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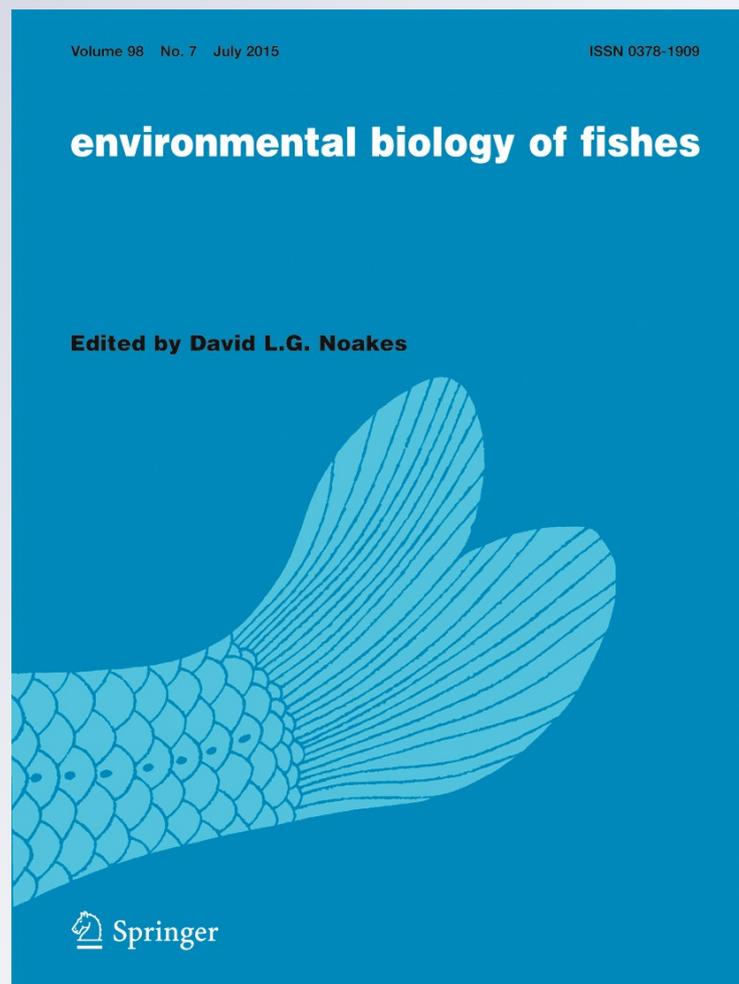
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# Evidence from data storage tags for the presence of lunar and semi-lunar behavioral cycles in spawning Atlantic cod

Timothy B. Grabowski · Bruce J. McAdam ·  
Vilhjálmur Thorsteinsson · Gudrún Marteinsdóttir

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**Abstract** Understanding the environmental processes determining the timing and success of reproduction is of critical importance to developing effective management strategies of marine fishes. Unfortunately it has proven difficult to comprehensively study the reproductive behavior of broadcast-spawning fishes. The use of electronic data storage tags (DSTs) has the potential to provide insights into the behavior of fishes. These tags allow for data collection over relatively large spatial and temporal scales that can be correlated to predicted environmental conditions and ultimately be used to refine

predictions of year class strength. In this paper we present data retrieved from DSTs demonstrating that events putatively identified as Atlantic cod spawning behavior is tied to a lunar cycle with a pronounced semi-lunar cycle within it. Peak activity occurs around the full and new moon with no evidence of relationship with day/night cycles.

**Keywords** Lunar cycle · Data storage tags · Reproductive ecology · Diurnal solar cycle · *Gadus morhu*

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T. B. Grabowski (✉)  
U.S. Geological Survey, Texas Cooperative Fish and Wildlife  
Research Unit, Texas Tech University, PO Box 42120,  
Lubbock, TX 79409, USA  
e-mail: t.grabowski@ttu.edu

