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Comparing Atlantic Cod Temporal Spawning Dynamics across a Biogeographic Boundary: Insights from Passive Acoustic Monitoring

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Abstract

Atlantic Cod *Gadus morhua*, which are overfished in the United States, are potentially vulnerable to disturbance from offshore wind energy (OWE) construction and operation during their spawning period. While many aspects of Atlantic Cod biology are well studied, little is known of their habitat use and spawning behavior at the extreme southern extent of the species' range. As Atlantic Cod form dense spawning aggregations and produce sounds associated with courtship behaviors, we used a combination of fixed-station and glider-based passive acoustic monitoring methods to evaluate the spatiotemporal spawning dynamics of Atlantic Cod in the Georges Bank stock. Additionally, we assessed potential interactions with OWE in designated offshore wind lease areas within southern New England waters of the western North Atlantic Ocean. Generalized linear modeling was used to evaluate correlations between cod grunt activity and multiple environmental cycles. Results from the southern New England spawning grounds were compared to similar data describing the geographically separated Massachusetts Bay winter-spawning subpopulation within the western Gulf of Maine stock. Temporal patterns in Atlantic Cod grunts suggest that spawning in southern New England waters is concentrated in November and December and is greatest near the new and full moons. Although there were fine-scale differences in the temporal dynamics of grunt presence between the two regions, the

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overall seasonality of inferred spawning was similar. Results suggest that Atlantic Cod spawning in southern New England overlaps with planned OWE construction in time and space. An understanding of cod spawning phenology in the western North Atlantic can be used to minimize disturbance to spawning through limiting construction timelines and consideration of turbine or cable placement.

To meet demand for a transition to renewable energy, offshore wind energy (OWE) development is rapidly expanding in the United States. As a result, there has been increasing effort to understand the potential interactions between marine ecosystems and offshore wind farms throughout all phases of development. Evidence suggests that interactions can include positive effects for some species, such as increased epibiont abundance (Hutchison et al. 2020) and fish densities (Bergström et al. 2013; Stenberg et al. 2015) around the turbine structure, as well as negative effects to existing complex habitat (Guarinello and Carey 2022). For marine animals, acoustic disturbance can result in masking of auditory communication, displacement, hearing loss (Popper and Hawkins 2019), and increased stress (Wysocki et al. 2006). Each phase of OWE development includes different sources of potential interactions with unique spatiotemporal risk zones. During project siting, operation, and decommissioning, most of the disturbance stems from vessel activity and associated noise at the wind energy area. This noise pollution generally has a small spatial effect but persists over multiple decades. Conversely, the construction phase involves numerous sources of potential disturbance that can occur at both small and large spatial scales and persist over multiple years. These disturbances include habitat effects from construction of turbine foundations and cable laying as well as acoustic effects from vessel activity and pile driving (Mooney et al. 2020).

Due to the risk of broad spatial and temporal overlap, interactions between the construction phase of OWE development and marine ecosystems have received the most attention. A priority concern is pile driving, which results in loud, impulsive noise pollution that is sustained during all times of day for multiple weeks and can propagate at elevated sound levels for tens of kilometers away from the source (Bailey et al. 2010; Andersson et al. 2017). Impulsive sounds have complex effects on the behavior, movement, and physiology of marine animals; the magnitude of these effects depends on distance from the sound source as well as the role of acoustic communication in the behavior and life history characteristics of the species (Madsen et al. 2006). For example, comparison of sound exposure criteria for bottlenose dolphins *Tursiops truncatus* to measured sound levels from pile driving revealed that auditory damage was possible within 100 m of the sound source, but behavioral effects could extend to 50 km (Bailey et al. 2010). Exposure to pile-driving sounds

has been shown to also affect the behavior of certain fish species, such as European Bass *Dicentrarchus labrax* and Atlantic Cod *Gadus morhua*, by negatively affecting group cohesion (Herbert-Read et al. 2017) as well as eliciting changes in depth and movement away from the sound source (Neo et al. 2016; van der Knaap et al. 2022). Moreover, experimental exposure to noise reduced spawning success in two goby species due to reduced acoustic courtship by males and a lack of spawning by females (de Jong et al. 2018). The combined effects of ground-disturbing activities on habitats and acoustic disturbance from construction on fish spawning are of particular concern for species that use acoustic communication during courtship and that are unlikely to successfully shift their reproduction to locations that are not disturbed, such as fishes that exhibit high fidelity to a spawning site (de Jong et al. 2020).

Of the U.S. OWE projects that are currently in development, many are located off southern New England and the Mid-Atlantic Bight in the western North Atlantic Ocean. As a result, an understanding of potential interactions between OWE and fisheries resources, specifically Atlantic Cod, has become a management priority in the region. Atlantic Cod have a complex metapopulation structure consisting of multiple subpopulations, each with multiple spawning components (Zemeckis et al. 2014a). Within these components, individuals exhibit high spawning site fidelity that is generally consistent in space and time each year (Robichaud and Rose 2001; Zemeckis et al. 2014b). During the spawning season, Atlantic Cod migrate to the spawning site and form dense aggregations within which reproductive males defend small territories (Nordeide and Folstad 2000; Fudge and Rose 2009). This aggregation behavior includes a courtship ritual in which males produce repetitive grunt-like sounds to attract a mate (Brawn 1961b; Finstad and Nordeide 2004). Sound production is thought to play a role in mate choice, as sound intensity and sound-producing muscle mass are correlated with male body size and mating success, respectively (Brawn 1961a; Hutchings et al. 1999; Rowe and Hutchings 2008). This combination of spawning site fidelity and use of acoustic communication during spawning could make Atlantic Cod vulnerable to acoustic and physical disturbances from OWE development.

Successful spawning is critical to sustain and rebuild populations, and experiments have shown that repeated exposure of Atlantic Cod to anthropogenic noise can

reduce the number of viable embryos produced by more than 50% due to decreased egg production and fertilization rates (Sierra-Flores et al. 2015). Furthermore, spawning disturbance associated with OWE development may have interactive effects with other anthropogenic and natural stressors. In the United States, Atlantic Cod spawning components have experienced consistent declines due to interacting pressures from overexploitation (Ames 2004; Zemeckis et al. 2014c), loss of stock stability (Reich and DeAlteris 2009), a mismatch between biological stock structure and management (Kerr et al. 2014), environmental variability (Brander 2005; Friedland et al. 2013), and range contraction due to climate change-induced thermal habitat loss (Nye et al. 2009; Friedland et al. 2020). In theory, a metapopulation structure should buffer against fluctuations in spawning success of discrete components while maintaining the overall stock complex (Stephenson 1999; Rose et al. 2011); however, attempts to rebuild the Atlantic Cod stock have been unsuccessful (Lilly et al. 2008; Lindegren et al. 2013; Zemeckis et al. 2014a) and much of the population structure has been lost (Ames 2004). In an attempt to improve the management and recovery of the Atlantic Cod stock, recent research has focused on expanding the understanding of connectivity between subpopulations and their relative roles in maintaining the stock. Atlantic Cod have historically been managed as two U.S. stocks—the Gulf of Maine stock and the Georges Bank stock, which includes the southern New England subpopulation—but a recent synthesis has identified five genetically distinct subpopulations (McBride et al. 2021). Current understanding suggests that most of the spawning stock biomass remains in the Gulf of Maine, which consists of distinct winter- and spring-spawning subpopulations. Southern New England supports its own distinct spawning group but also receives imports of eggs and larvae from Gulf of Maine winter spawners (McBride et al. 2021).

