suite of reproductive behaviors at large spatial and temporal scales and provide insight into how such behaviors that are core to population persistence are affected by fisheries management decisions made at the population level.

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