

-Not to be cited without prior reference to the author-

Lunacy in Atlantic cod: Assessing the timing of spawning in Atlantic cod using ocean models and electronic data storage tags

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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, such as Atlantic cod *Gadus morhua*, in the wild. The combination of oceanographic models and electronic data storage tags (DSTs) has the potential to provide insights into the behavior of fishes by allowing data collection over relatively large spatial and temporal scales that can be correlated to predicted environmental conditions. In this paper we present data retrieved from DSTs demonstrating that Atlantic cod spawning in Iceland is tied to a lunar cycle with a pronounced semi-lunar cycle within it. Peak spawning activity occurs around the full and new moon with no evidence of relationship with diel tidal or day/night cycles. We then use a Cartesian coordinate ocean model with three-dimensional adaptive mesh refinement and primitive equations (CODE) to assess the changes in environmental conditions at known cod spawning grounds associated with lunar and semi-lunar cycles and identify oceanographic conditions that might render this spawning strategy beneficial.

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Introduction

Entraining reproductive cycles to environmental cues is an essential adaptive strategy for marine fishes (Takemura et al. 2004, 2010) both on a relatively broad 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. Temperature and photoperiod have long been associated with the timing of reproductive cycles in temperate and higher latitude species (Peter and Yu 1997). Because temperature and photoperiod are relatively stable throughout the year at lower latitudes, many tropical species utilize lunar cycles for synchronizing spawning migrations and gonadal maturation (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 and 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 tidal cycle. 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.

Cyclical spawning behavior within a spawning season is an important aspect of the reproductive and evolutionary ecology of many tropical and intertidal spawning fishes. However, examples of temperate species exhibiting similar behavior are relatively rare. Species with an estuarine-dependent life history strategy may exhibit recruitment peaks coinciding with various lunar phases suggest newly settled individuals of these species were spawned during periods to take advantage of increased tidal flows which may facilitate transport into suitable estuarine nursery habitat (Miller 1988). The remaining evidence that is suggestive of cyclical patterns in the spawning behavior of temperate marine fishes seem to be reports of spawning occurring primarily at night in wide variety of taxa (Ferraro 1980; Migaud et al. 2010). There have been few attempts to thoroughly assess to what extent other environmental cycles may influence spawning behavior in temperate marine fishes.

We hypothesize that cyclical spawning behavior in temperate species is rarely reported because it is more difficult to detect than in tropical or intertidal spawning fishes. The selective pressures potentially favoring the development of cyclical spawning might be overwhelmed by the strong seasonal signals in temperature and photoperiod and thus mask underlying cycles on shorter temporal scales. It is also probable that the inherent difficulty in directly observing the spawning behavior of many of these species contributes to the lack of observations. Tropical marine fishes and intertidal spawners are considerably easier to directly observe during spawning, whereas similar research on temperate species is more reliant upon indirect methods. Furthermore, the

temporal resolution of these indirect methods, such as determining the developmental stage of eggs collected in ichthyoplankton surveys or hatch-date analysis, may not be sufficient to resolve what is likely to be a relatively subtle change in spawning frequency, particularly in thermally complex temperate marine environments.

The intensity of research conducted on Atlantic cod *Gadus morhua* renders it a unique model system to investigate the potential for the entrainment of these rhythms and their adaptive significance. Cod 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 (Kjesbu 1989; Hutchings et al. 1999; Marteinsdóttir et al. *personal observation*), 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 others have found that spawning activity can occur at all times of the day (T.B. Grabowski, unpubl. data). There has been no evidence presented that suggests spawning activity coincided with tidal, semi-lunar, or lunar cycles. Therefore our objectives were to determine if cod spawning behavior may be synchronized with other environmental cycles, evaluate whether the distinct behavioral or geographic components of a stock vary in this synchronization, and assess the adaptive significance of cyclical spawning on the early life history stages of Atlantic cod.

Methods

Data storage tag implantation and recovery — We used data storage tags (DST; DST Centi and DST Milli: Star-Oddi Marine Device Manufacturing, Reykjavik, Iceland) capable of recording temperature in the range of -2.0-40.0°C (resolution: 0.032°C) and depth in the range of 0-800 m (resolution: ± 0.32 m). The DSTs recorded paired temperature and depth measurements at 10-min intervals throughout the duration of the spawning season (March – June) and at either 10-min or 6-hr 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).