Studies of spatiotemporal spawning dynamics within the Gulf of Maine, Georges Bank, and other global Atlantic Cod stocks have identified that spawning generally occurs over a multiple-month period, with peaks in grunt activity at night near the new and full moons (Grabowski et al. 2015; Zemeckis et al. 2019). Studies of winter spawning aggregations throughout Massachusetts Bay (western Gulf of Maine) have identified that within the October–January spawning period, the seasonal timing of peak grunt activity varies among individual aggregations, with deeper sites exhibiting a peak later in the spawning season (Zemeckis et al. 2019; Caiger et al. 2020). Compared to the Gulf of Maine and Georges Bank, relatively few data exist regarding the dynamics and structure of cod in southern New England waters. To better understand interactions with OWE development and to support stock rebuilding, a broader understanding of the

spatiotemporal spawning dynamics of Atlantic Cod in southern New England is needed.

To fill the knowledge gap regarding potential interactions between Atlantic Cod and OWE development in southern New England, we employed multiple passive acoustic monitoring technologies to infer the spatiotemporal spawning dynamics of Atlantic Cod in and around planned OWE lease areas. Due to the role of sound production in cod spawning, passive acoustic monitoring offers multiple advantages, including access to long-term data from a noninvasive approach. The temporal dynamics of spawning-associated grunt activity identified near Cox Ledge in southern New England waters were also compared to those identified in an analogous study of the geographically separated winter-spawning subpopulation in Massachusetts Bay within the western Gulf of Maine. Given the lack of data on Atlantic Cod in southern New England, the goal of this comparison was to assess whether the observed dynamics were similar to those of other spawning groups. Our comparison may strengthen managers' ability to draw inferences about potential interactions between Atlantic Cod spawning and OWE from sparse data and may facilitate interpretation of our results in the context of the broader stock complex.

STUDY AREA

Passive acoustic monitoring of Atlantic Cod spawning-associated grunts was conducted in southern New England waters, with survey effort concentrated between Block Island and Martha's Vineyard and at depths between 30 and 50 m (Figure 1). The main bathymetric feature in the study area is Cox Ledge, an area of complex rocky substrate located southeast of Block Island. Cox Ledge is used by commercial and recreational fishing fleets and is included as essential fish habitat for all life stages of Atlantic Cod (Lough 2004; DeCelles et al. 2017).

To assess potential interactions between Atlantic Cod spawning and OWE, the study intentionally sampled multiple lease areas planned for development within the Rhode Island–Massachusetts Wind Energy Area, including the South Fork Wind Farm and portions of the Revolution Wind Farm and Sunrise Wind Farm (Figure 2). The South Fork Wind Farm spans 55.4 km² on Cox Ledge, with cable connections extending along the seafloor to New York. To date, the South Fork Wind Farm is the only project in the sampling area that has received full approval to begin construction, planned for late 2022, and will consist of up to 12 turbines and one substation (BOEM and NMFS 2021). The Revolution Wind Farm spans 334.8 km² on Cox Ledge and the surrounding region, with cables extending to Rhode Island. Construction of less than 100 turbines is anticipated to begin in 2023 (Revolution Wind 2021). The Sunrise Wind Farm

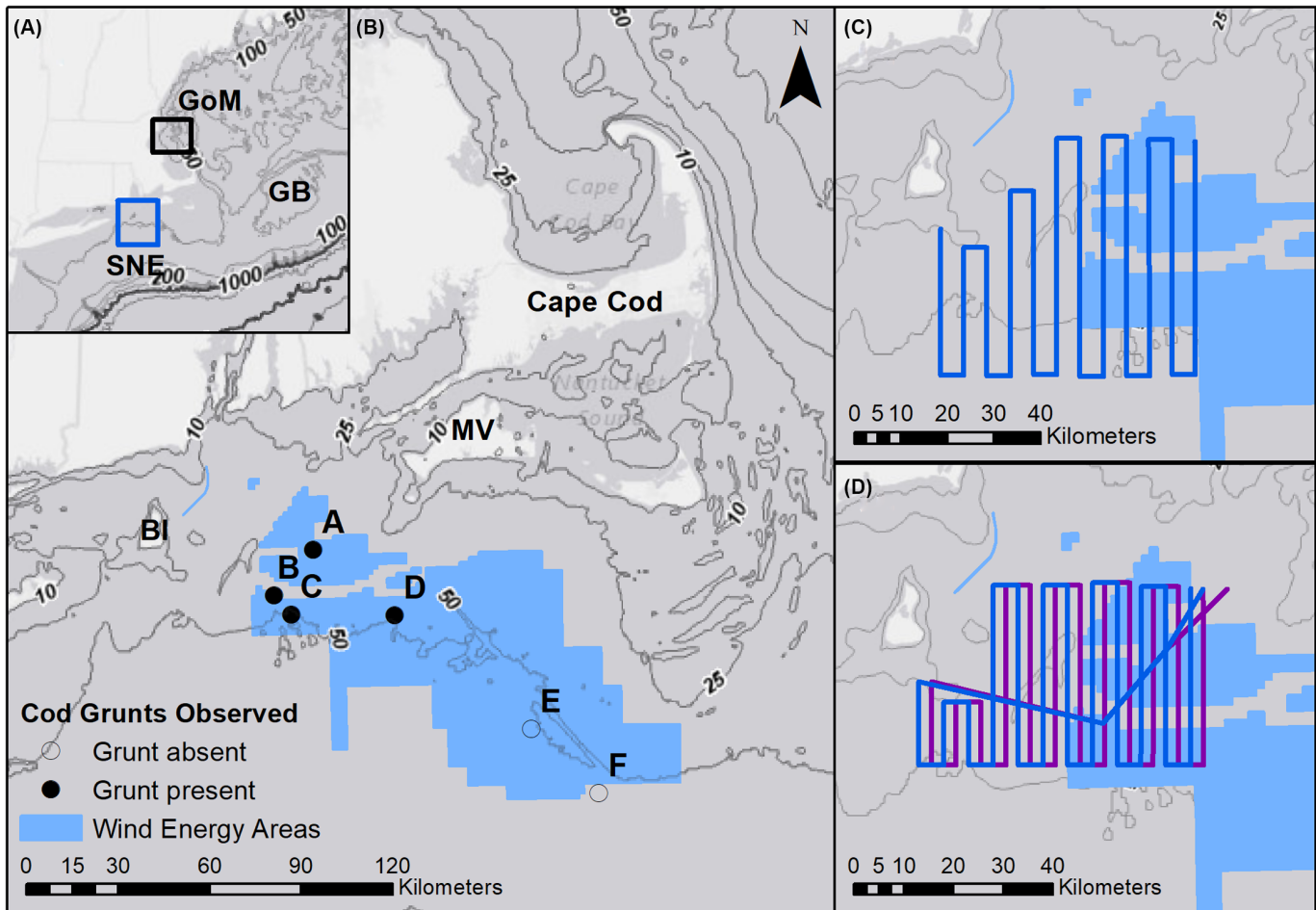


FIGURE 1. Maps of the study area and sampling effort: (A) regional context for comparison between Massachusetts Bay (black box) and southern New England (SNE; blue box) waters of the western North Atlantic Ocean, with text labels indicating the locations of general Atlantic Cod spawning regions in the Gulf of Maine (GoM), Georges Bank (GB), and SNE; (B) the SNE study area, including the full Rhode Island–Massachusetts Wind Energy Area and the locations of fixed-station receivers A–F (MV = Martha's Vineyard; BI = Block Island); (C) programmed glider track used during the 2019–2020 sampling effort; and (D) programmed glider tracks used during the 2020–2021 sampling effort. To improve spatiotemporal coverage, the glider alternated between the blue and purple tracks throughout the 2020–2021 deployment.

spans 351.4 km² south of Cox Ledge, with cables extending to New York. Construction of 59–122 turbines is proposed to begin in 2024 (Sunrise Wind 2021).

