



A decade of monitoring Atlantic cod *Gadus morhua* spawning aggregations in Massachusetts Bay using passive acoustics

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ABSTRACT: Atlantic cod *Gadus morhua* populations in the northeast USA have failed to recover since major declines in the 1970s and 1990s. To rebuild these stocks, managers need reliable information on spawning dynamics in order to design and implement control measures; discovering cost-effective and non-invasive monitoring techniques is also favorable. Atlantic cod form dense, site-fidelic spawning aggregations during which they vocalize, permitting acoustic detection of their presence at such times. The objective of this study was to detect spawning activity of Atlantic cod using multiple fixed-station passive acoustic recorders to sample across Massachusetts Bay during the winter spawning period. A generalized linear modeling approach was used to investigate spatio-temporal trends of cod vocalizing over 10 consecutive winter spawning seasons (2007–2016), the longest such timeline of any passive acoustic monitoring of a fish species. The vocal activity of Atlantic cod was associated with diel, lunar, and seasonal cycles, with a higher probability of occurrence at night, during the full moon, and near the end of November. Following 2009 and 2010, there was a general decline in acoustic activity. Furthermore, the northwest corner of Stellwagen Bank was identified as an important spawning location. This project demonstrated the utility of passive acoustic monitoring in determining the presence of an acoustically active fish species, and provides valuable data for informing the management of this commercially, culturally, and ecologically important species.

KEY WORDS: Atlantic cod · Passive acoustic monitoring · *Gadus morhua* · Massachusetts Bay · Spawning aggregations · Fisheries management

1. INTRODUCTION

Atlantic cod *Gadus morhua* L. is one of the most commercially, culturally, and ecologically significant fish species in the world (Kurlansky 1997) and has

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been a principal component of fisheries in the northwest Atlantic Ocean since at least the 17th century (Serchuk & Wigley 1992, Kurlansky 1997, FAO 2011). This long history of exploitation, combined with environmental variation (Brander 2005a, Halliday & Pin-
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horn 2009, Lambert 2011) and altered predator/prey dynamics (Frank et al. 2011, Friedland et al. 2013), has resulted in a major decline in many Atlantic cod stocks (NEFSC 2017). Therefore, discovering new methods to better understand, monitor, and protect these populations in cost-effective, low-impact ways is needed to support rebuilding efforts.

Atlantic cod are a demersal, aggregation-spawning species found on both sides of the North Atlantic, and have been known to reproduce in depths ranging from 10s to 100s of meters (Rose 2003, Brander 2005b, Meager et al. 2010) with a propensity for fine-scale bathymetric features such as cobble, rock, and boulder substrate (Meager et al. 2010, Dean et al. 2012, Siceloff & Howell 2013). Furthermore, this species exhibits strong fidelity to spawning sites (Robichaud & Rose 2001, Skjæraasen et al. 2011, Zemeckis et al. 2014c) that are often close to shore and predictable in space and time (Armstrong et al. 2013, Zemeckis et al. 2014b). These traits make them vulnerable to disruption from fishing pressure and have facilitated the serial depletion of semi-discrete spawning components in many stocks (Morgan et al. 1997, Ames 2004, Dean et al. 2012). Major disruptions to these site-associated spawning aggregations have lasting consequences for population structure and rebuilding. For instance, if a spawning component is exploited beyond its capacity to sustain itself, it may be extirpated, and the evolutionary knowledge to spawn at a given time and location can be lost forever, limiting the stock's capacity to generate future recruitment (Frank & Brickman 2000).

Many of the historical spawning components of Atlantic cod in the Gulf of Maine (GOM) have been extirpated through overfishing, habitat degradation, and declines in forage species, in particular along the mid-coast and eastern GOM (Ames 2004). In Massachusetts Bay, there are genetically distinct spring- and winter-spawning sub-populations (Kovach et al. 2010, Zemeckis et al. 2014a), and the overall population has declined by 60–70% within the past decade (MADMF 2017). A series of seasonal fishery closures has been implemented in Massachusetts Bay to reduce the likelihood of extirpating these remaining spawning components, including the Spring Cod Conservation Zone (SCCZ), Winter Cod Conservation Zone (WCCZ), and Framework 53 adjustment to the federal fisheries management plan (Armstrong et al. 2013, NEFMC 2017).

Traditional bottom trawl surveys are costly, extractive, and can impact the benthos. They also have limited spatial and temporal resolution, making them inefficient at describing fine-scale spatial or seasonal

patterns. Other methods of identifying spawning grounds, such as acoustic telemetry or maturity observations from directed sampling, require significant investments in equipment and ship/personnel time. In contrast, for a vocal spawning species such as Atlantic cod, passive acoustic monitoring (PAM) provides a cost-effective and non-lethal means of gathering fish presence and behavior data. Moreover, sampling can occur continuously over an extensive temporal scale and thus describe the spatial and seasonal extent of a spawning ground. Given the site fidelity of cod, specific spawning grounds (once identified) can be monitored over time for the presence and magnitude of spawning activity. Therefore, PAM can provide a valuable source of information to complement the biological observations of a trawl survey.

Long-term PAM is used to study decadal trends in the occurrence and distribution shifts of marine mammals (Van Parijs et al. 2009, Davis et al. 2017) and is increasingly being used to monitor fish occurrence and behavior (Locascio & Mann 2008, Mann et al. 2009, Širović et al. 2009, Nelson et al. 2011, Aalbers & Sepulveda 2012, Bolgan et al. 2018, Zemeckis et al. 2019). Calling activity has been linked to reproductive behavior in many other fishes, including pomacentrids (Mann & Lobel 1995), batrachoidids (McKibben & Bass 1998), sciaenids (Locascio & Mann 2008), and serranids (Rowell et al. 2015). Atlantic cod are well suited to the use of PAM for studying their spawning dynamics, because they aggregate during spawning, and males produce distinct vocalizations during courtship rituals (Brawn 1961a,b, Nordeide & Kjellsby 1999, Finstad & Nordeide 2004, Rowe & Hutchings 2006). Recording of cod sound production has primarily occurred in captivity, but there are some short-term or opportunistic *in situ* recordings (Nordeide & Kjellsby 1999, Fudge & Rose 2009). Furthermore, previous studies in Massachusetts Bay have demonstrated that PAM can be used effectively to study cod spawning dynamics (Hernandez et al. 2013). Hernandez et al. (2013) utilized one recording unit for 75 d in an area with known ripe tagged cod (Zemeckis et al. 2014c), and the acoustic analyses included subsampling the data and manual detection of cod grunts for the spring-spawning stock (*sensu* Kovach et al. 2010).