We collected spawning Atlantic cod from spring spawning aggregations around Iceland from 2002 through 2007 using gill nets and Danish seines and selected individuals displaying no indication of barotrauma or external injury for tagging. A DST was surgically implanted into each individual's abdominal cavity following the procedure described in Thorsteinsson and Marteinsdóttir (1998). Briefly, we removed each cod from a holding/observation tank and measured it to the nearest 10 mm total length (TL). We then placed the fish 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. We made a small (10-20 mm) incision into the abdominal cavity just off the ventral midline and inserted the DST. 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 and Kleiner 1982). We determined the sex of the individual through a visual examination of the gonads before closing the main incision using three interrupted 3-0 coated absorbable sutures. We administered approximately 100 mg kg⁻¹ of oxytetracycline (Engemycin: Intervet International, Boxmeer, The Netherlands) and 1.0 ml kg⁻¹ of a vitamin solution (Becoplex: Boehringer Ingelheim, Ingelheim, Germany) to each fish prior to release. The entire procedure took less than five minutes and the fish was returned to the sea immediately upon its completion. 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.

DST data interpretation — We used depth data from the recovered DSTs to identify behaviors of Atlantic cod consistent with those described for participation in spawning aggregations by Brawn (1961a,b), Rose (1993), Hutchings et al. (1999), Fudge and Rose (2009), and Meager et al. (2009). These studies, as well as visual observation of shallow water cod spawning aggregations around Iceland (*unpublished data*), suggest that the majority of cod courtship and male-male interactions take place on or near the bottom. Participation in a spawning aggregation or lek therefore should be associated with a DST-generated depth profile consisting primarily of a clear tidal signature of varying quality depending upon sea surface conditions. These signatures should occur between migratory periods (Fig. 1) and within the Atlantic cod spawning season of mid-March to early June in Icelandic waters (Thorsteinsson and Marteinsdóttir 1998; Marteinsdóttir et al. 2000). Events matching this description from the archived data were recorded for each individual along with the duration of time the individual displayed this pattern. The return to a more variable depth profile suggestive of moving fish or loss of a clear tidal signature was interpreted as the departure of an individual from a spawning aggregation.

Studies of captive Atlantic cod suggest that after a period of courtship, the male and female rise off the bottom, 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). In the wild, individuals that are presumably spawning travel as much as 150 m into the water column and can form large columns above the aggregation (Rose 1993; Fudge and Rose 2009). Based on these observations, we interpreted a spawning event from the DST data as a three-part process that occurred within a period identified as occupation of a spawning aggregation (Fig. 1). First we required the individual to occupy an initial depth ± 0.25 m for three consecutive observations to limit the possibility of identifying noise from rough sea conditions as a spawning event. During the next 10-min time step, the fish had to swim into the water column to a depth at least 1.50 m above that occupied during the previous three 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 almost certainly underestimates because of these requirements and the low probability of recording a spawning event due to its short duration. The dorsal mount behavior of cod under captive conditions lasts on average 9.9 ± 2.8 s (Hutchings et al. 1999). Although its duration in wild fish

is unknown, the time needed for gamete release is less than that taken to swim to the appropriate depth and back which seems to take several minutes (T.B. Grabowski, *unpublished data*). Therefore, the events we classify as potential spawning events are most likely not the actual gamete release, but instead reflect participation in a spawning column and capture the individual in transit to or from the depth of gamete release.

Analysis of cyclical behavior — We evaluated the relationship between cod reproductive behavior and four environmental cycles. The annual solar cycle was calculated with a period of 365.2424 days with time zero (t_0) placed at the winter solstice. The daily solar cycle (day and night) has a period of 1 day (84600 seconds) and t_0 was placed at midnight GMT. For the lunar cycle we used a period of 29.52812. 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 π 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 visually verifying that these distributions roughly fit a von Mises distribution, we estimated the dispersion, K , and peak angle, μ , 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.