METHODS

Data collection.—Passive acoustic monitoring data were collected from fixed-station recording instruments (2013–2015 and 2020–2022) and mobile autonomous underwater gliders (2019–2022; Table 1; Figure 2). Fixed-station data facilitated the interpretation of temporal patterns, while glider-based surveys offered broad spatial coverage. The sampling locations were selected to ensure sampling within and around the wind lease areas as well as at putative spawning sites that were identified from historical data in the region and fishery-dependent data.

From 2013 to 2015, fixed-station data in southern New England were collected by the Northeast Large Pelagic Survey Collaborative (consisting of the New England Aquarium, the Cornell University Bioacoustics Research Program, the University of Rhode Island, and the Center for Coastal Studies) to document ambient noise conditions and the occurrence of marine mammals in the context of eventual OWE development (Kraus et al. 2016). However, the recording equipment used was also capable of recording the presence of cod grunts. During the sampling period, five marine autonomous recording units (MARUs) were successfully deployed throughout the Rhode Island–Massachusetts Wind Energy Area (Figure 1B). The MARUs recorded continuously at a 2-kHz sampling rate with a 10–800-Hz band-pass filter to reduce electrical interference and prevent aliasing. The gain and sensitivity,

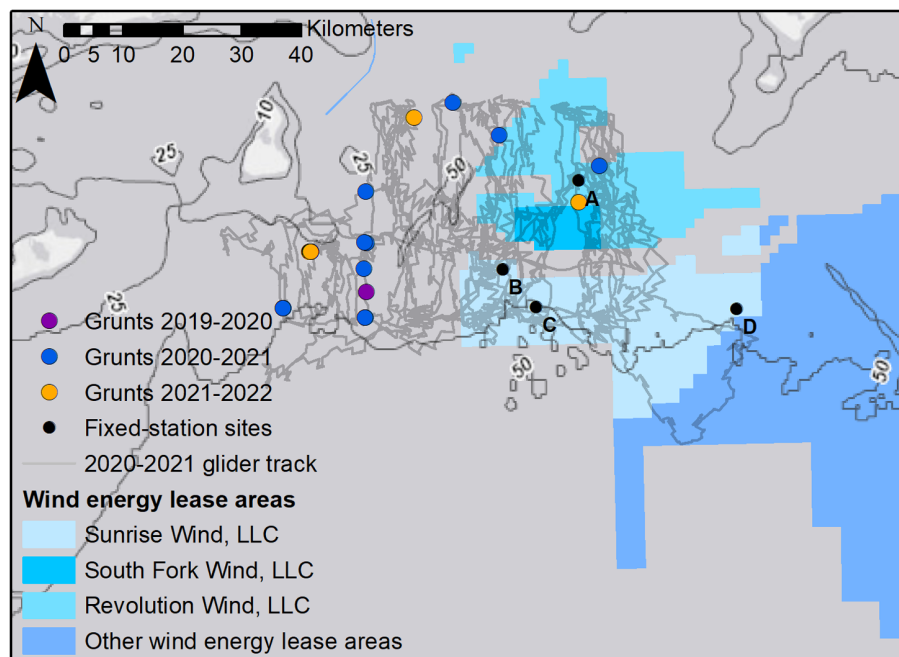


FIGURE 2. Locations of observed Atlantic Cod grunts during the glider survey in southern New England waters in all years. The realized glider track during the 2020–2021 deployment, the locations of fixed-station recorders, and relevant lease areas within the Rhode Island–Massachusetts Wind Energy Area are also plotted for spatial reference.

TABLE 1. Passive acoustic monitoring sites (see Figure 1) and deployment details for fixed-station receivers in southern New England waters of the western North Atlantic Ocean.

Site	Latitude (°N)	Longitude (°W)	Effort (d)	Years sampled	Depth (m)
A	41.1421	71.1038	156	2013–2015	33
A	41.1413	71.1013	202	2020–2022	32
B	41.0406	71.2195	202	2020–2022	41
C	40.9978	71.1683	73	2013–2014	51
D	40.9955	70.8642	73	2013–2014	50
E	40.7436	70.4607	26	2013	52
F	40.5993	70.5617	26	2013	59

respectively, were 23.5 dB referenced to (re) 1 μPa and -168 dB re 1 V/ μPa (± 3 dB between 10 and 1,000 Hz). Identical MARUs have been used previously in other regions to characterize the spawning-associated grunt activity of cod (Hernandez et al. 2013; Zemeckis et al. 2019; Caiger et al. 2020).

From 2020 to 2022, fixed-station sound data were recorded continuously during the presumed spawning season at two sites using SoundTrap ST500 recorders (Ocean Instruments, Warkworth, New Zealand) at a sampling rate of 48 kHz. These sites were selected as putative cod spawning sites based on analysis of the 2013–2015 fixed-station data as well as the telemetry and glider data

recorded during 2019–2020. Specifically, telemetry data from the 2019–2020 glider deployment identified the presence of multiple tagged cod at both sites, and analysis of the 2013–2015 data provided evidence of a local spawning aggregation at site A (Figure 1B). The hydrophone at site A had a gain of 1.8 dB and a sensitivity of -177 dB re 1 $\mu\text{Pa/V}$. The hydrophone at site B had a gain of 1.9 dB and a sensitivity of -177.4 dB re 1 $\mu\text{Pa/V}$.

The glider-based recorder was a digital acoustic monitoring instrument (Baumgartner et al. 2013) mounted to a Slocum mobile autonomous glider (Teledyne Webb Research, North Falmouth, Massachusetts; Rudnick et al. 2004). The digital acoustic monitoring instrument recorded at a 2-kHz sampling rate. The glider was programmed to follow a grid consisting of 12 north–south transects that were separated by 5 km. However, due to currents and oceanographic conditions, the glider deviated somewhat from this path. The programmed glider track was updated between deployments to improve spatial–temporal replication of the survey area. In 2019, the glider swam the grid from east to west and then reversed and traveled from west to east, covering a 2,400-km² area from December 21, 2019, to March 22, 2020 (Figure 1C). In 2020 and 2021, the glider swam the same 12 transects except that the southern extent was limited to the 50-m isobath (Figure 1D). Additionally, the glider swam from east to west and then flew back to start, passing directly over fixed-station sites A and B on the way, and repeated

the east-to-west circuit shifted 3 min east, covering an 1,800-km² area in total. The glider surveyed from November 11, 2020, to February 25, 2021, and from November 5, 2021, to February 7, 2022.

