



Acoustic monitoring of Atlantic cod (*Gadus morhua*) in Massachusetts Bay: implications for management and conservation

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Atlantic cod (*Gadus morhua*) stocks in northeastern US waters are depleted and stock recovery has been slow; research into the spawning behaviour of this species can help inform conservation and management measures. Male cod produce low-frequency grunts during courtship and spawning. Passive acoustic monitoring (PAM) offers a different perspective from which to investigate the occurrence, spatial extent and duration of spawning cod aggregations. A marine autonomous recording unit was deployed in the “Spring Cod Conservation Zone” (SCCZ) located in Massachusetts Bay, western Atlantic, to record cod grunts from April–June 2011. Cod grunts were present on 98.67% of the recording days ($n = 75$ days). They occurred across all 24 h, although significantly more grunts were found during the day than night-time ($p = 0.0065$). Grunt durations ranged from 57–360 ms, and the fundamental frequency and second harmonic had mean peak frequencies of 49.7 ± 5.6 and $102.9 \text{ Hz} \pm 10.9 \text{ sd}$, respectively. Cod grunt rates were low compared with those reported for other spawning fish, and may be indicative of diel movement patterns. Next steps will focus on expanding PAM coverage within the SCCZ, alongside prospecting for unknown spawning grounds within existing archival data.

Keywords: Atlantic cod, *Gadus morhua*, Gulf of Maine, passive acoustic monitoring, spawning behaviour.

Introduction

Atlantic cod (*Gadus morhua*) is a demersal predatory fish that has been targeted by both commercial and recreational fisheries for centuries (Lear, 1998). In the Northwest Atlantic, cod was heavily overfished throughout its range, resulting in a crash in several US and Canadian stocks during the early 1990s (e.g.

Serchuk and Wigley, 1992; Fogarty and Murawski, 1998; Frank *et al.*, 2011). In addition to the direct threat of overfishing, altered ecosystem dynamics may be negatively impacting cod recovery (Jackson *et al.*, 2001; Frank *et al.*, 2011). Historically, Atlantic cod was a top-tier predator, feeding upon forage fish and invertebrates, such as herring, capelin, shrimp and snow

crab (Swain and Sinclair, 2000; Jackson *et al.*, 2001; Frank *et al.*, 2011). With the large predatory fish depleted, a predator-prey reversal has occurred, whereby forage fish species have increased, potentially impacting the survival of cod eggs and fry (Swain and Sinclair, 2000; Frank *et al.*, 2011). In the Scotian Shelf ecosystem, abundances of predator and prey species appear to be reverting to pre-reversal levels (Frank *et al.*, 2011), although it remains to be seen if a similar trend occurs with cod stocks in US waters.

Additional threats to the recovery of cod stocks include a collapse in existing population structure and the disappearance of historic coastal spawning components (Ames, 2004), concurrent with the removal of reproductively active individuals. Reduction of genetic diversity in a spawning stock decreases the resiliency of the stock with respect to environmental influences, and increases the risk of recruitment failure (Begg and Marteinsdottir, 2000). There are three primary sympatric but distinct genetic groupings of Atlantic cod in US waters: the Northern Spring Complex, the Southern Complex, and Georges Bank (Kovach *et al.*, 2010). Multiple genetically distinct spawning groups can utilize the same spawning site, but vary temporally in their spawning (Howell *et al.* 2008).

Atlantic cod spawning behaviour is highly aggregated: fish gather in high concentrations in very small areas, sometimes forming vertical formations in the water column known as “spawning columns” (Rose, 1993). Cod also exhibit strong spawning site fidelity, returning to the same locations year after year (Skjæraasen *et al.* 2011). The discovery and protection of spawning aggregations is critical, as this concentrated behaviour can allow the reproductively active members of these stocks to be extracted or displaced within a relatively short time frame (Dean *et al.*, 2012). Although it is not well understood how fish localize the areas they use to spawn, aggregations that have been extirpated rarely reform in subsequent years (Ames, 2004; Dean *et al.*, 2012). This is significant because the inshore spawning components are believed to be major contributors to the overall abundance of the Gulf of Maine stock.