Estimating dispersal of eggs and larvae — We are currently processing particle tracking computations based on flow fields simulated by the ocean model CODE (Cartesian coordinates Ocean model with three-Dimensional adaptive mesh refinement and primitive Equations: Logemann and Harms 2006; Logemann 2007; Logemann et al. 2010; see <http://www.marice.is/code>) to evaluate the effects of any observed spawning rhythmicity on larval dispersal. CODE is a three-dimensional hydrodynamic model that covers the entire North Atlantic basin but has high spatial resolution for Icelandic waters of up to 1.0 km horizontal and 2.5 m vertical near shore. The temporal resolution is 20 minutes. CODE is capable of incorporating a particle tracking model that can be used to describe dispersal of fish eggs and larvae away from their place of origin (Jónasson et al. 2009; Logemann 2009).

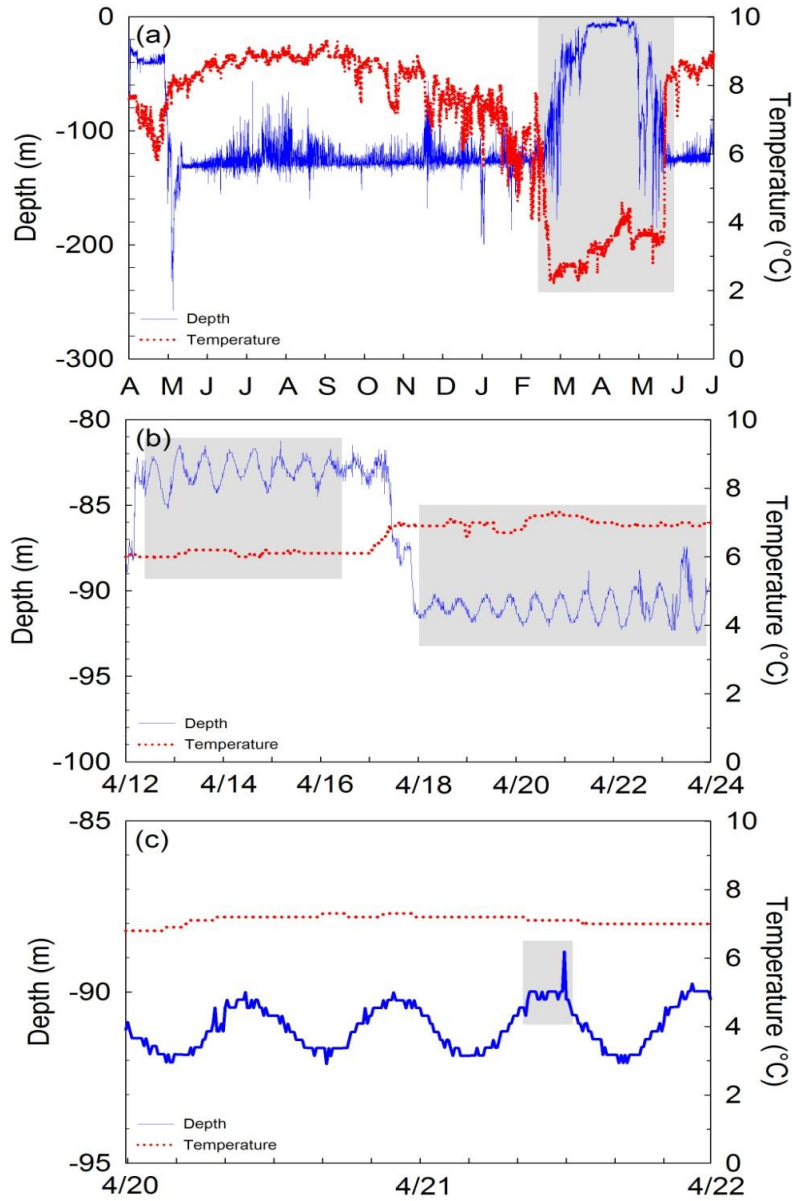


Fig. 1. The process to identify activity patterns consistent with Atlantic cod spawning events in depth profiles from DSTs (Grabowski et al. in review) based on descriptions of cod spawning behavior (Brawn 1961a; Rose 1993; Hutchings et al. 1999). (a) the period between migratory periods was identified. Because courtship occurs on or near the bottom, periods characterized by a clear tidal signature (b) were interpreted as participation in a spawning aggregation. Finally, a potential spawning event (c) was compared with a three-stage “template” representing an idealized spawning event. This template consisted of the individual occupying an initial depth ± 0.25 m for three consecutive observations (30 minutes), then swimming to a depth at least 1.50 m above that occupied during the previous three observations before returning to its initial depth ± 0.25 m on the next observation. Events matching this template were interpreted as participation in a spawning event. Modified from Grabowski et al. (*in prep*).