Atlantic Cod grunt detection.—All passive acoustic data were analyzed with a cod grunt detector (Urazghildiiev and Van Parijs 2016) that was executed in MATLAB and then manually validated in Raven version 1.5 (KLY-CCB 2014). The detector's performance was evaluated during development using data from a 24-h period at 19 MARUs. The probability of cod grunt detection ranged from 0.42 to 1.00, and the probability of false detection ranged from 0.0083 to 0.16 (Urazghildiiev and Van Parijs 2016). For the 2013–2015 data, sites A, C, and D were analyzed from October 1, 2013, to January 31, 2014, during the presumed spawning season based on fishery-dependent observations and maturity data from previous field studies (McBride et al. 2021). Because sites E and F were outside the focal region of the current study, they were analyzed during a shorter period of the presumed spawning season: from November 15 to December 10, 2013. During the 2013–2014 season, multiple cod grunts on consecutive days were only observed at site A; therefore, only site A was analyzed the following year from October 1, 2014, to January 1, 2015. Site A was also analyzed every Monday from February 18, 2013, to February 12, 2014, to confirm the bounds of the spawning season. All 2019–2022 fixed-station and glider data were analyzed for the full deployment.

After evaluation by the cod detector, all possible grunt detections were validated in Raven. For thorough review, all detections were visualized from 10 to 400 Hz in a 5 × 5 grid spectrogram and context spectrogram. The grid spectrogram was generated with a 256-point fast Fourier transform, 75% overlap, and a 1-s time-pad. The context spectrogram was generated with a 1,024-point fast Fourier transform, 75% overlap, and a 10-s time-pad. Positive cod detections were identified through auditory and visual confirmation only when (1) at least two harmonics were visible with the characteristic frequency down-sweep and (2) the fundamental frequency was between 40 and 80 Hz. The presence of grunts and the total number of grunts detected (i.e., grunt rate) were summarized by hour.

Statistical analysis.—Generalized linear mixed modeling was used to evaluate the temporal correlations between spawning-associated grunt activity of Atlantic Cod and multiple natural environmental cycles. Grunt activity was summarized as the presence of cod grunts each hour (hereafter, “grunt presence”) and the number of grunts per hour (hereafter, “grunt rate”). Grunt rate is inferred to indicate increased spawning activity, as experimental results indicated that higher grunt rates occur during the peak spawning period and are associated with

increased egg production (Rowe and Hutchings 2006). Statistical methods were analogous to those used by Caiger et al. (2020) to characterize spawning activity of winter-spawning cod in Massachusetts Bay, thus facilitating a comparison between the two regions. To prevent spurious correlations and facilitate comparisons, the criteria for data inclusion were grunt observations (1) on at least 10 d and (2) during at least 2% of hours in the spawning season, as used in previous passive acoustic monitoring of Atlantic Cod grunt activity (Zemeckis et al. 2019; Caiger et al. 2020). Grunt presence and grunt rate were summarized by hour, and their temporal correlations were evaluated separately. Grunt presence was modeled with a binomial distribution, while grunt rate was modeled with a zero-inflated negative binomial distribution.

The global models for grunt presence and grunt rate included the effect of multiple natural cycles (annual, seasonal, diel, and lunar) that have been identified as associated with the timing of cod grunt activity in other spawning stock components (Zemeckis et al. 2019). The spawning season year spanned October–January and was treated as a factor variable. Day of year and the diel, lunar, and semi-lunar cycles were treated as circular variables to facilitate the modeling of both the timing and magnitude of their effects (Zar 1999; Caiger et al. 2020). As such, each variable was converted to radians and its effect consisted of a sine and cosine term in the model. To reduce the effect of serial autocorrelation among the residuals, the effect of week was included as a random effect in the model.

The remaining candidate models for grunt presence and grunt rate consisted of the top models (difference in Akaike's information criterion corrected for small sample size [ΔAIC_c] ≤ 5) identified for each process in the Massachusetts Bay study (Caiger et al. 2020). Because the southern New England data set consisted of only one site, the candidate models for southern New England could not include the effects of site, depth, or the interaction between site and day of year. In addition, the random effect of week was dropped from the zero-inflated component of the grunt rate model but was retained in the conditional component. All models were evaluated using an information criterion-based model selection procedure with AIC_c . The effect of each natural cycle was calculated using estimated marginal means. To facilitate comparison of the temporal correlations between regions, the confidence interval ($\alpha = 0.05$) was estimated for the marginal mean of each variable for both Massachusetts Bay and southern New England. All statistical analyses were conducted in R version 4.0.3 (R Core Team 2020), the models were built using the glmmTMB package (Brooks et al. 2017), and estimated marginal means were calculated using the emmeans package (Lenth 2021).

RESULTS

For the 2013–2015 fixed-station data, three out of five sites had at least one cod grunt detection. Only site A had repetitive detections, inferred as an active spawning aggregation (Figure 1). In total, 1,035 grunts were observed at site A across the 2013–2014 and 2014–2015 spawning seasons; one grunt was observed at site C on December 13, 2013; and one grunt was observed at site D on December 25, 2013. No grunts were observed at site E or site F. Sites C–F were not evaluated during the 2014–2015 spawning season due to the lack of repetitive grunts during the 2013–2014 spawning season.

For the 2020–2022 data, six grunts were observed at the two fixed-station sites sampled. At site A, one grunt was observed on November 19, 2020, and one grunt was observed on December 22, 2021. At site B, one grunt was observed each day on November 29, December 1, and December 15, 2020, as well as on January 4, 2021. The 2020–2022 deployments at site A were intended to resample the aggregation that was observed in the 2013–2015 data; however, due to oceanographic conditions at the time of deployment, the recorder locations at site A unintentionally differed by approximately 228 m, with the 2020–2022 site located 113° to the southeast. The low number of grunts observed from 2020 to 2022 did not meet the threshold for data inclusion, so all further temporal analysis only includes the 2013–2015 data.

The glider-based survey observed a total of 31 cod grunts across three deployments, with one grunt observed on January 19, 2020 (2019–2020 deployment); 12 grunts observed between November 15, 2020, and January 8, 2021 (2020–2021 deployment); and 18 grunts observed between November 6, 2021, and January 4, 2022 (2021–2022 deployment). Grunts were observed at all times of day, but 9 of the 12 grunts during the 2020–2021 spawning season were observed at night. During the 2021–2022 spawning season, 16 grunts were observed within a 45-min period on December 9. Across all deployments, three grunts were observed within or adjacent to the wind lease areas, while the remaining grunts were concentrated in the western half of the study area in water between 25 and 50 m deep (Figure 2).

The analysis of 1 d/week at site A from February 2013 to February 2014 did not identify any cod grunts outside of the October–January period, suggesting that analysis during this period was sufficient to capture spawning-associated grunt activity. For the 2013–2015 spawning season data at site A, grunt activity was concentrated in November and December, with only 36 grunts (3.5% of the total observed) detected in October and January. More grunts were observed during 2013–2014 compared to 2014–2015. In 2013–2014, the maximum number of grunts per day was 125 on November 26, 2013, while in 2014–2015, the maximum was 60 grunts on December 24, 2014

(Figure 3). During months when the maximum grunt activity was observed, grunts were detected at all times of day; otherwise, the observed grunt rate per hour was highest during the day (Figure 4A,B). During 2013–2014, observed grunt activity appeared to be associated with the lunar cycle, with most grunts occurring between the full moon and waning moon (Figure 4C). In 2014–2015, grunt activity was more variable, with the greatest number of grunts observed between the new moon and full moon (Figure 4D).