B. J. McAdam  
Institute of Aquaculture, University of Stirling, Stirling FK9  
4LA, UK

V. Thorsteinsson  
Marine Research Institute, Skulagata 4, 121 Reykjavik,  
Iceland

G. Marteinsdóttir  
Institute of Biology, University of Iceland, Askja, Sturlugata  
7, 101 Reykjavik, Iceland

## Introduction

Entraining reproductive cycles to environmental cues is an essential adaptive strategy for marine fishes (Takemura et al. 2004, 2010) both on a relatively gross temporal scale, e.g., initiating gonadal maturation or establishing the start of the spawning season at a particular time of year, and finer temporal scales, e.g., governing the timing of gamete release within a spawning season. However, the precise environmental cues and triggers that regulate reproductive behavior are not fully understood for most species. Temperature and photoperiod have long been associated with the timing of reproductive cycles in species inhabiting temperate and higher latitudes (Peter and Yu 1997). In contrast, many tropical species utilize lunar cycles, or the 29.52812 d cycle between the full and new moon, for

reproductive cues because temperature and photoperiod are relatively stable throughout the year at these lower latitudes (Takemura et al. 2004). There is also extensive evidence that these same tropical marine fishes link cyclical spawning behavior within a reproductive season to lunar cycles (see Takemura et al. 2004, 2010 for reviews). This within-season synchronization is not limited to tropical marine fishes, as many intertidal spawning species such as California grunion *Leuresthes tenuis* (Clark 1925) and mummichog *Fundulus heteroclitus* (Taylor et al. 1979; Marteinsdóttir and Able 1992) spawn almost exclusively on a 14-day cycle corresponding to the semi-lunar cycle, or the 14.7906 d period between spring and neap tides. These species deposit their eggs at or above the high tide line during spring tides where development can occur in an environment with reduced predation risk. Species with an estuarine-dependent life history strategy may exhibit recruitment peaks coinciding with various lunar phases thus improving egg survival through lowered predation but also facilitating transport of newly hatched larvae into suitable estuarine nursery habitats at high tides (Miller et al. 1988). Lunar or semi-lunar spawning periodicity has been directly observed in a wide range of taxa, including clupeids (Hay 1990), atherinopsids (Conover and Kynard 1984), sparids (Wakefield 2010), and sciaenids (Aalbers 2008). Also, a number of studies have identified lunar or semi-lunar periodicity in the recruitment and settlement of larval fishes (Robertson et al. 1990; Takemura et al. 2004, 2010). However, evidence of other environmental cycles influencing within-season spawning behavior in temperate marine fishes, such as the diurnal solar cycle (i.e., day-night cycle), are more common (Ferraro 1980; Migaud et al. 2010).

Atlantic cod *Gadus morhua* is amongst the most intensively studied marine fish species in the world, yet many aspects of its reproductive behavior and biology are poorly known. The seasonal nature of cod spawning is well documented throughout its range (Brander 2005), but there is little information available regarding whether cyclical behavior exists within a spawning season. There are reports that cod spawning occurs primarily at night or twilight (Kjesbu 1989; Hutchings et al. 1999), but these observations have been based primarily on captive fish. Field studies suggest that a day-night cycle exists in some populations (Fudge and Rose 2009); while other populations may exhibit behaviors consistent with spawning during daylight

hours (Grabowski et al. 2012). While there has been no evidence presented that suggests activity in spawning Atlantic cod coincides with tidal, semi-lunar, or lunar cycles, it is unclear whether this is because cod do not entrain these celestial cycles or because of a lack of sufficient data or direct evaluation. Increasing knowledge on spawning behavior has particular relevance to the management and conservation of Atlantic cod fisheries as intensive fishing effort for this species is often focused on their spawning aggregations (Morgan et al. 1997; Begg and Marteinsdottir 2003).

Furthermore, Atlantic cod can exhibit high levels of behavioral diversity and plasticity both across their range (Brander 2005) and at more local scales. For example, the Icelandic cod stock has distinct geographic components, one in the waters off northern Iceland and another off southern Iceland (Pampoulie et al. 2006). Two distinctive behavioral ecotypes occur within each geographic component. Coastal cod tend to remain in the relatively shallow water of the continental shelf, while frontal cod move to deeper waters along the shelf break and exhibit large daily vertical migrations (Pálsson and Thorsteinsson 2003; Pampoulie et al. 2008; Grabowski et al. 2011). These stock components exhibit differences in their reproductive phenologies (Grabowski et al. 2011) and thus it is possible that their reproductive behavior has responded differently to environmental cycles.