We will use these models to evaluate the adaptive significance of cod timing their reproduction to environmental cycles by testing the hypothesis that oceanographic conditions during certain periods of the various cycles result in cod eggs and larva experiencing different dispersal/diffusion rates, probabilities of reaching known nursery areas, transport times, or environmental conditions during transport compared to that during other periods. We first evaluate this hypothesis under “idealized” conditions where meteorological factors were held constant and simulating the release of eggs into this “ideal” ocean from known cod spawning grounds at various points in the cycles of interest and simulate their drift for 90 days. The same trials will be repeated in a “realistic” ocean where meteorological conditions were allowed to vary.

Results

Spawning database and comparison to reported values — We tagged 1,188 Atlantic cod from spawning aggregations around Iceland during the five-year period spanning 2002-2007. 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 and had depth profiles clear enough to discern tidal signatures. In total, we identified 822 events from the DST depth profiles that matched our criteria to be interpreted as participation in a spawning event. While our measures of spawning activity were generally consistent with those available from the literature, they do seem to represent a conservative estimate of these behaviors (Grabowski et al., *in prep.*; Table 1).

Cyclical behavior present in DST spawning event database — Atlantic cod spawning activity seemed to coincide 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 spawning differed significantly from a uniform distribution over an annual period (Fig. 2a; Rayleigh test, $p < 0.0001$) the bootstrapped maximum likelihood estimates of spawning behavior peaked on an annual cycle in late April to early May (95% CI of day 117-120 after 1st Jan). Cod tagged from spawning aggregations in southern Iceland demonstrated an annual peak in spawning activity that was approximately 10-14 days earlier than counterparts captured from aggregations in northern Iceland (95% CI: day 116-118 in the south and 126-132 in the north). However, there was no indication that Atlantic cod exhibiting the coastal behavioral patterns described by Palsson and Thorsteinsson (2003) and Pampoulie et al. (2008) differed in their timing of peak spawning from those exhibiting a frontal behavioral pattern (95% CI: day 116-119 for southern coastal and day 113-118 for south frontal). 117-120 after 1st Jan).

There was no indication of Atlantic cod spawning activity being tied to a diurnal cycle (Fig. 2b; Rayleigh test, $P = 0.53$). Individuals were equally likely to spawn during daylight or nighttime hours.

Table 1. Comparison of aspects of spawning behavior in Atlantic cod based interpretation of depth profiles from recovered electronic data storage tags described in this study and published findings from laboratory and field-based studies.

	Present study	Other studies
Sample size		
Females	31	3 ^{1†} ; 10 ² ; 5 ³ ; 27 ⁴ ; 12 ⁵
Males	27	21 ⁴ ; 12 ⁵
Total length of individuals [mean ± SD (range)]		
Females	89 ± 10 cm (69 – 110 cm)	65 ± 10 cm (56 – 75 cm) ¹ 57.0 ± 5.7 cm (45.5 – 67.5 cm) ² (42 – 67 cm) ³ (64 – 87 cm) ⁴ 65.2 ± 9.6 cm ⁵
Males	91 ± 11 cm (72 – 112 cm)	(67 – 88 cm) ⁴ 66.0 ± 6.6 cm ⁵
Spawning events participated in/egg batches produced per season [mean ± SD (range)]		
Females	5.8 ± 3.9 (1 – 20)	18.0 ± 1.0 (17 – 19) ^{1†} 7.0 ± 2.5 (4 – 11) ² 15.8 ± 4.9 (10 – 21) ³
Males	13.0 ± 10.9 (1 – 67)	no <i>in situ</i> observations available
Interval between spawning events/egg batches**[mean ± SD (range)]		
Females	39.4 ± 38.4 h (0.7 – 901.0 h)	75.1 ± 5.2 h (23 – 280 h) ^{1†} 134.4 ± 156.2 h (72 – 216 h) ²
Males	19.9 ± 15.1 h (0.7 – 975.0 h)	no <i>in situ</i> observations available
Residence time in spawning aggregations per year [mean ± SD (range)]		
Females	7.5 ± 4.5 d (0 – 31.3 d)	18.6 d ^{4‡} 17.8 ± 13.5 d ^{5††}
Males	13.2 ± 8.3 d (0 – 40.9 d)	9.5 d ^{4‡} 22.0 ± 12.4 d ^{5††}
Date of entrance into a spawning aggregation	11 Apr 2003*; 17 Feb 2004; 01 Mar 2005; 15 Mar 2006	mid-March ^{6,7,8}
Date last fish exited a spawning aggregation	12 Jun 2003; 9 Jun 2004; 10 Jun 2005; 24 May 2006	mid-June ^{7,8}