Compared to other gadoid fishes such as haddock (Hawkins & Amorim 2000), cod have a limited vocal repertoire, using a single low-frequency 'grunt' to function in multiple social contexts (Finstad & Nordeide 2004, Rowe & Hutchings 2006). Both male and female cod produce grunts during the year; however, during the spawning season, only male cod

grunt, both as part of an aggressive display to keep other males out of their territory and to attract females (Finstad & Nordeide 2004, Rowe & Hutchings 2006). Grunts are produced by the vibration of 3 pairs of muscles along the swimbladder wall (Brawn 1961b, Rowe & Hutchings 2008). The calls consist of short grunts (about 200 ms) with peak amplitudes at frequencies ranging between approximately 50 and 500 Hz (Brawn 1961b, Midling et al. 2002, Finstad & Nordeide 2004). More specifically, the fundamental frequency is usually around 45–60 Hz, with 2 or more bands of energy concurrent at higher frequencies (Brawn 1961b, Hernandez et al. 2013). Source levels for Atlantic cod have not been estimated *in situ*; however, a tank study measured source levels of one cod at 127 dB re 1 $\mu\text{Pa m}^{-1}$ (see Nordeide & Kjellsby 1999). The expanding record of Atlantic cod vocalizations, coinciding with the identifiable sound characteristics, allows for the easy recognition of cod and the development of more automated means of analysis (e.g. Urazghildiiev & Van Parijs 2016).

This project represents an unprecedented long-term investigation of the acoustic behavior of Atlantic

cod in Massachusetts Bay. The high spatial and temporal resolution PAM in this study, when used to inform a linear model, can provide insights into the spawning ecology of Atlantic cod. These data can be valuable to fishery managers by elucidating the factors that influence the spatio-temporal patterns of spawning behavior. Such information is necessary for crafting effective fishery closures to protect the remaining spawning aggregations of the critically depleted GOM stock of Atlantic cod.

2. MATERIALS AND METHODS

2.1. Study site

Acoustic recordings were leveraged from 3 separate projects that covered the areas both within and outside designated fishery closures intended to protect Atlantic cod spawning aggregations in Massachusetts Bay in the western GOM (Fig. 1). This area encompasses some of the last known winter spawning grounds for Atlantic cod in the GOM (Kovach et

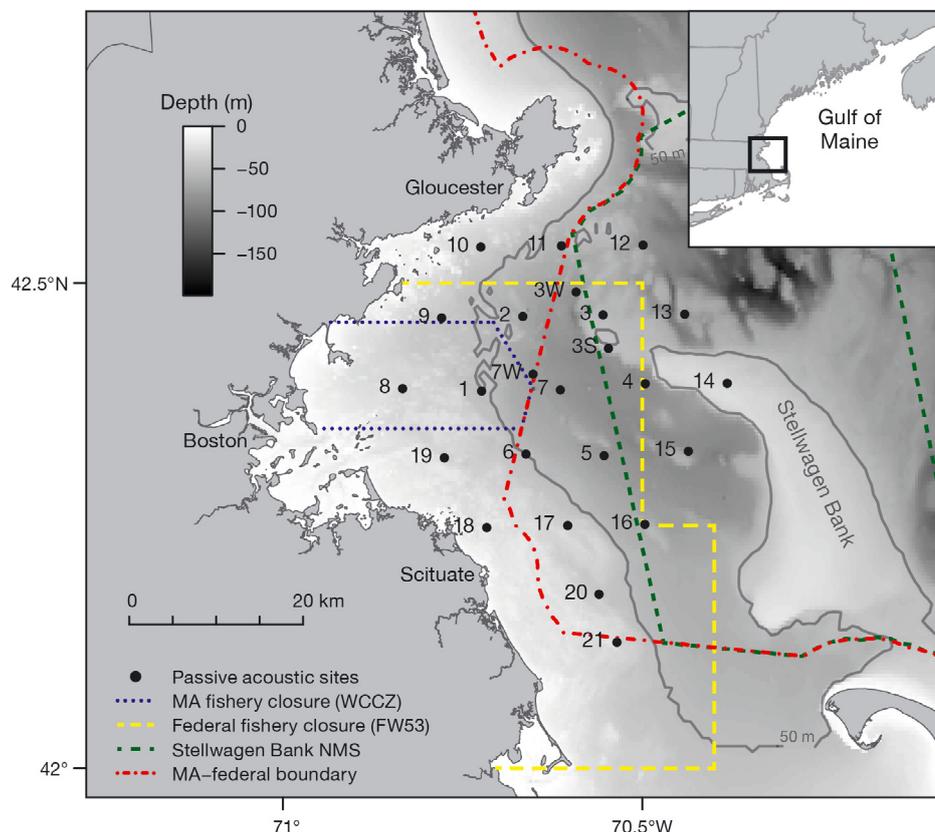


Fig. 1. Study area showing deployment sites for passive acoustic recorders in Massachusetts Bay, southern Gulf of Maine, western North Atlantic Ocean. Dashed lines represent fishery closures (WCCZ: Winter Cod Conservation Zone; FW53: Framework 53 to the Federal Fishery Management Plan) and jurisdictional boundaries (Stellwagen Bank National Marine Sanctuary [NMS] and the break between Massachusetts and Federal Waters). Solid line: 50 m isobath

al. 2010, Zemeckis et al. 2014a), as well as the spatial management areas designed to protect this vulnerable group.

Massachusetts Bay is bordered on the north by Cape Ann, to the south by Cape Cod, to the east by Stellwagen Bank, and to the west by Boston Harbor (NEFMC 2007). The maximum depth of the area approaches 100 m in the center of the bay, just west of Stellwagen Bank, which rises as shallow as 20 m. This forms a basin with 2 passages on either side of Stellwagen Bank that link the bay to the greater GOM. The sea floor in this area is predominantly fine-grained sediment, with a patchwork of cobble and boulder deposits amongst large bedrock outcrops (Butman et al. 2007). The Stellwagen Bank National Marine Sanctuary (SBNMS) and the state/federal boundaries are both within the study area, which present overlapping authorities for managing the stock and its habitat.

2.2. Data collection

Data from 2007–2012 were collected by Cornell University’s Bioacoustics Research Program (Morano et al. 2012); data from 2013–2015 were collected by a collaborative project between fishermen, state and

federal scientists, and non-profit organizations (Zemeckis et al. 2019); and 2016 data were collected by the SBNMS’s Four Sanctuaries Project (NOAA). The locations and sampling efforts do not correspond completely between the 3 studies; however, collectively they represent a decade-long time series that encompasses an area of approximately 1200 km². The timing of data collection was focused on the acoustic presence of Atlantic cod across the winter spawning season (details of specific dates below). At certain times of the deployments, recordings were compromised due to technical faults (e.g. battery/software/hardware failings), or inoperable recorders (damaged or detached via weather and/or commercial fishing gear). When this occurred, the data were removed from analyses. Table 1 provides information on site numbering, sampling effort, depth, and coordinates.