Our objective was to test the hypothesis that Atlantic cod activity during the spawning season may be synchronized with four environmental cycles: annual solar cycle, diurnal solar cycle, lunar cycle, and semi-lunar cycle. Secondly, we evaluated whether there were differences in the relationship between activity and environmental cycles amongst the geographic and behavioral components of the Icelandic cod stock.

## Methods

### DST depth profile collection and interpretation

We used a data set of 822 putative spawning events identified from the depth profiles of 58 data storage tags (DSTs; DST Centi and DST Milli: Star-Oddi Marine Device Manufacturing, Reykjavik, Iceland) recovered from Atlantic cod in Icelandic waters during 2002–2007 as described by Grabowski et al. (2014). Briefly, we tagged 1,188 Atlantic cod from spawning aggregations

around Iceland following the procedure described in Thorsteinsson and Marteinsdóttir (1998). While a total of 449 individuals have been recovered, only 58 individuals (27 males; 31 females) were at liberty for a sufficient time to encompass at least one full spawning season. Most of these individuals were from the southern component of the Icelandic cod stock, and there were about twice as many cod exhibiting the coastal behavioral type as individuals exhibiting the frontal behavioral type (Table 1). No coastal behavioral types were recovered from the northern stock component with usable DST depth profiles during the spawning season. The DSTs recorded paired temperature and depth measurements at 10-min intervals throughout the duration of the spawning season (mid-February – 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.

Putative spawning events were identified from the depth profiles of recovered DSTs based on published descriptions of Atlantic cod spawning behavior, primarily Brawn (1961a, b), Rose (1993), Hutchings et al. (1999), Fudge and Rose (2009), and Meager et al. (2009). 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 low levels of vertical movement produce a DST depth profile with a clear tidal signature (Righton et al. 2001). Therefore, a DST-generated depth profile consisting primarily of a clear tidal signature lasting at least 12.5 h was interpreted as participation in a spawning aggregation if occurring between migratory periods and within the

Atlantic cod spawning season of mid-February to early June in Icelandic waters (Thorsteinsson and Marteinsdóttir 1998; Marteinsdóttir et al. 2000). Migratory events consisted of a directed change in the depth occupied by an individual (Grabowski et al. 2011; Thorsteinsson et al. 2012; Grabowski et al. 2014; Fig. 1), indicated by a shift in the mean daily depth to the shallower waters occupied during spawning from the deeper water occupied during the remainder of the year. Periods of clear tidal signature did occasionally occur outside of the spawning period but tended to be shorter in duration and lacked the vertical behavior characterized as putative spawning events.

Vertical behaviors identified as putative spawning events were characterized as a three-part process that occurred within a period of a clear tidal signature (Grabowski et al. 2014). First we required the individual to occupy an initial depth  $\pm 0.25$  m for three consecutive observations at 10 min intervals, followed by an ascent into the water column of at least 1.50 m, and a return to its initial depth  $\pm 0.25$  m. Spawning cod in laboratory settings have been observed to swim into the water column after courtship and release their gametes before returning to the substrate (Brawn 1961b; Rose 1993; Hutchings et al. 1999). Hydroacoustic surveys actively spawning cod have observed individuals traveling as much as 150 m from the bottom, sometimes forming large columns above the aggregation (Rose 1993; Fudge and Rose 2009). However, vertical movements of < 10 m may be more common (Grabowski et al. 2012, 2014). The counts of putative spawning events are subject to error from false positives and false negatives, i.e. missed events, due to the short duration of a spawning event, about 10 s in captive conditions (Hutchings et al. 1999), and relatively rapid ascent rate (12–15 m min<sup>-1</sup>; Grabowski et al. 2012) relative to the DST sampling interval. At the same time, activity could be overestimated due to the fact that these short duration vertical movements could be due to a number of factors unrelated to spawning. However, there are sex-specific differences in the number of putative spawning events recorded per spawning season and intervals between events that suggest the database represents a reasonable estimate of spawning activity (Grabowski et al. 2014).