Animals utilize vocalizations to communicate in several contexts, including recognition of conspecifics, agonistic interactions, and reproductive behaviour (Bradbury and Vehrencamp, 1998). Despite lacking the expansive repertoires of birds and marine mammals, many fish produce sounds in the context of agonistic interactions (e.g. Brawn, 1961a; Winn, 1964; Ladich, 1997), and especially during courtship behaviours and spawning (e.g. Brawn, 1961a, 1961b; Winn, 1964; Lobel, 1992). Sound-producing fish species are known from at least 100 families, several of which are fished for recreational or commercial purposes (e.g. Rountree *et al.*, 2006; Luczkovich *et al.*, 2008; Širovič *et al.*, 2009). The cod family (Gadidae) contains several acoustically active species such as the haddock (*Melanogrammus aeglefinus*, Hawkins and Amorim, 2000), pollock (*Pollachius virens*, Hawkins and Rasmussen, 1978) and Atlantic cod (*Gadus morhua*, Brawn 1961b, 1961c).

Cod acoustic behaviour has been studied for several decades. Early work included tank experiments detailing sound production mechanisms, as well as observations of cod behaviour in agonistic interactions and reproduction (Brawn, 1961a, 1961b, 1961c). These studies showed that both sexes produce a low frequency (<500 Hz) pulsed sound, termed a “grunt”, during agonistic interactions (Brawn, 1961a), but only males do so during the spawning season (Brawn, 1961b, 1961c). During this period, males produce grunts as part of courtship displays and in agonistic

interactions with conspecific males (Brawn, 1961a, 1961b). The grunt is produced by a pair of sound-producing muscles that vibrate against the swimbladder wall (Brawn, 1961c; Rowe and Hutchings, 2004). The lack of an in-depth description of cod grunts in these earlier studies (Rountree *et al.*, 2006) prompted further work which expanded upon the reproductive behaviour of cod, as well as the acoustic properties and mechanisms of species-specific vocalizations (Fudge and Rose, 2009; Rowe and Hutchings, 2004, 2006). Rowe and Hutchings (2006) found that sound production of captive cod peaked with spawning activity; therefore, sound production has the potential to serve as a proxy for spawning activity.

Compared to other gadoid fishes, such as haddock (Hawkins and Amorim, 2000), cod have a limited vocal repertoire, using a single sound (the grunt) in multiple social contexts (Finstad and Nordeide, 2004; Rowe and Hutchings, 2006). However, recent work has described possible additional sounds in the cod repertoire: a high frequency (>2 kHz) “click” produced in the presence of potential predators (Vester *et al.*, 2004), “knocks” produced singularly in association with intraspecific interactions (Midling *et al.* 2002) and a low frequency “hum” produced during the ventral mount (Rowe and Hutchings, 2006). These results were based upon recordings conducted *ex situ*, so the presence of these sounds, with the exception of the “knocks”, in a natural setting has yet to be confirmed. Midling *et al.* (2002) also recorded knocks from wild cod in Norway, and found that the long series of knocks associated with territorial or investigative behaviour were only produced from wild individuals, not those in captivity, which led them to conclude that captivity restricts their vocal repertoire. Only two studies have recorded cod *in situ*, one in a Norwegian fjord (Nordeide and Kjellsby, 1999) and the other on a spawning ground off the coast of Newfoundland (Fudge and Rose, 2009). Grunts could not be distinguished within a low frequency “rumble” recorded in the fjord, which the authors attributed to many cod (on the order of thousands of individual fish) vocalizing simultaneously (Nordeide and Kjellsby, 1999), while only ten grunts were recorded in 18.5 hours of recordings from a single day off Newfoundland (Fudge and Rose, 2009).

Long-term studies (on the scale of weeks to months) of fish presence using passive acoustic monitoring (PAM) are increasingly being used to study their occurrence, spatial use and behaviour (e.g. Locascio and Mann, 2008; Mann *et al.* 2009; Širovič *et al.*, 2009; Nelson *et al.*, 2011; Aalbers and Sepulveda, 2012). However, to date no long-term PAM studies of cod behaviour and occurrence have been conducted in the North Atlantic region. The aims of this study were to demonstrate the utility of PAM to survey for cod in their natural habitat and establish a base line upon which to build by: (i) using PAM to survey a known cod spawning ground for cod grunts, and (ii) providing a detailed quantitative description of cod grunts recorded *in situ*.