2.2.1. 2007–2012

Marine autonomous recording units (MARUs) (Calupca et al. 2000) were used from 2007–2012. All MARUs were programmed to record continuously at a sampling rate of 2000 Hz and had a 10 Hz high-pass filter to reduce electrical interference from the recording unit and an 800 Hz low-pass filter to prevent alias-

Table 1. Site of passive acoustic recording of Atlantic cod, including depth (average depth of hydrophone deployment), sampling effort (hours of recordings yr⁻¹), and overall percent of recorded hours with grunts (% positive). Note that no data were recovered from deployments at Sites 3W and 7W

Site	Depth (m)	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	% Positive
1	50	648	648	552	624	624	624	0	1896	1896	0	15.7
2	67	600	648	552	624	624	624	0	0	0	0	2.8
3	54	648	0	552	624	600	576	0	0	0	0	7.9
3W	73	0	0	0	0	0	0	0	0	0	0	–
3S	49	0	0	0	0	0	0	0	0	1896	1176	60.4
4	87	648	648	552	624	216	0	0	0	0	0	0.6
5	79	648	648	552	624	624	144	0	1896	0	0	1.2
6	51	648	648	552	624	624	624	1680	0	1896	0	13.4
7	80	648	648	96	624	624	48	0	0	1896	0	2.4
7W	80	0	0	0	0	0	0	0	0	0	0	–
8	33	48	648	552	624	624	624	0	0	0	0	4.9
9	43	648	648	552	624	624	624	0	0	0	0	3.8
10	38	648	0	552	624	624	624	0	0	0	0	3.6
11	62	552	648	96	624	408	624	0	0	0	0	1.6
12	82	48	648	384	624	600	576	0	0	0	0	0.1
13	69	648	648	552	624	408	624	0	0	0	0	4.7
14	30	456	0	456	0	216	576	0	0	0	0	44.9
15	81	648	648	552	624	624	624	0	0	0	0	1.6
16	57	648	648	552	624	624	624	0	0	0	0	7.4
17	35	648	648	456	624	624	624	1680	1896	0	0	7.2
18	21	48	0	0	0	120	0	0	0	0	0	82.7
19	31	600	648	96	576	408	576	0	0	0	0	6.4
20	41	0	0	0	0	0	0	1680	0	0	0	12.1
21	24	0	0	0	0	0	0	1680	1896	1896	0	16.7

ing. The MARUs had a flat frequency response of -151.2 dB re $1 \mu\text{Pa}$, between 15 and 585 Hz. All recorders were weighted to the seafloor, with flotation lifting the hydrophone elements 1 m off the seafloor. Recorders were positioned at 19 locations throughout Massachusetts Bay (sites are labelled 1–19) covering an area of approximately 38 km west to east and 32 km north to south in a hexagonal grid array (Fig. 1). These sites were originally chosen to monitor North Atlantic right whales *Eubalaena glacialis* in Massachusetts Bay (Morano et al. 2012). Within the 893 km^2 array, each MARU was positioned approximately 9.3 km apart at depths ranging from 20–90 m. Continuous data were recorded over 24 h periods, approximately every 2–3 d, year-round.

2.2.2. 2013–2015

Recording instruments during 2013–2015 were also MARUs, with the same sampling rate and calibration settings as the 2007–2012 project. A total of 17 MARUs were deployed, of which 13 provided usable data. The sites were chosen as part of a multidisciplinary study investigating Atlantic cod spawning sites which paired telemetry-based movement of tagged individuals with both bottom-mounted and mobile passive acoustics to target cod spawning aggregations (Zemeckis et al. 2019). Site selection was based on various sources, including previous PAM (Morano et al. 2012, Hernandez et al. 2013), trawl survey data, fishery observer data, and ecological knowledge from collaborating commercial fishermen. Any site that was within 2 km of an original deployment location (i.e. Sites 1–19; 2007–2012) was treated as the same location; otherwise, new sites were given a unique label (i.e. 3S or 7W) and treated as a separate location (Table 1). Although admittedly an arbitrary threshold, 2 km appeared to be a reasonable resolution given the spatial scale and patterns observed in Zemeckis et al. (2019). Most sites that retained their original labels moved far less than 2 km. Continuous sound data for this project were available every day from 14 October–31 December.

2.2.3. 2016

Only one recorder was deployed in 2016 (3S; Fig. 1, Table 1) and consisted of an omnidirectional SoundTrap hydrophone (ST300, Ocean Instruments). The SoundTrap recorded continuously at a sampling rate of 48 000 Hz with a 20 Hz high-pass filter and a flat

frequency response of -171.4 dB re $1 \mu\text{Pa}$ between 20 and 60 000 Hz. The decision to deploy an added year of recording at site 3S in 2016 was due to the high number of cod grunts at this location in 2015. Continuous data was available every day for the sample period 14 October–7 December (recordings were stopped earlier in the winter than the other 2 studies due to project-specific logistics).

2.3. Data analyses

2.3.1. Grunt detections

All sound files were processed using a custom-built automated Atlantic cod grunt detection algorithm (Urazghildiiev & Van Parijs 2016) executed in MATLAB (R2014b; MathWorks). All detections classified as Atlantic cod grunts by the detector were subsequently manually verified using the acoustic analysis software program Raven Pro 1.5 (Bioacoustics Research Program). Detections were viewed in a 5×5 spectrogram grid adjacent to a context spectrogram. Each detection was viewed from 10–400 Hz using a fast Fourier transform (FFT) of 256 points and 75% overlap, and a 1 s time pad, while the context spectrogram was viewed at a 10 s time window with a FFT of 1024 points and 75% overlap from 0–500 Hz. All detections that met the following criteria were marked as positive for cod: (1) at least 2 bands of energy present, (2) a fundamental frequency range within 40–60 Hz, and (3) a distinct audible recognition of the grunt. Waveforms were also checked to substantiate certain grunts.

2.3.2. Year-round analysis

The duration of the winter spawning season for Atlantic cod in Massachusetts Bay (Howell et al. 2008, Kovach et al. 2010, Zemeckis et al. 2014a) and, more specifically, in the WCCZ (Hoffman et al. 2012, Armstrong et al. 2013) was previously reported as spanning the period from October through January, based on a combination of acoustic telemetry, maturity observations (i.e. ripe gonads), and/or the presence of large aggregations. To ensure that the acoustic recordings of cod grunts were associated with spawning activity, one full year (3 August 2009 to 3 August 2010) of data were analyzed from Site 1 for the acoustic presence of Atlantic cod. There were 3 data gaps (21–26 August, 8–17 and 20–26 December) due to non-usable data. We chose this year and site, as there was

a complete year of recording for this site, and the site encompassed a spawning aggregation. The seasonal data profile was compared with the other descriptions of cod spawning activity and used to set the seasonal extent of subsequent analyses.

2.3.3. Spatio-temporal patterns

Spatio-temporal patterns in cod grunting activity were examined by first summarizing the verified grunts by hour for each site. Circular histograms were used to visualize the observed data for diel and lunar cycles. In order to disentangle the simultaneous effects of multiple variables, generalized linear mixed models (GLMMs) were then fit to both the presence of cod grunts (grunt presence/absence in hourly bins), as well as grunt rate (number of cod grunts per hour). The grunt presence model assumed a binomial error distribution to predict the probability of grunts occurring in a specific hour, while a zero-inflated negative binomial (ZINB) GLM was used to predict the number of grunts per hour. Initial attempts at a negative binomial grunt rate model without zero-inflation revealed that model to be highly over dispersed, which justified the choice of the ZINB modeling approach. Model forms were evaluated using Akaike's information criterion (AIC), and models with $\Delta AIC < 5$ were used to create model-averaged predictions, weighted by their Akaike weight (Burnham & Anderson 2002). Candidate predictors included year, site, depth, and multi-

ple natural cycles (diel, lunar, semi-lunar, seasonal). An interaction between site and seasonal cycle was also included because it appeared that some sites had a seasonal pattern that was consistently different from the rest. To minimize the influence of serial autocorrelation, week was treated as a random effect. Natural cycles were represented using circular variables, which involved converting time to radians according to the period of the cycle and applying the sine and cosine functions (Zar 1999, Zemeckis et al. 2019). Thus, each circular variable required 2 parameters and enabled estimation of the magnitude of the effect and where in the cycle the peak response occurred. Sites that recorded data on less than 10 d yr^{-1} or had grunts on less than 2% of hours overall were omitted from analyses, as the observations were deemed too sparse to inform the models. All models were fit using the 'glmmTMB' package (Brooks et al. 2017) in R v.3.4.1 (R Core Team 2017). The marginal mean effect of each variable was estimated using the 'emmeans' package in R.