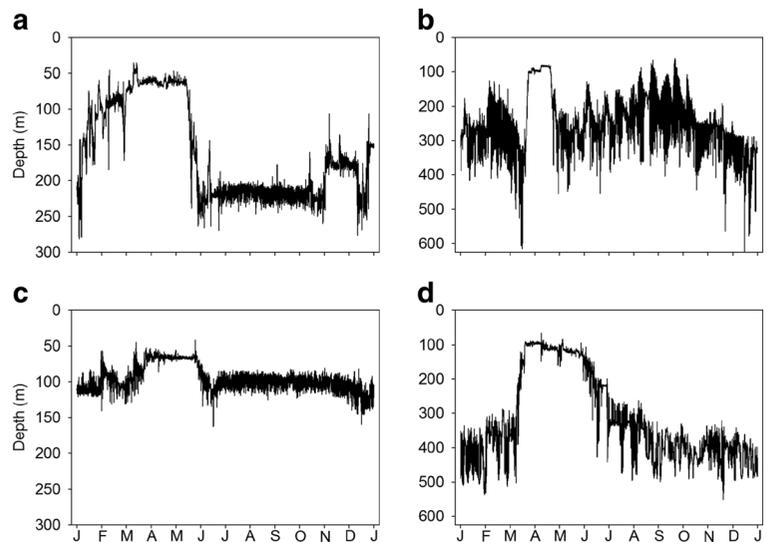
#### Analysis of cyclical behavior

We evaluated the relationship between the timing of putative spawning events and four environmental

**Table 1** Population, behavioral type, and sex of Atlantic cod from Icelandic waters tagged with electronic data storage tags and recovered after at least one full spawning season during 2002–2007

	Males	Females	Total
Northern	2	4	6
Frontal	2	4	6
Southern	25	27	52
Coastal	15	19	34
Frontal	10	8	18
Total	27	31	58

**Fig. 1** Representative annual depth profiles collected from Atlantic cod in Icelandic waters using electronic data storage tags deployed during 2005. The depth profiles in panels (a) and (c) were from cod exhibiting a coastal behavioral type and the depth profiles displayed in panels (b) and (d) were from cod exhibiting a frontal behavioral type



cycles. The annual solar cycle was calculated with a period of 365.2424 d, obtained by dividing the time between the winter solstice in 2004 and winter solstice 2010 by 6 years, with time zero ( $t_0$ ) placed at the winter solstice. For the lunar cycle we used a period of 29.52812 days obtained by dividing the time between the full moon in January 2004 and full moon January 2010 by the 75 lunar periods between. The full moon was used as  $t_0$  for this cycle. As tides are influenced by a semi-lunar cycle, with spring tides around both the full and new moon, we also included a semi-lunar cycle in our analysis with period of 14.7906 days and  $t_0$  at both the full and new moon. The position of every spawning event within each natural cycle relative to its  $t_0$  was expressed as an angle in radians, e.g., an event occurring at 06:00 has an angle of  $\pi/2$  radians on the daily solar cycle, and an event occurring at the first quarter moon has an angle of  $\pi$  radians on the semi-lunar cycle and  $3\pi/2$  radians on the lunar cycle. In order to detect whether behavior was cyclic with particular periods, Rayleigh (1919) tests were used to test for uniformity of the distribution of angles. For the periods that were significantly different from uniformity, after verifying that these distributions roughly fit a von Mises distribution, we estimated the dispersion,  $K$ , and peak angle,  $\mu$ , using a maximum likelihood method and used bootstrapping to generate the confidence intervals around these estimates. The best-fit annual and semi-lunar distributions were combined into a predictive model simply by multiplying the probability densities from each.