Generalized linear mixed modeling of the 2013–2015 data when an inferred spawning aggregation was observed elucidated clear temporal patterns in grunt activity. Modeling of grunt presence identified the global model as providing the best fit for the southern New England data (Table 2). The candidate model without the semi-lunar cycle as a predictor yielded the second-best fit and was nearly indistinguishable from the global model. Grunt presence was estimated to be most likely during mid-day between the full moon and waning moon (Figure 5). The asymmetrical lunar pattern suggests an effect of the semi-lunar cycle, with a second, smaller increase in grunt probability between the new moon and waxing moon. Seasonally, the highest probability of grunt occurrence was on December 5 (Figure 6A).

Overall, the temporal correlations of grunt presence with multiple natural cycles were similar to those in Massachusetts Bay, although the magnitude of the correlations tended to be stronger at the southern New England site.

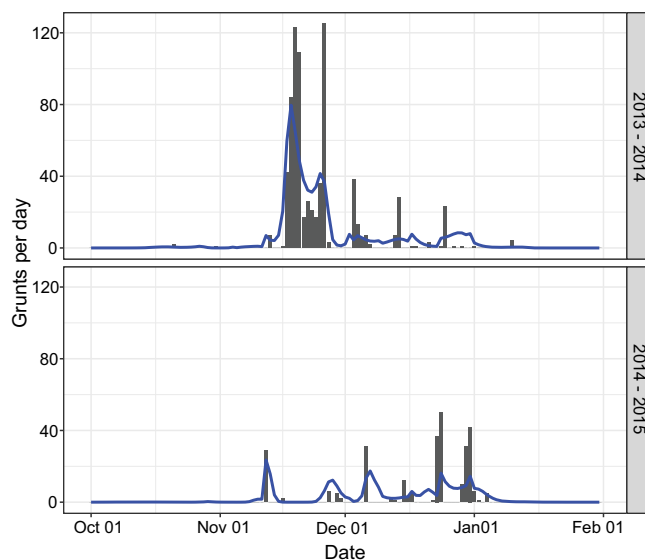


FIGURE 3. Seasonal and interannual variability in the total number of observed Atlantic Cod grunts per day at site A in southern New England waters during the 2013–2015 sampling periods (bars) and the predicted number of grunts per day (blue line) under the global model for grunt rate.

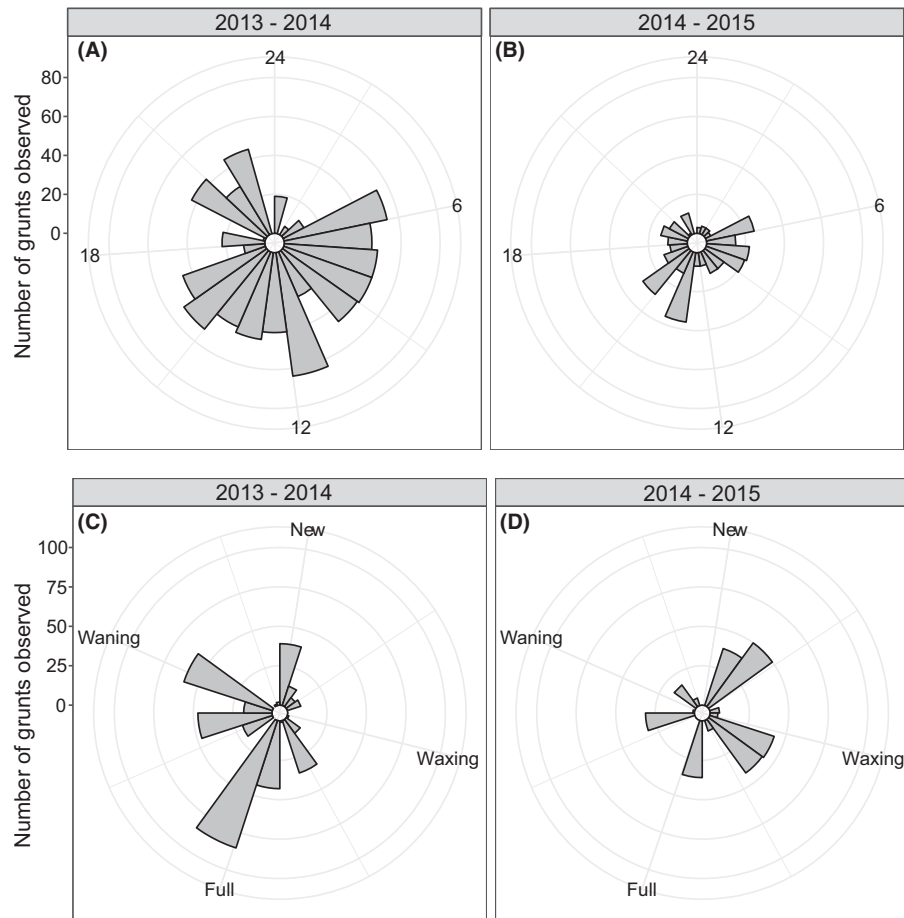


FIGURE 4. Number of Atlantic Cod grunts observed at site A in southern New England waters (A), (B) per hour and (C), (D) throughout the lunar cycle during each spawning season sampled.

Specifically, data from both regions identified similar support for multiple models with varying lunar terms included, but the Massachusetts Bay data suggested a much weaker effect of the diel and lunar cycles on grunt presence (Figure 5). Both regions followed a similar seasonal pattern, with grunt activity concentrated in November and December, though the peak in grunt presence in Massachusetts Bay had a significant interaction with site and was estimated to occur on November 20 overall—approximately 2 weeks earlier than the peak at the southern New England site (Figure 6A).

The temporal correlations with grunt rate in southern New England were also best explained by the global model, where both the grunt rate terms and the zero-inflated terms included all candidate predictor variables (Table 2; Figure 3). Due to the high proportion of zeroes in the grunt rate data set, inclusion of the zero-inflated negative binomial substantially improved model fit over a negative binomial distribution alone. The highest grunt rate was estimated to occur at noon near the full moon

(Figure 7B,D). Similar to grunt presence, the asymmetrical lunar pattern indicated an effect of both the lunar and semi-lunar cycles, with the highest grunt rates estimated to occur just after the full and new moons and lower grunt rates estimated to occur near the waxing and waning moons. Seasonally, the maximum grunt rate was estimated to occur on November 26, about 1 week before the peak in grunt presence (Figure 6B).

The grunt rate model that was best supported by the Massachusetts Bay data included the same temporal correlations as the grunt rate model for southern New England but did not include the semi-lunar cycle as a zero-inflated term. Although the overall grunt rate was higher in Massachusetts Bay and the two regions exhibited different diel correlations (Figure 7A,B), the correlations with lunar cycle were very similar between the two regions (Figure 7C,D). Similarly, the seasonal trend followed the same pattern, but the peak grunt rate in Massachusetts Bay was estimated to occur on December 5, approximately 2 weeks later than that in southern New England waters (Figure

TABLE 2. Candidate models for temporal correlations of Atlantic Cod grunt activity in southern New England waters of the western North Atlantic Ocean. The model with the best fit (in bold) for grunt presence or grunt rate was used for all comparisons with Massachusetts Bay (AIC_c = Akaike's information criterion corrected for small sample size; ΔAIC_c = difference in AIC_c between the given model and the best-performing model). Included predictor variables are year (Y), hour of the day (H), lunar cycle ($L1$), semi-lunar cycle ($L2$), day of the year (J), and week of the year (rW).