Material and Methods

A single marine autonomous recording unit (MARU) (Calupca *et al.*, 2000) was deployed at a depth of 51.4 m within the Spring Cod Conservation Zone (SCCZ), a seasonal fishery closure area established to protect a coastal cod spawning aggregation in northern Massachusetts Bay, 5 km south of Gloucester, Massachusetts, USA. Recordings were obtained for 75 days (14 April–27 June 2011) during the spring spawning season (Dean *et al.*, 2012; Figure 1, this study). The unit recorded continuously at a sampling rate of 5000 Hz. The MARU has a flat frequency response of

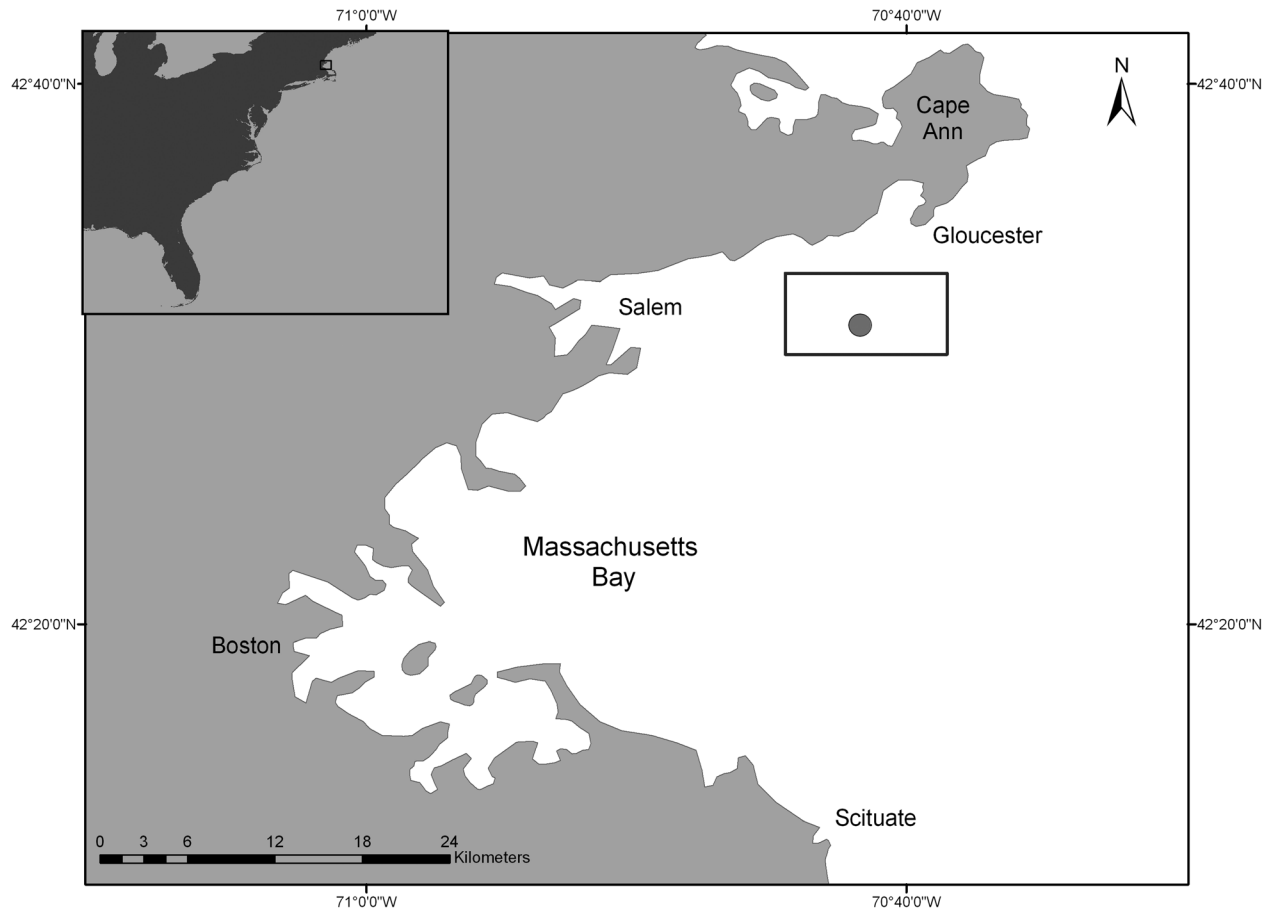


Figure 1. Map of study site region, Massachusetts Bay, Western Atlantic. Gray circle indicates the location of the marine acoustic recording unit (MARU) deployed from 14 April–27 June 2011. The black rectangle corresponds to the boundaries of the Spring Cod Conservation Zone (SCCZ).

~ 151.2 dB re 1 μ Pa (± 1 dB) across the 10–585 Hz frequency range (HTI-94-SSQ, High Tech, Inc., Gulfport, MS, USA). Spectrograms of sound files (Hann Window, FFT: 2048 points, FFT overlap: 90%, window size: 52 s) were viewed using the eXtensible Bioacoustics Tool (XBAT) (Bioacoustics Research Program, 2011b). The first ten minutes of each hour for every recording day were examined for the presence of cod grunts in order to subsample the continuous dataset. Cod were confirmed to be within the vicinity of the MARU, based on confirmed captures of cod in the vicinity of the MARU as part of a concurrent tagging study conducted by the Massachusetts Division of Marine Fisheries (D. Zemeckis, pers. obs.). Cod grunts were identified based on careful comparison of spectrograms and measurements of frequency and duration to those published in the literature (Brawn, 1961c; Hawkins and Rasmussen, 1978; Finstad and Nordeide, 2004; Rowe and Hutchings, 2006). Presence or absence of grunts in each ten-minute bin was recorded to determine broad-scale diel and seasonal trends in grunt occurrence.