We used three approaches to evaluate whether the timing of potential spawning events was associated with a diurnal solar cycle. First we evaluated whether there were peaks in activity associated with a particular time of day by assigning the daily solar cycle (day and night) a period of 1 d (84,600 s) and placing  $t_0$  at midnight GMT following the approach described above. However, the Atlantic cod spawning season in Iceland occurs during a period of rapidly changing day length, as there are approximately 8 h of daylight at the start of the season in mid-February and almost 20 h by its conclusion in late May-early June. Therefore, we needed to account for shifts in sunrise and sunset during this period. We evaluated whether cod activity was more likely to occur during daytime or nighttime than dawn and dusk by assigning local midday and midnight angles of 0 radians and 18:00 GMT and 06:00 GMT angles of  $\pi$  radians, then performing Rayleigh tests as described above. While this approach addresses whether cod activity does not peak during dawn and dusk, it would still not definitively identify a crepuscular pattern due to the shifting times of sunrise and sunset. To account for these shifting times, we also divided the dataset into two parts: events that occurred  $\pm 4$  h of sunset and events that occurred  $\pm 4$  h of sunrise. The times of sunrise and sunset at 63.50.0°N were defined daily using the NOAA Earth System Research Laboratory solar calculator (NOAA, <http://www.esrl.noaa.gov/gmd/grad/solcalc>) and were assigned an angle of 0 radians. The time 4 h before and after sunrise and sunset were each assigned

an angle of  $\pi$  radians. Intervals between each potential spawning event and sunrise/sunset were assigned an angle between 0-  $\pi$  radians and evaluated using the Rayleigh tests as described above.

## Results

Atlantic cod activity coincided with several environmental cycles based on the interpretation of depth profiles generated from recovered DSTs. When all of the individuals were considered as a single unit, we found that the distribution of putative spawning events differed from a uniform distribution over an annual period (Rayleigh test,  $P < 0.01$ , Fig. 2a) and the bootstrapped maximum likelihood estimates of spawning behavior peaked on an annual cycle in late April to early May (95 % confidence interval of day 117–120 after 01 January). However, cod tagged from spawning aggregations in southern Iceland seemed to exhibit an annual peak in activity that was approximately 10–14 days earlier than counterparts captured from aggregations in northern Iceland (day 126–132), but no further statistical analysis was conducted due to small sample size from northern spawning aggregations. Time of peak spawning on an annual cycle did not differ between cod exhibiting coastal vs frontal behavior (95 % confidence intervals: day 116–119 for southern coastal and day 113–118 for south frontal).

There was no indication of activity being tied to a diurnal solar cycle (Rayleigh test:  $P = 0.53$ ; Fig. 2b). Individuals were equally likely to exhibit putative spawning behavior during daylight or nighttime hours, and there did not seem to be any tendency for activity to peak during dawn (Rayleigh test:  $P = 0.50$ ) or dusk (Rayleigh test:  $P = 0.40$ ).

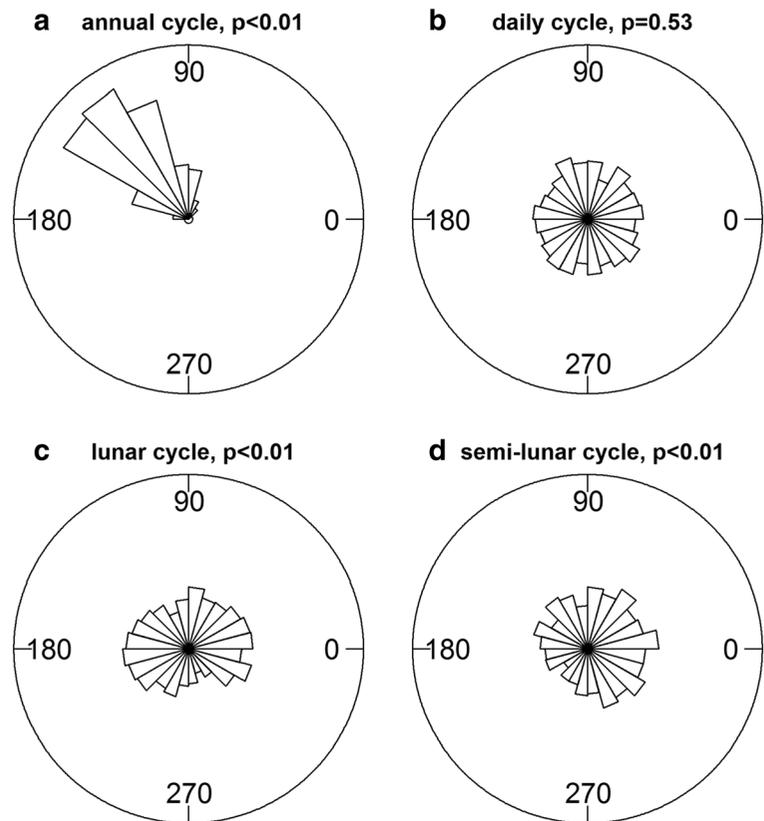
In contrast to the solar cycle, Atlantic cod activity seemed to have relationships with both the lunar and semi-lunar cycles (Rayleigh tests:  $P < 0.01$  for lunar cycle;  $P < 0.01$  for semi-lunar cycle; Fig. 2c and d). The peak in the semi-lunar cycle coincided with the spring tide about 0.5–1.6 d after a full or new moon, and in addition we detected a peak in the lunar cycle 6–11 d after the full moon, suggesting that cod may spawn more frequently during the waning phases of the moon (from full to new) with peaks during both spring tides. However, the relationship with the lunar cycle was weaker than that of the semi-lunar cycle as evidenced by the higher dispersal of events throughout the cycle