3. RESULTS

The year-round acoustic analyses (2009–2010) confirmed that the presence of Atlantic cod grunts aligned with the winter spawning season described in previous studies, and that the available data set encompassed the winter spawning season almost completely (Fig. 2). There were only 4 d outside of the targeted winter sampling regime that detected

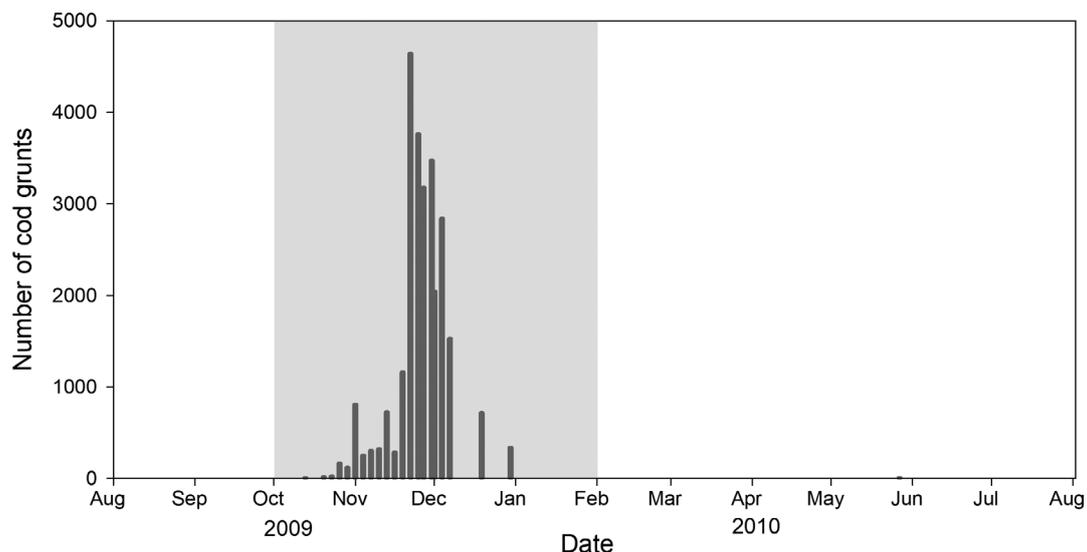


Fig. 2. Number of Atlantic cod grunts positively identified from automated detections between 3 August 2009 and 3 August 2010 using data from Site 1 (see Fig. 1 for location). Each day that the detector was run over the 12 mo period is presented (approximately every second day). Shaded area: reported cod winter spawning periods from the literature; vertical check marks on x-axis: first day of the month

the presence of cod grunts (5 Aug, 29 Sep, 13 Oct, 27 May), and each of those days recorded less than 10 grunts. As a result, all further acoustic analyses focused on the months of October, November, and December.

In total, 194 880 Atlantic cod grunts were manually verified from the 110 passive acoustic receivers which had successful deployments over the 10 yr of this study. This represented 38.6% of the total number of automated detections, although this rate of true positives varied year to year from a low of 6.3% (2012) to a high of 70.8% (2015). The majority of these grunts were detected at a few stations (e.g. 27 934 grunts at Site 1 in 2009; 30 501 at Site 1 in 2010; 9370 at Site 14 in 2010; 91 363 at Site 3S in 2015).

Atlantic cod were acoustically active throughout the course of a 24 h period but consistently showed the highest grunting activity near sunset and at night ($\bar{X}_{H16 \rightarrow H5} = 3.74 \text{ grunts h}^{-1}$; $\bar{X}_{H6 \rightarrow H15} = 1.82 \text{ grunts h}^{-1}$; Fig. 3a). Lunar patterns were less apparent in the observed data, with the highest number of grunts recorded at various points in the lunar cycle in different years. However, the observed data suggest an association with the full moon in that the years with

the highest number of grunts (2009, 2010, 2015) all had highest grunt activity during this lunar phase, and thus in general (with all years combined) the highest number of grunts were detected at the end of the full moon period (Fig. 3b).

Several grunt presence models were similarly supported by the data (i.e. $\Delta AIC < 2$) and only differed in which lunar parameters were included (Table 2). Given the lack of a clear 'best' model, the top 4 were used collectively to make predictions, using the Akaike weights approach to model averaging (Burnham & Anderson 2002) (Fig. 4a). Although a single grunt rate model was most supported by the data, a second likely model was also found. As such, both models were used to make predictions, again using the Akaike weights approach to model averaging. Depth was omitted from both the conditional and zero-inflated components of the grunt rate model because its inclusion created model convergence issues. The highest probability of grunt presence and grunt rate occurred during the night, between sunset and midnight (Fig. 5a,c). Grunt rate was more influenced by lunar cycles than grunt presence, and the inclusion of the semi-lunar effect in the grunt rate