*Most fish were tagged during the first week of April 2003

**Numbers for present study reflect number spawning events participated in as inferred from DST data. In other studies, this number reflects egg batches and does not record number of egg releases.

†Reports number of batches of eggs released and interval between batches as assessed from daily sampling from tanks. Actual spawning events not enumerated. Only three fish were allowed to finish their spawning season.

††Excludes fish present for less than three days.

‡Results of telemetry study with sufficient resolution to determine presence/absence on known spawning grounds, but not to evaluate participation in an aggregation.

¹Kjesbu (1989)

²Chambers and Waiwood (1996)

³Kjesbu et al. (1996)

⁴Robichaud and Rose (2003)

⁵Meager et al. (2009)

⁶Jonsson (1982) – estimated from proportion of mature females on spawning grounds

⁷Marteinsdóttir et al. (2000) – estimated from hatch date analysis and proportion of mature females on spawning grounds, varies around Iceland

⁸Brander (2005)

In contrast to the solar cycle, Atlantic cod spawning activity seemed to have strong relationships with lunar and semi-lunar cycles (Fig 2c-d; Rayleigh tests: $p=0.0002$ for lunar cycle, $p<0.0001$ for semi-lunar cycle). The peak of spawning activity in the lunar cycle was 6-11 d after the full moon (bootstrapped 95% CI) while the peak in the semi-lunar cycle coincided with the spring tide about 0.5-1.6 d after a full or new moon (bootstrapped 95% CI). These results suggest that cod tend to spawn more frequently during the waning phases of the moon (from full to new) with peaks during both spring tides. There were no differences in the timing of spawning as related to lunar and semi-lunar spawning in northern and southern Icelandic cod. Likewise there were no differences between coastal and frontal cod in their timing as it related to lunar or semi-lunar cycles (95% CI from bootstrapping overlap).

Results of particle tracking experiments — At the time of writing, these analyses were in the process of being performed. Results will be presented during the conference.

Discussion

The use of electronic data storage tags to assess the spawning behavior of Atlantic cod seems to have potential. It is important to note, that direct observations of cod spawning behavior have only been made on captive individuals and that observations in wild fish have been confined to relatively low resolution acoustic telemetry and active hydroacoustics. However, the pattern interpreted as participation in a spawning event results in realistic, if somewhat conservative compared to reported values (Table 1), estimates of spawning activity. This is not particularly surprising given the relatively low temporal resolution of the DST depth profiles. There also seems to be substantial variation among cod populations in their reproductive biology and behavior (see Brander 2005 for review), leaving open the possibility that our low estimates reflect inherent differences among Icelandic cod and other stocks. These uncertainties highlight the issue that at present there is no way to independently confirm that the patterns observed in the depth profiles correspond to participation in spawning events and thus may incorporate an unknown quantity of false positives. Furthermore while we do not feel there is a reason to suspect that the detection of spawning events is biased towards particular times of day, lunar phases, etc., there remains no way to independently verify this assumption. Future technological improvements in the capabilities of DSTs (Metcalf et al. 2009) should allow for a more thorough assessment of spawning behavior and refinement of our approach.