Model terms	Zero-inflated terms	df	AIC_c	ΔAIC_c
Grunt presence				
$Y + H + L1 + L2 + J + rW$		11	1,398.8	0.00
$Y + H + L1 + J + rW$		9	1,402.8	4.00
$Y + H + L2 + J + rW$		9	1,445.6	46.75
$Y + H + J + rW$		7	1,452.3	53.51
Grunt rate				
$Y + H + L1 + L2 + J + rW$	$Y + H + L1 + L2 + J$	22	2,271.9	0.00
$Y + H + L1 + L2 + J + rW$	$Y + H + L1 + J$	20	2,351.8	79.92

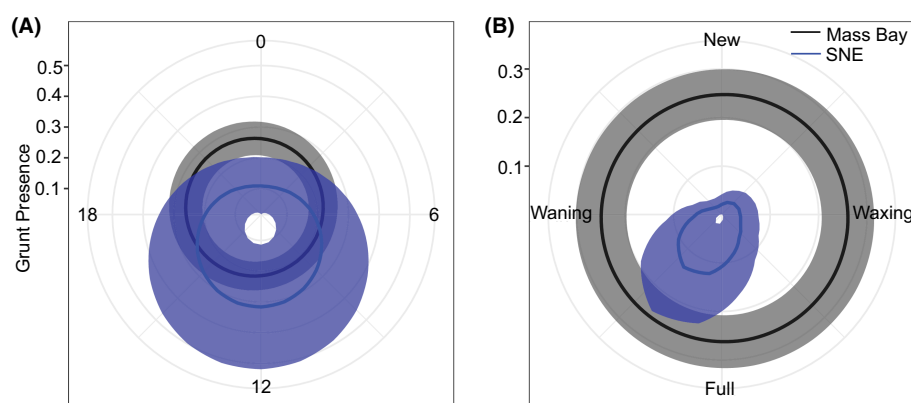


FIGURE 5. Estimated marginal mean effect of (A) diel and (B) lunar cycles on Atlantic Cod grunt presence at fixed stations, compared between Massachusetts Bay (Mass Bay) and southern New England (SNE) waters. The shaded regions represent the 95% confidence interval of the estimates.

6B). However, there was significant spatial heterogeneity in the seasonal profile of cod spawning activity in Massachusetts Bay, and the present results for Atlantic Cod in southern New England are well within this range.

DISCUSSION

The use of multiple passive acoustic monitoring strategies to assess the spatiotemporal spawning dynamics of Atlantic Cod in southern New England recorded the presence of occasional cod grunts throughout the study area and successfully captured the dynamics of a spawning aggregation during two consecutive years. Analysis of spawning-associated grunt dynamics identified that peak grunt activity occurred during the day and near the full moon in late November to early December. While there were fine-scale differences between the temporal patterns of grunt activity observed in southern New England versus Massachusetts Bay, the broadscale seasonality was very similar. Over the sampling period, the number of grunts detected at the inferred spawning aggregation at site A

decreased and the aggregation was not detected during the 2020 or 2021 sampling period; however, the glider results suggested that spawning Atlantic Cod were still present throughout the region. Overall, evidence from the fixed-station and glider data in southern New England suggests that Atlantic Cod spawning overlaps with wind lease areas in the region.

Some temporal dynamics of inferred spawning identified in the southern New England study area aligned with those in Massachusetts Bay. For example, the peak spawning season for winter Atlantic Cod in Massachusetts Bay consistently occurred between November and December, with intermittent grunts extending into October and January at certain sites. Studies have reported correlations between grunt activity and lunar cycles, with grunt presence associated with the lunar cycle and grunt rate associated with both the lunar and semi-lunar cycles (Zemeckis et al. 2014a; Grabowski et al. 2015). Although the southern New England data revealed an association between grunt presence and both the lunar and semi-lunar cycles, the probability of grunt presence was much higher

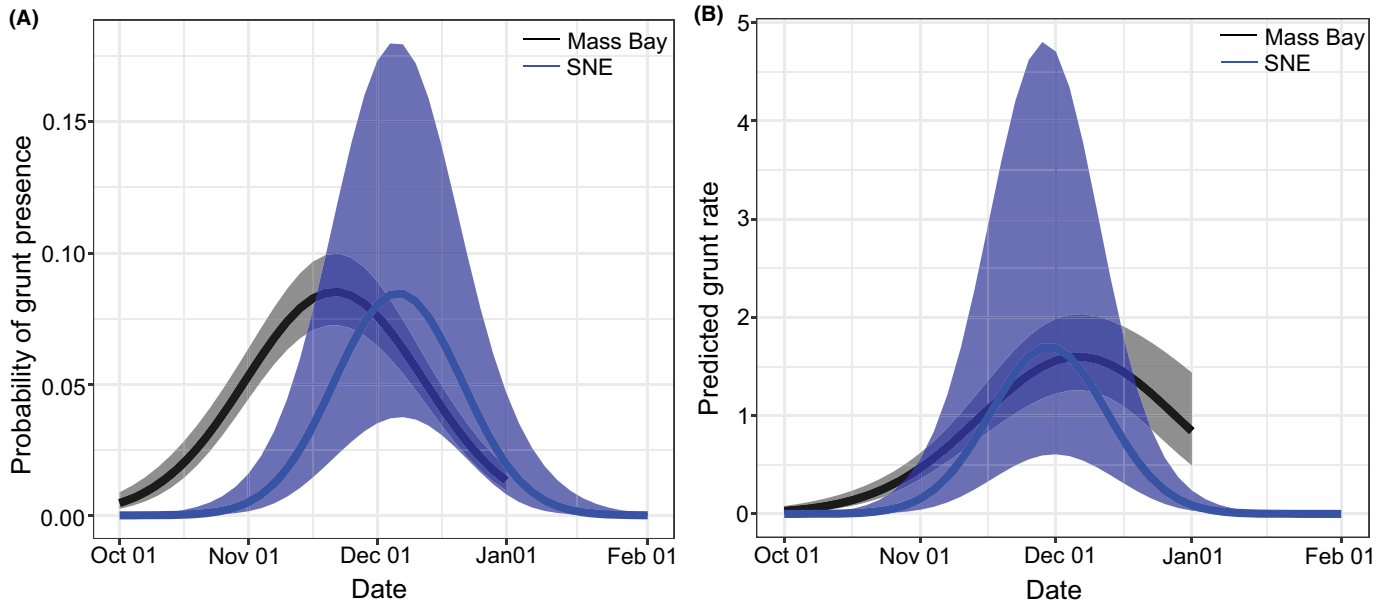


FIGURE 6. Estimated marginal mean effect of calendar date on Atlantic Cod (A) grunt presence and (B) grunt rate at fixed stations in Massachusetts Bay (Mass Bay) and southern New England (SNE) waters. The shaded regions represent the 95% confidence interval of the estimates.