The numbers of grunts present in each hour were quantified for six days across the recording period (17 and 24 April, 10 and 19 May, 8 and 15 June) and were annotated by hand to observe finer-scale trends. Grunts were grouped into four periods based on the altitude of the sun, and hourly counts were assigned to the predominant light level. Light levels (dawn, daylight, dusk, night) were based on the definitions of nautical twilight, obtained

from the US Naval Observatory Astronomical Applications website (<http://aa.usno.navy.mil>) for Gloucester, Massachusetts (42°37'N 70°40'W). All time periods are reported in Eastern Standard Time (EST). Dawn (0250–0510 h) was defined as the period when the sun's altitude was between -12 and 0° , daylight (0410–1920 h) was when the sun's altitude was $>0^\circ$, dusk (1820–2040 h) was when the sun was between 0 and -12° , and night (1930–0250 h) when the sun's altitude was $<-12^\circ$. For the purpose of the statistical tests, the light levels represented by dawn and dusk were grouped into one light regime, twilight. For these six days, differences in grunt occurrence between each light period were not normally distributed (Shapiro-Wilk test). Therefore, we used a non-parametric Kruskal-Wallis test to assess whether there were significant differences between light levels. Wilcoxon Rank-Sum tests were used for *post hoc* comparisons between individual light levels. Bonferroni corrections were applied to adjust for multiple comparisons.

Several parameters were measured to describe cod grunts quantitatively. In order to maximize the likelihood of sampling grunts from different individuals, the entire analysis period (74 days) was subsampled such that two grunts separated by at least 12 hours were chosen for analysis, for a total of 148 grunts available for analysis. When calls with a signal-to-noise ratio (SNR) <10 dB [as measured in Osprey 1.7 (Mellinger and Bradbury, 2007)] were removed, a total of 89 calls were left for analysis. Grunts