The entrainment of an annual cycle in cod reproduction was not unexpected. 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 (Jonsson 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. 2005). The differences between northern and southern Icelandic cod in their timing of spawning have been previously noted by Marteinsdóttir et al. (2000). Overall, these

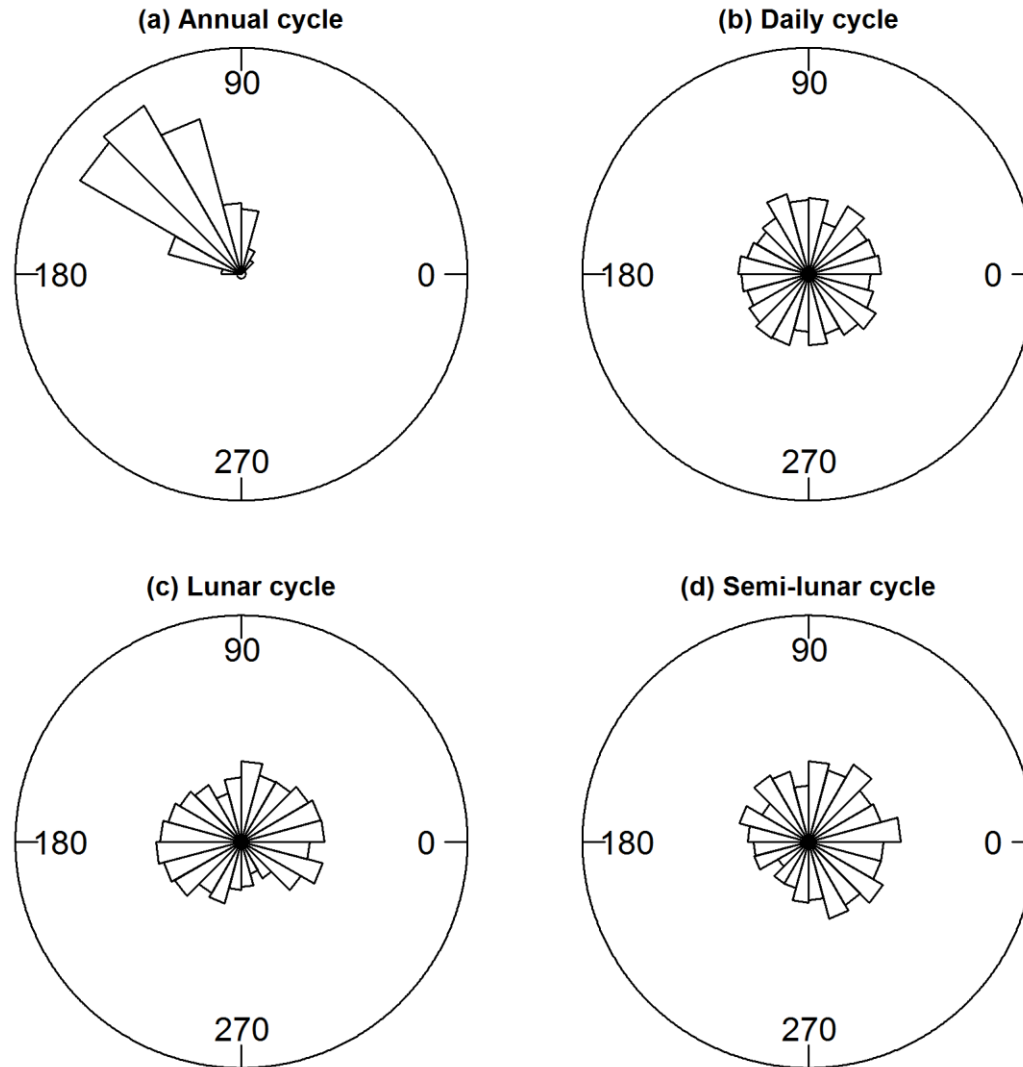


Figure 2. Distribution of angles representing the position of Atlantic cod spawning events relative to each environmental cycle period of interest. The annual, lunar, and semilunar cycles are significant, while daily cycle was not significantly different from a circular (uniform) distribution.