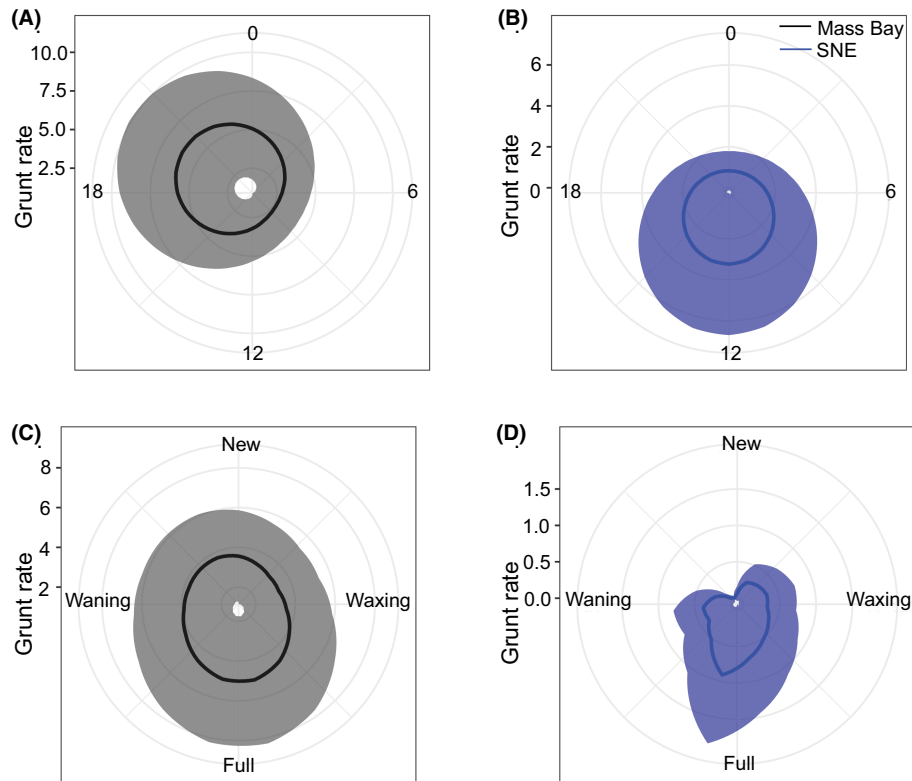


FIGURE 7. Estimated marginal mean effects of (A), (B) the diel cycle and (C), (D) the lunar cycle on the Atlantic Cod grunt rate at fixed stations in Massachusetts Bay (Mass Bay) and southern New England (SNE) waters. Note the change in the y-axis scales. The shaded regions represent the 95% confidence interval of the estimates.

between the full moon and waning moon than between the new moon and waxing moon, suggesting that the semi-lunar cycle has a smaller effect on grunt presence relative to the lunar cycle. Conversely, the grunt rate in the Massachusetts Bay and southern New England data revealed a stronger effect of the semi-lunar cycle, with peaks near the full and new moons. The timing of spawning is thought to occur when oceanographic and ecological conditions are best suited to the success of the released eggs and subsequent larvae (Cushing 1990). These consistent correlations with the semi-lunar cycle may be indicative of larval transport to favorable habitats or retention and settlement of larvae during times of unique oceanographic conditions (Lough et al. 2006).

In the scope of identifying the peak spawning period, both regions were consistent, with peaks in grunt presence and grunt rate estimated to occur within a 3-week period from late November to early December. Within the spawning season, however, the peak grunt rate occurred before peak grunt presence in southern New England, while the opposite was true in Massachusetts Bay. This slight difference in grunt trend throughout the spawning season may indicate aggregation-level differences between spawning components or interannual variation in lunar cycle timing within the month rather than reflecting a regional difference. For example, the magnitude of grunt activity at the southern New England aggregation in 2013 was much higher than the magnitude of activity in the subsequent spawning season. Additionally, the peak in grunt activity was observed in November during 2013 and in December during 2014. This variation between the 2 years sampled likely explains the different relationship between maximum predicted grunt presence and grunt rate. In contrast to the single aggregation sampled in southern New England, the Massachusetts Bay data set captured spawning dynamics over a much broader area and period by sampling 16 sites across 10 years. Both the comparison study and additional studies of Atlantic Cod temporal grunt dynamics in Massachusetts Bay have identified a significant interaction between site and seasonal peak grunt rate, with the peak in grunt activity occurring later at deeper sites (Zemeckis et al. 2019; Caiger et al. 2020). This significant interaction suggests that individual spawning aggregations within a subpopulation may exhibit their own unique temporal correlations that maximize the success of spawning in their specific oceanographic conditions. Lastly, grunt activity in Massachusetts Bay was not summarized in January and a few sites had increasing observed grunts throughout the month of December, suggesting that there may have been grunts missed during January. This difference in sampling period may also contribute to the difference in grunt patterns within the spawning season.

One difference between the two regions was that grunt presence had a stronger association with the diel and lunar

cycles in southern New England than in Massachusetts Bay. Due to the large difference in the number of aggregations sampled between the two studies, it is difficult to discern whether this pattern is a regional difference or indicative of aggregation-level differences. Because the Massachusetts Bay results summarize the average temporal dynamics across all sites, it could be expected that the estimated marginal means for Massachusetts Bay would report a weaker association with a specific natural cycle. As previously mentioned, the timing of peak grunt activity is known to vary among aggregations within a subpopulation, so it is plausible that discrete aggregations have unique correlations with other natural cycles as well. It is also useful to note that while the strength of temporal associations with grunt rate was similar between the regions, the magnitude of grunt rate was higher for Massachusetts Bay, likely due to greater abundances.

Of the natural cycles explored, the diel cycle was the most inconsistent between the two regions, as peak grunt activity occurred at night in Massachusetts Bay and during the day in southern New England. Many field (Zemeckis et al. 2019; Caiger et al. 2020) and laboratory (Brawn 1961b; Kjesbu 1989; Hutchings et al. 1999) studies have reported cod spawning and grunt activity increasing at night, especially for winter-spawning cod stocks. Despite this, passive acoustic monitoring of the spring-spawning subpopulation in Massachusetts Bay also identified an increase in grunt activity during the day (Hernandez et al. 2013). Similar to the present study in southern New England, that study consisted of a single MARU. Because cod grunts are relatively quiet compared to other marine sound sources, successful detection of a cod grunt requires the fish to be very close to the receiver. The only documented source level for Atlantic Cod grunts is 127 dB re 1 μ Pa at 1 m, and estimates of their communication radii under a variety of background and anthropogenic noise conditions ranged from 1.3 to 21.6 m (Nordeide and Kjellsby 1999; Stanley et al. 2017). Moreover, Atlantic Cod are known to exhibit diel movements whereby individuals aggregate in one location during the day and travel to surrounding areas or shift their position within the aggregation to defend a territory at night (Dean et al. 2014). Hernandez et al. (2013) suggested that one explanation for the discrepancy in grunt activity was that the receiver could have been located near the daytime aggregation site and diel movements caused individual cod to move outside of the detection radius of the receiver at night, leading to an apparent lack of grunt activity. Similar behavioral migrations and receiver locations could explain the uncommon diel association observed in southern New England.