are comprised of series of rapidly produced pulses, and can appear as continuous signals with several harmonics depending on spectrogram parameters. The appearance of harmonics is directly related to the Interpulse interval (IPI) within a call. The fundamental frequency (F_0) and second harmonic were logged individually and together, so as to obtain measurements for each separately, and to determine which harmonic was of higher amplitude. Low and high frequency, bandwidth, median frequency, the first frequency quartile (the frequency at which 25% of the total energy of the sound occurs), and the peak frequency were measured for each harmonic in Osprey 1.7 (FFT: 1024 points). This software automatically computes robust measurements based on the distribution of energy in the selection box. Temporal measurements, specifically IPI, as well as the duration of each grunt and the individual pulses within a grunt, were made from the waveform using Avisoft-SASLab Pro 5.1 (Specht, 2010) and Raven Pro 1.4 (Bioacoustics Research program, 2011a), respectively. Specific call parameters measured were chosen in order to expand upon previous measurements of cod grunts as well as to compare these values to those reported in the literature [e.g. Finstad and Nordeide (2004)]. For these measurements all reported values are mean \pm standard deviation (s.d.), unless otherwise indicated.

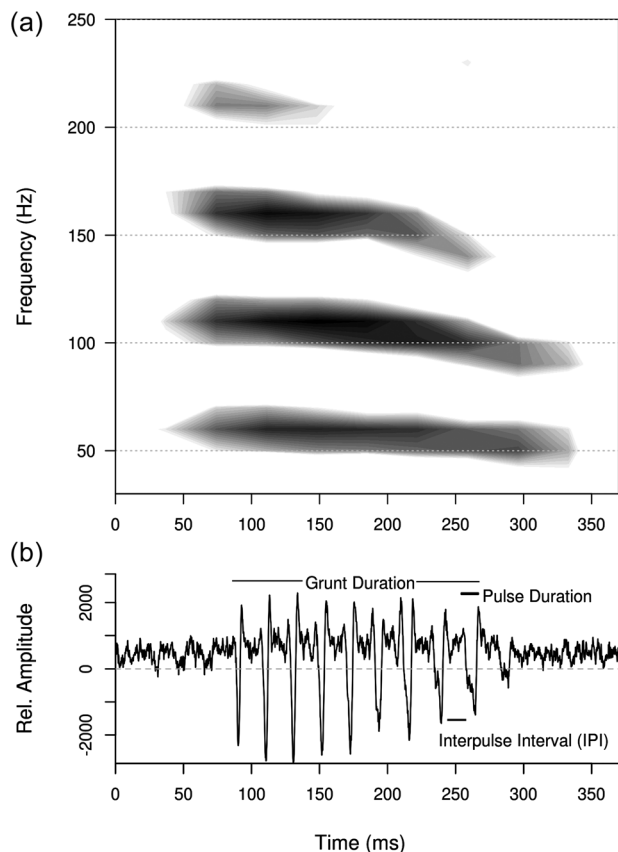


Figure 2. Spectrogram (a) and waveform (b) of an Atlantic cod (*Gadus morhua*) grunt recorded in the Spring Cod Conservation Zone (SCCZ), Massachusetts Bay, Western Atlantic (5 kHz sampling rate, 2048 FFT, Hann window). Temporal measurements that were made in this study are indicated by black bars.

Results

Cod grunts (Figure 2) were recorded on almost every day of the analysis period (98.67% of days) (Figure 3). Number of hours with cod grunts increased over the analysis period, with the highest occurrence of grunts occurring in late May to early June 2011 (Figure 3). Detections of grunts appeared to decrease towards the end of the MARU deployment, although cod were observed on the spawning ground until 1 August 2011 (D. Zemeckis, pers. obs.), one month after the unit was retrieved. Calculated rates of grunt occurrence for each month, based on six days, increased over the recording period (692 ± 9.6 s.e. (standard error) grunts day^{-1} in April, 1101 ± 3.1 s.e. grunts day^{-1} in May, 1979 ± 5.2 s.e. grunts day^{-1} in June).

Grunts were present throughout the entire 24-h period. The occurrence of grunts during the 6 days that were analysed in detail showed that grunts were most prevalent during daylight hours (79.4 ± 69.9 s.d. grunts hr^{-1}) when compared to twilight (31.7 ± 27.6 s.d. grunts hr^{-1}), and night (9.6 ± 9.6 s.d. grunts hr^{-1} , Figure 4). The difference in grunt rates between light periods was statistically significant (Kruskal-Wallis test: $\chi^2 = 11.9$, d.f. = 2, $p < 0.0025$). *Post hoc* comparisons between each light period revealed that the daylight period was significantly different from night ($p = 0.0065$). Daylight and twilight were not significantly different from one another, ($p = 0.0779$), nor were night and twilight ($p = 0.0779$).