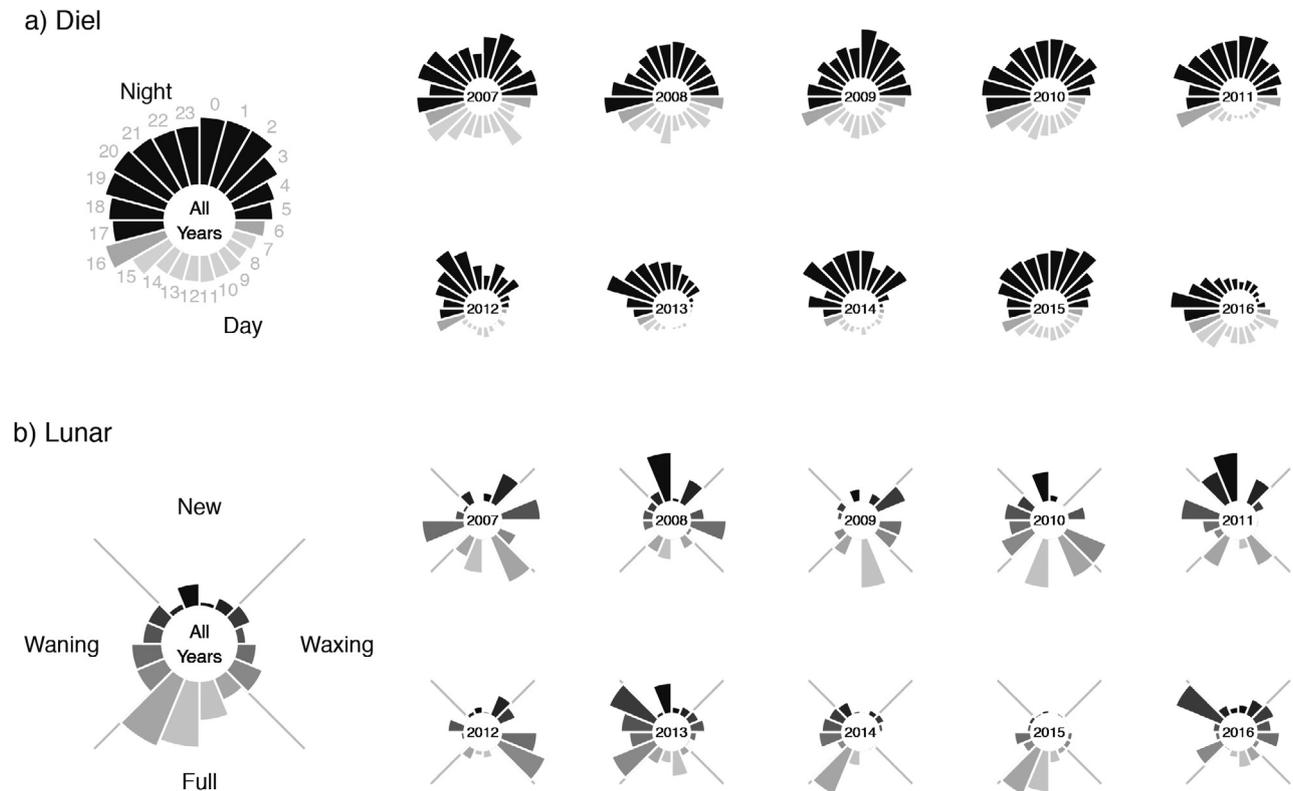


Fig. 3. Circular histograms showing total number of Atlantic cod grunts in Massachusetts Bay overall and by year for (a) diel and (b) lunar patterns. In (a), black: night; light gray: day; dark gray: sunrise or sunset. In (b), darker colors indicate darker moon phases (i.e. new moon) and lighter colors indicate brighter moon phases (i.e. full moon)

Table 2. Top 5 best-fitting models for Atlantic cod grunt presence and grunt rate, ranked by AIC. Models in **bold** were considered plausible and used to create model-averaged predictions, weighted by the Akaike weight (w). Model terms: Y = year; S = site; H = diel cycle; L1 = lunar cycle; L2 = semi-lunar cycle; D = depth; rW = random week effect; S:J = site \times seasonal interaction. Additional information including a table of parameter estimates (i.e. effect sizes, SE, and p-values) can be found in the Supplement at www.int-res.com/articles/suppl/m635p089_supp.xls. Each cyclical term is represented by 2 parameters, and therefore accounts for 2 df. For example,

$$H = \sin\left(2\pi \frac{\text{hour}}{24}\right) + \cos\left(2\pi \frac{\text{hour}}{24}\right)$$

Grunt presence						
Model terms	df	AIC	Δ AIC	w		
Y + S + H + D + L1 + J + rW + S:J	63	33774.3	0	0.36		
Y + S + H + D + J + rW + S:J	61	33774.5	0.3	0.31		
Y + S + H + D + L1 + L2 + J + rW + S:J	65	33775.8	1.5	0.17		
Y + S + H + D + L2 + J + rW + S:J	63	33775.8	1.5	0.16		
Y + S + H + L1 + J + rW + S:J	62	33862.3	88.0	0.00		
Grunt rate						
Model terms	Zero-inflated terms		df	AIC	Δ AIC	w
Y + S + H + L1 + L2 + J + rW + S:J	Y + S + H + L1 + J + rW + S:J		127	81201.4	0.0	0.82
Y + S + H + L1 + L2 + J + rW + S:J	Y + S + H + L1 + L2 + J + rW + S:J		129	81204.5	3.2	0.17
Y + S + H + L2 + J + rW + S:J	Y + S + H + J + rW + S:J		123	81211.2	9.8	0.01
Y + S + H + L2 + J + rW + S:J	Y + S + H + J + L2 + rW + S:J		125	81214.2	12.8	0.00
Y + S + H + J + rW + S:J	Y + S + H + J + L2 + rW + S:J		123	81216.0	14.6	0.00

model created an asymmetrical lunar pattern overall, with the lowest activity between the new and waxing moon and the highest activity near the full moon (Fig. 5b,d).

The most active sites (Sites 1, 3S, 14, and 21) were near the 50 m isobaths or shallower (Fig. 6). Very few grunts were detected at depths greater than 60 m, despite approximately one-third of recordings coming from these sites (Fig. 6). The overall estimated marginal mean peak grunt presence occurred on 20 November, with the peak in grunt rate following 2 wk later on 25 November (Fig. 7). Most sites had a seasonal profile similar to this general pattern that was remarkably stable across years (Figs. 4 & 6). However, some shallow sites (Sites 19 and 21) were consistently active earlier, while some deeper sites (Sites 3, 7, and 13) were consistently active later (Fig. 6). Across the entire data set, the dates of peak grunt rate were significantly correlated with depth (Pearson's $r = 0.88$, $p < 0.0001$). The estimated marginal mean inter-annual trend in grunt presence declined over the course of the study, with the highest values in 2009 and 2010 (Fig. 7b), while the equivalent trend for grunt rate had a peak value in 2011. It should be noted that the small number of sites with recordings after 2012 and the addition of some new sites in later years limited our ability to describe a continuous inter-annual trend through 2016. As such, we make a distinction between the earlier time period with more consistent

spatial coverage (2007–2012) and the full time series (2007–2016). The inter-annual trend in grunt presence was significantly correlated with the trajectory in spawning stock biomass (SSB) from the most recent stock assessment for GOM cod (2007–2012: Pearson's $r = 0.83$, $p = 0.0415$; 2007–2016: $r = 0.89$, $p = 0.0006$), while the trend in grunt rate was not (2007–2012: $p = 0.39$; 2007–2016: $p = 0.53$).

4. DISCUSSION

The acoustic presence of winter-spawning Atlantic cod in Massachusetts Bay was examined over a broad spatial scale and across more than a decade of study. The modeling approach employed allowed us to quantify the simultaneous influence of multiple natural cycles on vocal spawning behavior; the overall peak in activity occurred at night, under a full moon, and between late November and early December. At a finer scale, the grunt presence models captured most of the primary spatial and temporal patterns of the observed data set. For instance, synchronous periods of high activity across sites (e.g. mid-November 2010) and consistent seasonal patterns within sites could both be explained by the combination of lunar and seasonal circular variables. The consistent spatial pattern in grunt presence was captured by the site and depth variables, whereas overall inter-annual