(Fig. 2c and d). There were no apparent differences in the timing of spawning as related to lunar and semi-lunar spawning in northern and southern Icelandic cod based upon 95 % confidence intervals of the estimates of peak activity, but the small sample size of individuals from the northern stock component precluded further statistical analysis. Likewise there seemed to be no differences between coastal and frontal cod from the southern stock component in their timing as it related to lunar or semi-lunar cycles as 95 % confidence intervals from bootstrapping overlap. The observed frequency of activity relative to the probability density of activity from the multiple cycles is illustrated in Fig. 3.

## Discussion

Atlantic cod activity during the spawning season in Iceland seems to be strongly tied not only to an annual solar cycle as expected, but also to lunar and semi-lunar cycles. This may be the first evidence for the entrainment of lunar and semi-lunar cycles in this species. Although the exact timing differs among populations and locations, Atlantic cod exhibit distinct spawning seasons throughout its range (Brander 2005). In Iceland, cod are reported to spawn between mid-March and mid-June (Jónsson 1982; Marteinsdóttir et al. 2000; Brander 2005) with a peak in the season generally occurring in mid-April on the main spawning grounds off southern Iceland (Marteinsdóttir et al. 2000). The potential differences between northern and southern Icelandic cod in their timing of spawning observed in this study have been previously noted by Marteinsdóttir et al. (2000) and Grabowski et al. (2011). Overall, these observations are similar to our results suggesting a protracted spawning season in Icelandic waters running from February to June. However, our observation of activity peaking in late April-early May was slightly later than that noted in the literature (Jónsson 1982; Marteinsdóttir and Björnsson 1999; Marteinsdóttir et al. 2000), but this difference might be attributable to our sampling protocol. Our tagging was typically restricted to April due to various logistical considerations, and thus might be biased towards individuals that spawn relatively late in southern Iceland and relatively early in northern Iceland. The similarity in peak activity between coastal and frontal cod was not unexpected. The two behavioral types seem to initiate spawning behavior at

**Fig. 2** Observed frequency of putative Atlantic cod spawning events inferred from electronic data storage tags, by time offset in four different natural cycles (**a**) annual (0 degrees = midwinter), (**b**) daily (0 degrees = midnight), (**c**) lunar (0 degrees = full moon), and (**d**) semi-lunar (0 degrees = full or new moon)