Haddock (*Melanogrammus aeglefinus*) knocks, and humpback whale (*Megaptera novaeangliae*) vocalizations, were also occasionally recorded in the data set. However, due to the dissimilarity in call structure and careful aural analysis, there was little to no risk of mistaking either of these species' sounds for cod.

Frequency- and time-based measurements of cod grunts are summarized in Table 1. There were a mean of 5 harmonics (range, 2–8) visible across calls. Average SNR was 12.9 ± 1.8 s.d. and 12.5 ± 1.7 s.d. dB for the fundamental frequency and second harmonic, respectively. The number of pulses comprising

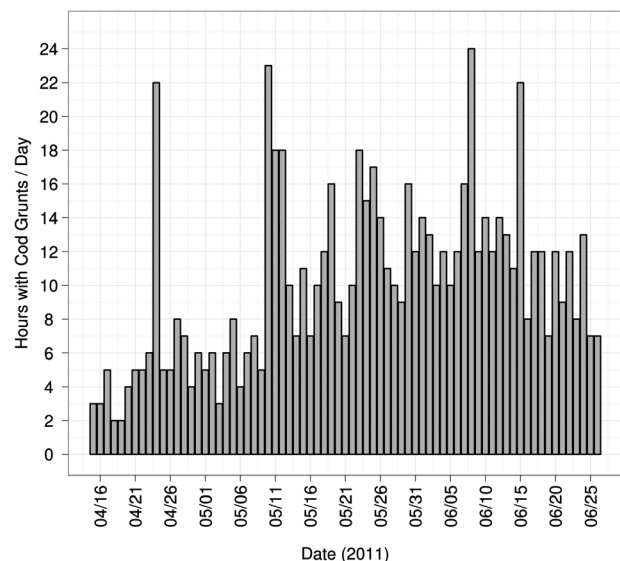


Figure 3. Graphic representation of the seasonal pattern of Atlantic cod grunts recorded in the Spring Cod Conservation Zone (SCCZ), Massachusetts Bay, Western Atlantic. The figure depicts the number of hours with cod grunts (based on analysis of the first 10 minutes of each hour) for each day of the recording period ($n = 75$ days).

each grunt varied (range, 3–18 pulses), but on average, grunts consisted of 9 ± 3 pulses (Figure 5a). Grunts lasted on average 167.6 ± 56.1 s.d. ms (range, 57–360 ms). Mean interpulse interval (IPI) within a grunt was $19.6 \text{ ms} \pm 4.8$ s.d. and ranged from 4.6–46.2 ms (Figure 5b). Individual pulse duration (8.9 ± 2.9 s.d. ms) increased steadily for sequential pulses within a call (Figure 6). Peak frequencies of the first two harmonics were bimodally distributed (Figure 5c), and had mean values of 49.7 ± 5.6 s.d. and 102.9 ± 10.9 s.d. Hz, respectively (Figure 5c).

Discussion

This study represents the first attempt at utilizing PAM to record spawning cod *in situ* over an extended period of time. Previous attempts to record cod in their natural environment were only on an opportunistic basis or for short (i.e. single day) time periods (Nordeide and Kjellsby, 1999, Fudge and Rose, 2009). Our results suggest that we acoustically captured the start of the 2011 spawning period, although we were not able to capture the

endpoint of the season. While the MARU was only deployed until the end of June, cod were observed on the spawning ground from mid-April until the beginning of August 2011 (D. Zemeckis, pers. obs.). Rowe and Hutchings (2006) found that captive cod grunted most frequently during the peak of spawning activity. Assuming this relationship between sound production and spawning is valid, it appears that peak spawning in the SCCZ occurred in late May or early June. This is in contrast to the 1 April peak spawning date used in the recent Gulf of Maine cod stock assessment (NEFSC, 2012). Future deployments will be sent out for longer periods (5–6 months) to encapsulate the entire spawning season.