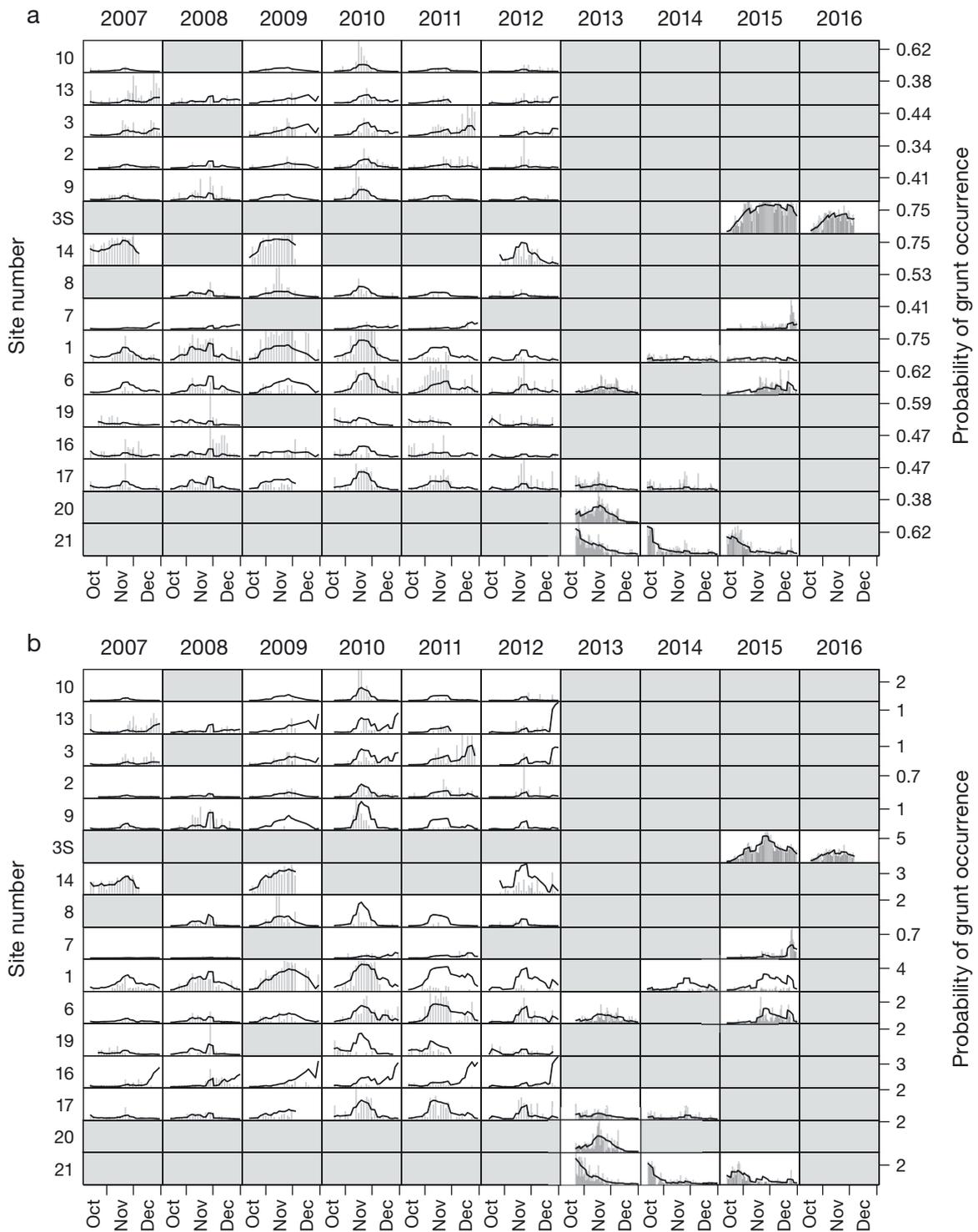


Fig. 4. Observed (grey bars) versus predicted (black line) seasonal patterns in Atlantic cod (a) grunt presence (mean daily probability of grunts occurrence) and (b) grunt rate (mean daily grunts per hour). All stations with very few grunts (<2% of recorded hours with zero grunts) were omitted. Calendar months are bound by check marks on x-axes

trend was captured by the year variable. The grunt rate model captured the observed temporal patterns particularly well for sites that had consistently high levels of vocal activity (e.g. Sites 1, 3S, 14, and 21). Al-

though the greatest number of grunts was recorded in 2015 (primarily at Site 3S), the linear model revealed a general decline in cod acoustic activity over the course of the study, after accounting for the

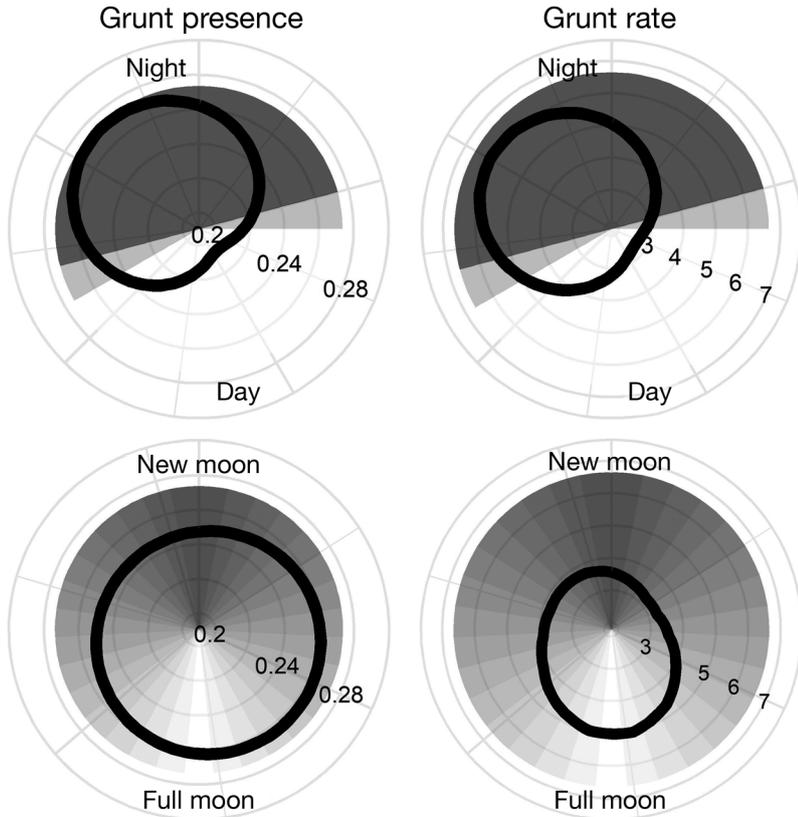


Fig. 5. Marginal mean effects of diel and lunar cycles on Atlantic cod grunt activity. Grunt presence depicts the probability of grunts being detected in any given hour; grunt rate is the number of grunts per hour. For each radial plot, the portion of the thick black line farthest from the center indicates where the peak acoustic activity occurs. Shading represents ambient light levels for time of day (night darkest, dawn/dusk intermediate, and day brightest) and lunar period (full moon brightest to new moon darkest)

effects of site and natural cycles. This inter-annual trend is consistent with the recent decline in the GOM cod stock suggested by the stock assessment (NEFSC 2017). The results presented here demonstrate the potential for PAM to be used towards addressing fisheries management objectives, which includes setting fishing closures in key areas during times of aggregation.