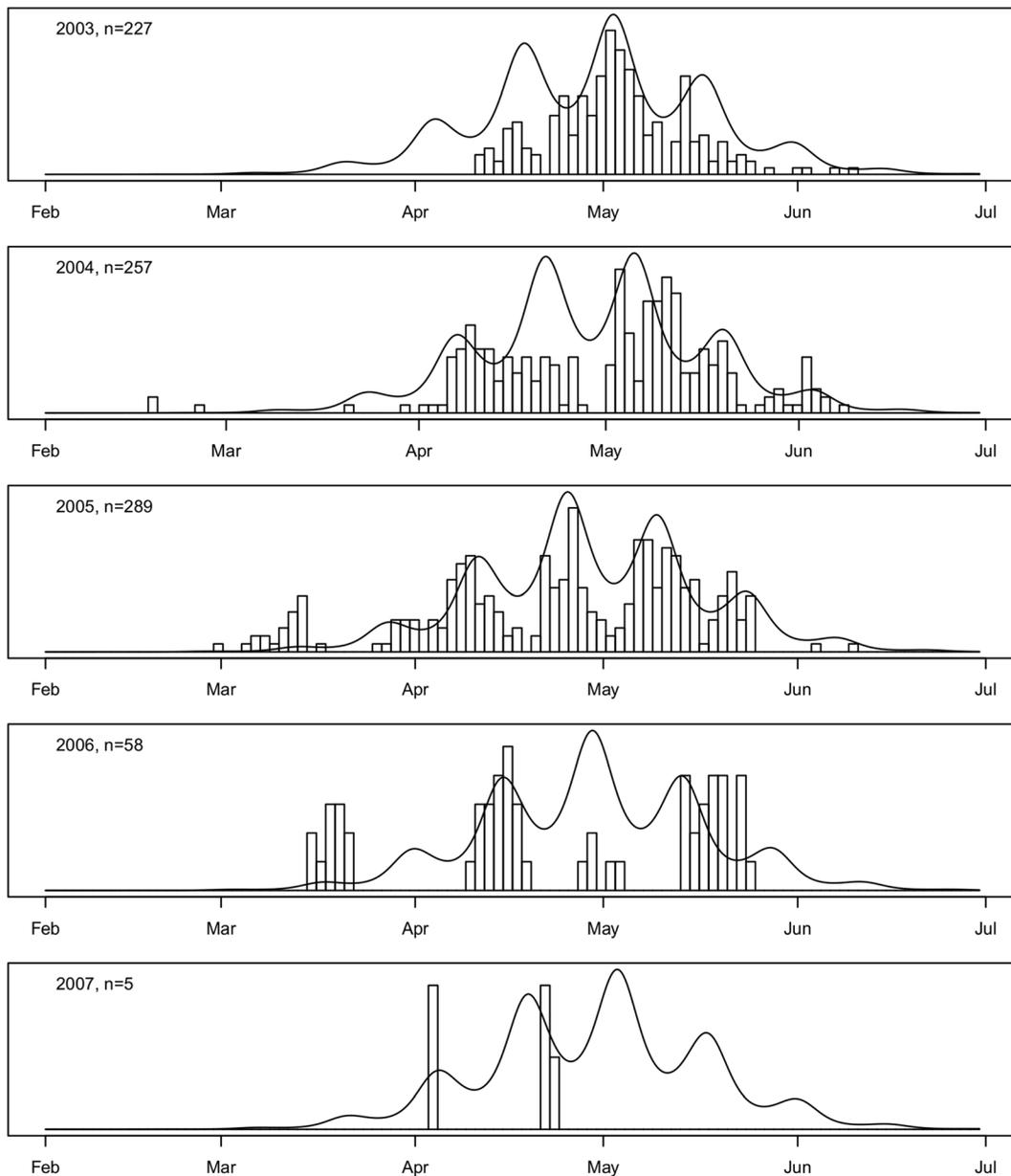


approximately the same time despite experiencing dramatically different temperature regimes (Grabowski et al. 2011).

Icelandic cod seem to lack a diurnal solar cycle in their activity during spawning. Previous observations of Icelandic cod spawning seem to support the lack clear diurnal solar cycle in the DST depth profiles. Using a split-beam echosounder and dual-frequency identification sonar, Grabowski et al. (2012) found distributions of cod consistent with those described for spawning column formation during daylight hours, but did not investigate whether this phenomenon also occurred at night. Observations of Icelandic cod in production and laboratory facilities have noted spawning occurs mostly at night similar to that for captive individuals from other populations of cod (Brawn 1961b; Kjesbu 1989; Rowe and Huchings 2006). Field studies of other cod populations either suggest primarily nocturnal reproduction in cod (Fudge and Rose 2009) or do not directly quantify or observe spawning behavior (Siceloff and Howell 2013) making it difficult to directly compare with our results. While Fudge and Rose (2009) describe cod spawning columns forming at only night in

Newfoundland, the study was only conducted over an 18.5-h period making it difficult to conclude that these columns form only at night throughout an entire spawning season. Ultimately, the entrainment of a diurnal solar cycle into spawning behavior may vary among populations as individuals experience differential selective pressures that favor spawning at specific times in a given location (Yamahira 2004). However, this warrants further investigation due to the limitations of interpreting behavior from DST depth profiles as there is no way to confirm gamete release. The activity recorded by the tags could include other behaviors, such as courtship or agonistic displays.