Following identification of a spawning aggregation at site A in 2013–2015, the goal of resampling that site in 2020 and 2021 was to evaluate whether temporal grunt dynamics were stable over time. However, only one grunt was detected at

site A in 2020 and 2021. Given the 5-year gap in sampling, it is possible that the populations declined below detectable levels of abundance or were no longer detectable by passive acoustic monitoring due to a shift in aggregation location, accidental changes in sampling location, or the use of different recorder types. The U.S. Atlantic Cod stocks have been classified as overfished since 2010 (Zemeckis et al. 2014c). Additionally, because the southern New England spawning components are situated at the southern extreme of the species' range, they are the most vulnerable to climate impacts, including thermal habitat loss, loss of prey biomass, and increased species interactions (Fogarty et al. 2008; Nye et al. 2009; Friedland et al. 2013). As such, the spawning aggregation observed in 2013–2015 reflects the dynamics of a smaller baseline population. Successful formation of a spawning aggregation in some species is density dependent, such that the aggregation does not form at low abundances (Domeier 2012). The small number of observed grunts in 2019–2022 may be indicative of a highly disorganized spawning population in which the aggregation behavior has been further disrupted. The high site fidelity of Atlantic Cod poses challenges for aggregation recovery following disruption. For example, the onset of a gill-net fishery in Massachusetts Bay fully disrupted an aggregation of spawning cod, causing most individuals to leave the aggregation site and not return (Dean et al. 2012). Despite this, results from a recent review of extirpated fish spawning aggregations suggest that recovery of the aggregation is possible if given enough time following strict enforcement of spatial protection or temporal moratoria on fishing (Chollett et al. 2020). In the absence of management protections for spawning cod, the combination of historically low population sizes, high spawning site fidelity, and increasing climate impacts makes the recolonization of an extirpated spawning aggregation unlikely for Atlantic Cod in the region.

Beyond the possibility that the aggregation was no longer present, the lack of observed grunts may be due to limitations of passive acoustic monitoring for Atlantic Cod. Spawning aggregations of Atlantic Cod are typically spatially consistent between years, with variation generally less than 1 km. Despite this, because cod grunts are relatively quiet, even shifts on the order of 100 m could cause grunts to occur outside the detection radius of the hydrophone. Similarly, due to the gap in sampling from 2015 to 2020, the aggregation was monitored with two different recorder types for which the geographic position varied by 228 m. The realized recording radius of passive acoustic monitoring can be difficult to assess, and whether an acoustic signal is detected depends on multiple factors, including the source level of the signal, the distance from the receiver, and the ambient background noise. As such, it is quite possible that the shift in sampling location or a change in cod detector performance on different acoustic data sources was responsible for the lack of detections in

2020–2022. To that end, the lack of detections is not necessarily indicative of a true absence of spawning cod in the vicinity of the historical spawning site.

This study intentionally leveraged multiple passive monitoring technologies to provide a broad spatiotemporal sample of Atlantic Cod grunt activity in southern New England. Each methodology used includes a trade-off between spatial and temporal coverage, and the multi-method approach and adaptive sampling between years were intended to balance these trade-offs and improve sampling coverage. For example, during the 2020–2022 glider deployments, the glider was programmed to travel directly over the two fixed-station sites. During these deployments, a grunt was observed on November 16, 2020, and another was observed on November 6, 2021, in the vicinity of the historical aggregation at site A. Given that the detection date was near the onset of increased grunt activity in 2013, if the aggregation was still present in large numbers and actively spawning, we would expect to have observed more grunts in this area. Overall, the sparse data observed by the glider and fixed-station sites in 2019–2021 as well as deviations of the glider from the planned path make it difficult to conclude whether the lack of grunts is a result of insufficient sampling locations and timing or reflects true absences. Future research with a denser array of fixed-station receivers or a finer-scale glider survey could reduce uncertainty regarding whether the patterns observed in the present study (i.e., diminished activity at historical spawning sites in 2020, the lack of grunts in the eastern portion of the study area, and the unique diel trend) are a result of gaps in the sampling coverage or true ecological patterns.

Between previous studies of Atlantic Cod spawning dynamics and population structure in the western North Atlantic Ocean (Zemeckis et al. 2014a; McBride et al. 2021), annual trawl surveys for groundfish by the Northeast Fisheries Science Center (Lough 2004), and local ecological knowledge of fishers (DeCelles et al. 2017), it is known that southern New England waters—specifically Cox Ledge—host critical habitats for Atlantic Cod eggs, larvae, and spawning adults. However, little was known of the specific location and timing of spawning in the region. During the present study, passive acoustic monitoring in 2013–2015 revealed the dynamics of a spawning aggregation near Cox Ledge and within wind lease areas. Moreover, comparison with Massachusetts Bay winter-spawning Atlantic Cod confirmed that the dynamics observed in southern New England are largely the same as those in other regions, with the peak spawning period in November and December. As a result, spatial and temporal interactions between OWE construction and Atlantic Cod in southern New England are likely. Despite the limited number of cod grunts observed during the 2019–2022 sampling periods, the results of the regional comparison

reduce uncertainty regarding the likelihood of temporal overlap between current construction timelines and cod spawning.

Among the many possible interactions between OWE development and fisheries, fine-scale habitat effects and broadscale acoustic effects are the greatest concerns for Atlantic Cod spawning aggregations. Due to the high site fidelity of Atlantic Cod spawning aggregations, the status of the stock as overfished, and the southern range contraction due to climate change, if a turbine foundation or underground cable is located at the aggregation site, the spawning aggregation would be disrupted and may fail to relocate to an undisturbed area (de Jong et al. 2020). On a broader scale, the acoustic disturbance from pile driving overlaps in frequency with cod grunt activity (Popper and Hawkins 2019), increasing the risk of auditory masking and the disruption of cod behavior over a scale of tens of kilometers (Hammar et al. 2014; Mooney et al. 2020). There have been recent advances in technologies to minimize the acoustic impacts from pile driving (i.e., bubble curtains); however, temporal restrictions on disruptive activities are among the most successful measures for mitigating disturbance to and facilitating recovery of aggregation-spawning fishes during vulnerable periods (Erisman et al. 2017; Chollett et al. 2020; Mooney et al. 2020). Although these measures have had limited success for rebuilding Atlantic Cod stocks after overfishing has occurred (Clarke et al. 2015), temporal restrictions on fishing have had numerous successes for other fish populations (Burton et al. 2005; Nemeth 2005; Hamilton et al. 2011). Under the Marine Mammal Protection Act, current construction plans for OWE in the region only restrict pile driving from January to April to mitigate disturbance for North Atlantic right whales *Eubalaena glacialis* (BOEM and NMFS 2021). Although some Atlantic Cod spawning does occur in January, the results presented here show that the vast majority of inferred spawning activity occurs in November and December, leaving cod vulnerable to disturbance from pile driving and other construction activity.

At large population sizes, Atlantic Cod spawning aggregations have been recorded producing a loud, persistent rumbling that is frequently referred to as a “fish chorus” (Brawn 1961b; Nordeide and Kjellsby 1999). The lack of persistent cod grunts throughout the region and the relatively small number of grunts at an inferred aggregation are likely a result of low abundances in the region and limitations of passive acoustic monitoring for Atlantic Cod. The quiet nature of a cod grunt requires a recorder to be in very close proximity to the individual, while the aggregating behavior among small populations makes it challenging to sample in the right place at the right time. Despite these limitations, the use of multiple passive acoustic monitoring technologies offers spatial and temporal data from a noninvasive method that is specific to spawning individuals and does not require physical

capture and dissection (Van Parijs et al. 2009; Rowell et al. 2015; Zemeckis et al. 2019). Moreover, while many vessel-based surveys are not able to operate during the construction and operation of a wind farm, passive acoustic monitoring remains a viable survey option. This advantage results in baseline data that can be compared to data collected both during and after construction, thus facilitating long-term assessment of interactions between OWE and fishery resources.

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