Both the observed data and model predictions revealed an association between cod spawning grunts and the lunar cycle. There are different strategies among fish species as to which phase of the moon is best to release fertilized eggs into the water column, dependent on whether light level or current strength and/or direction is a driving factor (for reviews on lunar spawning see Lowerre-Barbieri et al. 2011, Farmer et al. 2017). Ciannelli et al. (2010) and Stanley et al. (2013) both showed that Atlantic cod time their spawning to periods when currents have minimal advection; however, both of these studies occurred in isolated fjord populations where strong local retention of eggs and larvae would be favored. In our more open

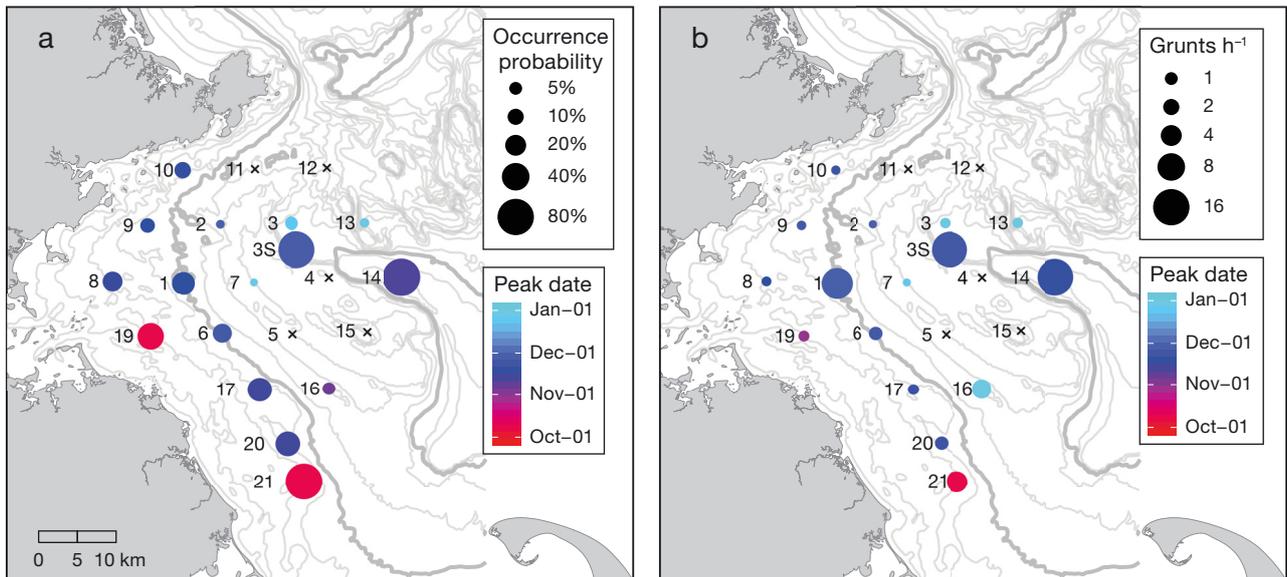


Fig. 6. Effects of site on Atlantic cod grunts across the entire winter season in Massachusetts Bay. Size of bubbles represents marginal mean site effect for (a) probability of grunt presence and (b) grunt rate. Color represents when each site peaks in activity. 'x' represents stations that were dropped due to >98% zeros

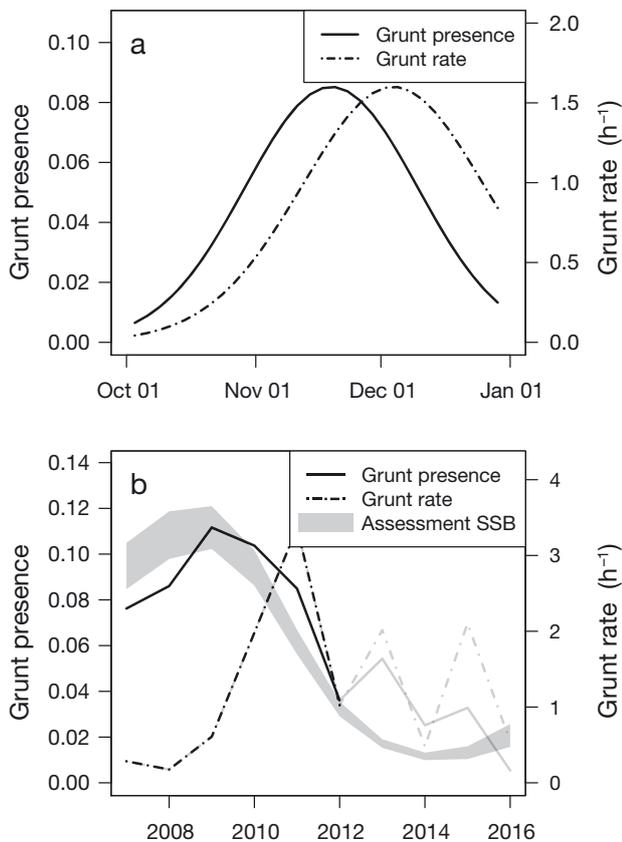


Fig. 7. (a) Marginal mean seasonal patterns of Atlantic cod vocal activity in Massachusetts Bay across all sites and years and (b) marginal mean inter-annual trend in Atlantic cod vocal activity in Massachusetts Bay across all sites; 2013–2016 is shown in lighter gray because the trend in these years is more uncertain due to fewer and less consistent sampling sites. Shaded gray region: 95% confidence interval surrounding the estimate of spawning stock biomass (SSB) from the most recent stock assessment for Gulf of Maine cod

study area, the primary juvenile nursery ground is 50–80 km to the south (southern Cape Cod Bay; Howe et al. 2002), likely making some amount of advection beneficial. The influence of the semi-lunar cycle would support the hypothesis that currents influence cod spawning activity in Massachusetts Bay, yet the dominant association with the full moon suggests that light levels may also play a role. Interestingly, Grabowski et al. (2015) found similar associations between cod spawning behavior in Iceland and the lunar/semi-lunar cycles and concluded that peak activity was related to the strong tidal currents that occur near full and new moons. Further investigation is required to determine which mechanism(s) underlie this lunar influence in our study system.

There is evidence that Atlantic cod exhibit high inter-annual fidelity to spawning location at a re-

markably fine scale, often returning to the same exact seafloor feature each year (Robichaud & Rose 2001, Skjæraasen et al. 2011), including evidence within Massachusetts Bay (in the SCCZ) (Zemeckis et al. 2014c). However, it may be possible that the focal point of a specific aggregation site shifts somewhat from year to year, affecting the probability of detection at a fixed recording location. Our findings support this notion in that we found a spatial pattern that was consistent over time but with periods of negatively correlated deviations at some adjacent sites (e.g. Sites 1 and 6; 2009–2011). This underscores the need for an array of multiple fixed-location hydrophones deployed over several years to investigate spatial/temporal patterns, as in the present study. Targeted fine-scale mobile surveys of autonomous underwater vehicles (AUVs) equipped with hydrophones can also be useful, although this trades spatial information at the expense of temporal (e.g. Zemeckis et al. 2019).