Within a spawning season, the activity of cod in Iceland seems to peak in association with the spring tide, which can lag several days after the full and new moons. Over the course of a full lunar cycle, vertical movements consistent with spawning behavior are most concentrated during the waning phases of the moon, but also peak again during the full moon. While behavioral synchronization with lunar and semi-lunar cycles has been previously noted in Atlantic cod during other parts of the years, such as during the summer or migratory



**Fig. 3** Observed frequency of putative Atlantic cod spawning events as inferred from electronic data storage tags (*bars*) compared to an illustration of the combined effects of probability density of spawning from annual and semi-lunar cycles (*line*) aggregated from 2003 to 2007

periods (Godø and Michalsen 2000; Stensholt 2001; Neat et al. 2006), it is not entirely clear why Icelandic cod would synchronize their activity to these cycles. Numerous hypotheses have been proposed to explain the advantages of synchronizing reproductive behaviors with lunar and semilunar cycles. A semi-lunar spawning cycle is thought to enable spawning fish to enhance or limit dispersal during spring or neap tides (Takemura

et al. 2004), or otherwise reduce mortality by giving the developing larva access to protected habitats (Clark 1925; Taylor et al. 1979; Marteinsdóttir and Able 1992; Takemura et al. 2004). Fishes timing their spawning behavior with a lunar cycle may be using this cycle to synchronize spawning in order to swamp predators, minimize intra-cohort competition, facilitate movement to or from spawning grounds, allow more

effective guarding of nest sites at night, or to provide settling larva the cover of darkness during a new moon (Taylor 1984; Robertson et al. 1990; Takemura et al. 2004). However, few if any of these hypotheses seem directly applicable to what is known about Atlantic cod spawning behavior and early life history. More recently, Hernández-León (2008) proposed that spawning on a lunar cycle might enable larval fishes to both feed more effectively at night ultimately leading to higher growth and survival rates as well as avoid planktivorous fishes, which tend to remain in deeper water during the full moon. While this is an intriguing possible explanation for the entrainment of lunar and semi-lunar cycles in Icelandic cod, further research is needed to fully evaluate the effects of this spawning pattern on cod growth and recruitment.

The use of DSTs to assess the spawning behavior of marine fishes seems to have great potential (Kawabe et al. 2009; Metcalfe et al. 2009; Yasuda et al. 2013) and our methodology seemed to produce realistic, if somewhat conservative (Grabowski et al. 2014), estimates of activity in spawning Atlantic cod. The use of DSTs enables behavioral data to be collected across wide temporal and spatial scales, though the resolution of the data may not be as fine as other approaches. However, the ability to identify peaks in activity during spawning has important implications for the conservation and management of commercial fisheries for cod and potentially other marine species. Atlantic cod has a complex mating system (Hutchings et al. 1999; Nordeide and Folstad 2003) that can be sensitive to anthropogenic disturbances, such as commercial fishing activities (Morgan et al. 1997; Rowe and Hutchings 2004). Current management practices for Atlantic cod and many other marine species include times or areas that are closed to exploitation. For example, current management of the Icelandic cod stock mandates a closed two-week period (Fiskistofa 2014). The start date of these closures varies around the island depending on time of peak spawning in each area (Marteinsdóttir et al. 2000). Our results suggest that these practices might not always incorporate the peak of activity in Iceland. Furthermore, incorporating our results into a stock assessment program might allow for the refinement of conservation and management activities to ensure the protection of spawning stocks during the periods where their reproductive output is highest, while at the same time potentially minimizing impacts on the commercial fishery.

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