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. This difference might be attributable to our sampling protocol. Due to the various logistical considerations, our tagging has typically been restricted to April and thus might be biased towards individuals that spawn relatively late in southern Iceland and relatively early from northern Iceland.

While we recognize a need to refine our approach to account for the fact the cod spawning season take place during a period of rapidly changing daylength, our preliminary results suggest

Icelandic cod seem to lack a day-night cycle in their spawning activity or if present, it is not a particularly strong behavioral cycle. Observations made of Icelandic cod using a split-beam echosounders and dual-frequency identification sonar in, found distributions of cod during daylight hours (T.B. Grabowski, unpubl. data) consistent with those described for spawning column formation (Rose 1993; Lawson and Rose 2000; Fudge and Rose 2009). This is in contrast to most laboratory studies and several field studies of Atlantic cod spawning behavior that suggest spawning activity occurs primarily at night. The nocturnal behavior in tank studies may be an artifact of the artificial lighting conditions of a tank environment. Cod held in shallow laboratory tanks likely experience brighter conditions than wild fish at depth and may adjust their spawning activity accordingly. Studies suggesting nocturnal reproduction in wild cod are either limited in their duration or do not attempt to directly quantify spawning behavior making it difficult to directly compare with our results. For example, Fudge and Rose (2009) describe cod spawning columns forming at only night in Newfoundland. These fish exhibited a dramatic day-night differences in the mean depth individuals were distributed around and changes in the intensity of sound production. However, this study was only conducted over an 18.5-hour period making it difficult to conclude that these columns form only at night throughout an entire spawning season. Furthermore, there is the possibility that the entrainment of a daily cycle of spawning behavior is a trait that varies among populations and locations cannot be discounted as differential selective pressures may favor spawning at different times at given locations (Yamhira 2004). The stronger the selective pressures, the more distinctive the behavioral signal.

In the Icelandic marine environment, it seems that Atlantic cod spawning behavior is tied to lunar and semi-lunar cycles in Icelandic waters. Cod spawning seems to peak in association with the spring tide which occurs approximately two days after the full and new moons in Iceland (Tomasson and Karadóttir 2005). Over the course of a full lunar cycle, cod spawning is more concentrated during the waning phases of the moon and that activity tends to be higher during the full moon. Lunar and semi-lunar spawning cycles are relatively common in tropical reef species (Takemura et al. 2004, 2010). Intertidal spawning fishes, such as mummichog *Fundulus heteroclitus* and California grunion *Leuresthes tenuis*, also exhibit a similar rhythm in their spawning behavior associated with semi-lunar cycles. In most of these species, a semi-lunar spawning cycle enables their offspring to take advantage of the spring tides to enhance dispersal or otherwise reduce mortality by giving the developing larva access to protected habitats (Takemura et al. 2004, 2010). Fishes timing their spawning activity with a lunar cycle seem to be utilizing this cycle to synchronize spawning activity (Takemura et al. 2004, 2010). However, this sort of synchronization with lunar and semi-lunar cycles has not been previously noted in other temperate fishes and it is unclear why Atlantic cod might be employing this strategy. The results of our initial particle tracking exercises should provide some insight as to why Icelandic cod synchronize their spawning with semi-lunar and lunar cycles.

Acknowledgements

We thank all of the captains and crew members from vessels used in this study for their assistance with sampling and tagging; H. Karlsson and B. Gunnarsson of the Icelandic Marine Research Institute for their assistance with tagging; S. Guðbjörnsson and S. Gunnlaugsson at Star-Oddi Marine Device Manufacturing for assistance with DST deployment, data recovery, and data analysis; and of the Icelandic fishermen who participated in this study by returning tags. Funding for this project was provided by the Marine Research Institute, Iceland; the University of Iceland Research Fund; the EU-projects “CODYSSEY” (Q5RS-2002-00813; 2003-2006) and “METACOD” (Q5RS-2001-00953; 2002-2005); the Icelandic Research Fund (grant number: 070019023); and the Fisheries Project Fund of the Icelandic Ministry of Fisheries and Agriculture. Fish tagging activities conducted by V.T. under license number 0304-1901 issued by the Icelandic Committee for Welfare of Experimental Animals, Chief Veterinary Office at the Ministry of Agriculture, Reykjavik, Iceland.

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