The highest predicted grunt rate occurred 2 wk later than the highest predicted grunt presence. This suggests that it could take a critical number of cod to elicit the onset of spawning activity. For instance, certain pre-spawning male behaviors such as territorial display and courtship routines (often accompanied with grunting; Rowe & Hutchings 2006) likely do not take place outside of an aggregation. The low level of grunts recorded early in the spawning season may help coordinate the movements of cod about the spawning ground by communicating which locations have attracted the greatest number of fish. Similarly, grunting during daylight hours when aggregation members may be more dispersed (Dean et al. 2014) could serve to keep this line of communication open. Vocal activity occurred later at deeper depths, which is where the warmest bottom temperatures can be found at this time of year. This is in contrast to other studies of the association of cod reproductive phenology and water temperature, which found that spawning occurred earlier in warmer waters (McQueen & Marshall 2017). The spatial variation in the seasonal profile of vocal activity could be a consequence of the limitation of grunts as a method of group coordination, with the early spawners at the shallower southern sites beyond the range of communication with the late-spawners at the deeper northern sites. Such seasonal heterogeneity could also be related to oceanography (i.e. timing of currents) or fishing pressure (i.e. seasonal closures). Regardless of the mechanism, these patterns highlight the seasonal variability in spawning activity within this system, which should be considered when developing fishery management measures.

One potentially important environmental factor not addressed in this study is that of water temperature. This could be important given that these animals are ectothermic, and particularly so as the vocalizations are produced by muscle contractions (Brawn 1961b). Sea surface temperature (SST) from NOAA weather station buoy 44013 (close to Site 1) showed 2015 to be the warmest winter over the course of the study (https://www.ndbc.noaa.gov/station_page.php?station=44013). Furthermore, there was a broad inverse relationship between SST and overall inter-annual grunt rate and presence. Therefore, temperature is potentially an important driver of Atlantic cod spawning and/or vocalizations and warrants further investigation.

There was a clear depth association with cod vocal activity in this study, with very few grunts recorded below 60 m. This apparent depth threshold falls within that reported elsewhere for Atlantic cod spawning activity, which ranges from around 20 m (Brander 2005b) to deeper than 100 m (Rose 2003). The depth preference seen in the present study could be related to the unique bathymetry and the varied topographic complexity in the area. The northwestern portion of Stellwagen Bank in particular is classified as an area of high topographic complexity relative to the deeper area at the center of the basin, which also has more silt than on the bank (Battista et al. 2006).

Depth is also related to light, as light levels diminish rapidly with depth, which could suggest that visual components of the mating system influence the depth of spawning activity. The lunar pattern, with higher activity near the full moon, would also support this idea. However, the diel and seasonal patterns, with more vocal activity at night and near the winter solstice, would indicate that if light levels influence cod spawning activity, it is through a non-linear relationship (i.e. dark, but not too dark). It has been established that cod are active nocturnally (Brawn 1961b, Rowe & Hutchings 2006), which was confirmed by the nighttime peak in the current study. Nocturnal spawning is a general strategy to reduce egg predation, as visual predators will be less active around spawning events/egg dispersal (e.g. Reeb 2002, Šmejkal et al. 2018). Moreover, nocturnal vocalizing has been specifically linked with spawning in a diversity of fishes ranging from tropical to temperate, schooling to individual, and reef and non-reef species (e.g. Lobel 1978, Luczkovich et al. 1999, McIver et al. 2014, Rice et al. 2017).

The greater number of grunts detected during daylight hours by Hernandez et al. (2013) contradicts our findings of a strong nocturnal pattern to cod vocaliza-

tions. This was based on the deployment of a single hydrophone directly adjacent to the daytime aggregation focal point. However, although this spring-spawning aggregation was contained within a small area (100–200 ha) for the entire spawning season, the extent varied substantially from day to night (based on high-resolution telemetry; Dean et al. 2014). Therefore, much of the nocturnal spawning behavior may have been out of range of this one hydrophone, and thus care should be taken when interpreting the results from a single hydrophone deployment. This also highlights that the relatively quiet nature of cod grunts means they are only detectable on the scale of 10s of meters (Stanley et al. 2017), creating limitations for the use of PAM in monitoring spawning activities and a challenge for the interpretation of data. The present study overcomes these limitations through an extensive spatial and temporal scale of data collection (20+ locations over 10 yr), which allowed the underlying patterns to be revealed.

The number of hydrophone deployments in this study resulted in exceptionally large data sets (>80 000 h of passive acoustic recordings), which necessitated the use of an automated detector. Although this critical step effectively filters out the vast amount of recorded data without cod grunts, it still requires a substantial commitment for a human analyst to review and verify each putative grunt detected by the algorithm. This is especially so given the fraction of automatic detections that were verified as true grunts was highly variable. As this and other automated detectors are refined (including feedback from the present study), and the sensitivity of receivers improves (as long as the received levels are above the ambient sound), the need for (and cost associated with) manual verification of cod grunts may be reduced. This is especially key in areas that experience high anthropogenic noise such as Massachusetts Bay (Stanley et al. 2017).

Getting reliable quantitative estimates of fish relative abundance using PAM is hindered by several factors, including masking, uncertainty around source levels and transmission distances, deciphering how many fish in the population are actually calling, individual call rates, and how to disentangle overlapping calls/chorusing. It has been attempted with some success by pairing active (i.e. sonar) and passive acoustics with visual technologies (Širović et al. 2009, Sprague & Luczkovich 2012, Rowell et al. 2017). Ultimately, there is still much work to be done before more precise abundance estimations are produced, especially independent of other technologies such as sonar, fishing, or visual surveys.

In the case of monitoring Atlantic cod spawning aggregations, PAM provides a more tangible management application. Although there is some evidence that cod produce sound during non-spawning agonistic encounters (Brawn 1961b, Finstad & Nord-eide 2004), most studies describe a strong association between grunting and spawning (Brawn 1961b, Hutchings et al. 1999, Rowe & Hutchings 2006). Our year-round analysis would support this idea, given that we found only a small number of isolated grunts outside of the October–December spawning period. As such, sites with high grunt rates are likely indicative of where spawning behaviors take place (i.e. spawning aggregations). This approach of using high call rates to identify spawning aggregations has been applied elsewhere for other vocal-spawning fish species (e.g. sciaenids; Saucier & Baltz 1993, Luczkovich & Sprague 2002, Gannon 2003). However, for Atlantic cod it is important to consider that the spatial pattern of grunt rates is influenced by the exceptionally high density of cod spawning aggregations and limited detection range of cod grunts; in other words, small-scale inter-annual shifts in aggregation or receiver location could have a large effect on the recorded grunt rate. For this reason, the presence of grunts may be a more reliable and consistent indicator of spatial and temporal patterns in cod spawning behavior, because this metric is less vulnerable to large shifts in the observed magnitude of vocal activity.

In conclusion, this project utilized the vocal behavior of Atlantic cod to undertake an unprecedented look at the long-term spatio-temporal spawning distribution of this species in Massachusetts Bay. An extensive data set of passive acoustic recorders, combined with a powerful modeling approach, found strong cyclical patterns in grunt activity in addition to spatial and broader inter-annual trends. Our description of this spawning ground is corroborated by other sources of information, including maturity observations and a contemporaneous acoustic telemetry study that found similar spatial and seasonal patterns (Zemeckis et al. 2019). Furthermore, a significant correlation between the probability of grunt occurrence and SSB from the stock assessment suggests that this spawning ground may be a critical component of the stock's remaining reproductive capacity, further emphasizing the continued need for protection. These supporting lines of evidence provide confidence that PAM can be an informative and cost-effective means of describing the presence of an acoustically active spawning fish, even in an area of high human usage.

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