In contrast to many reports of diel trends in fish sounds (e.g. Locascio and Mann, 2008), cod grunts were most prevalent during daylight hours as opposed to twilight and night-time hours. Whereas most fish species that are known to be soniferous (e.g. toadfish, *Opsanus spp.*) increase their vocal activity at night, cod in the SCCZ produced fewer grunts at night. Similarly, a captive study of the reproductive behaviour of haddock found that sound production was highest during the day and a combined dawn/dusk period, and lower at night (Hawkins and Amorim, 2000). In this study, the apparent decrease in cod grunting activity at night could be due to a diel pattern in movement away from the main daytime aggregation sites within the SCCZ, or a decrease in grunting activity at night. There is evidence based on the movement of acoustically tagged individuals to support the diel movement pattern hypothesis (M. Dean, unpublished data). Studies of spawning cod in captivity have found that vocalizations were most frequent at night, further suggesting that the observed diel pattern in vocal activity could be a function of fish movements (Brawn, 1961c; Rowe and Hutchings, 2006). Future MARU deployments consisting of multiple units over a larger geographical area, in conjunction with further tagging studies, will help to determine the movement trends in cod as well as the true spatial extent of the SCCZ spawning area.

Grunt occurrence over the analysis period was relatively low when compared to reports of other sound-producing fishes (e.g. Hawkins and Amorim, 2000; Locascio and Mann, 2008). One possible explanation for this is that there may be few males vocalizing within recording range of the MARU. Captive studies of cod reproductive behaviour have shown that there are typically a few dominant males in a spawning group that are actively defending territories from satellite males (e.g. Brawn, 1961b; Rowe and Hutchings, 2006). While most males can grunt, regardless of dominance rank, it is likely that the majority of grunts could be

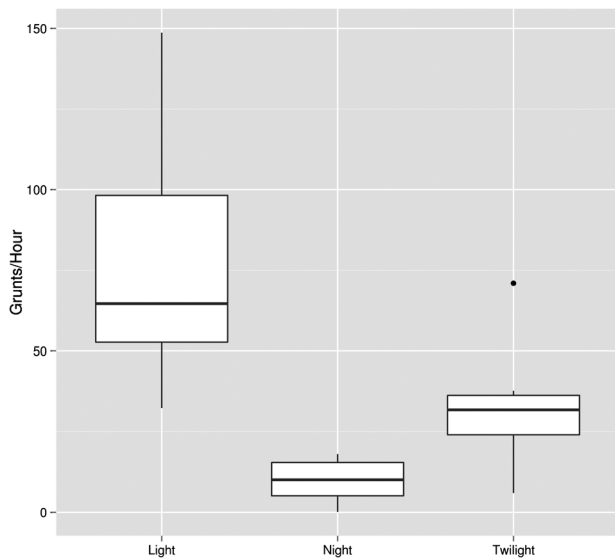


Figure 4. Box-and-whisker plot of the diel occurrence of Atlantic cod (*Gadus morhua*) grunts per hour for each light period ($n = 6$ days). Lower and upper bounds of boxes represent lower and upper quartiles, respectively. Solid lines represent medians. Whiskers represent the furthest data points within 1.56 interquartile range (IQR) of the lower and higher quartile, respectively. Dots are outliers.

Table 1. Measurements of the first and second harmonics of Atlantic cod grunts ($n = 89$) recorded during the spring spawning period in the Spring Cod Conservation Zone (SCCZ), Massachusetts Bay, Western Atlantic.

Harmonic		LF	HF	DUR	BW	MF	1.FQ	PF	SNR
First	Mean	38.9	60.1	6.8	21.1	47.5	5.8	49.7	12.9
	s.d.	5.8	6.9	1.9	5.3	5.3	1.0	5.6	1.8
	Min	26.9	46.4	3.0	14.7	36.1	3.7	39.1	10.0
	Max	51.3	95.2	14.0	53.7	57.8	9.9	58.6	18.2
Second	Mean	89.5	114.9	6.9	25.5	99.8	7.0	102.9	12.5
	s.d.	10.1	10.6	1.9	5.7	10.5	1.3	10.9	1.7
	Min	70.8	90.3	3.0	19.5	75.4	4.6	78.1	10.1
	Max	109.9	144.0	13.0	48.8	120.4	12.4	122.1	17.5

LF = Low Frequency, HF = High Frequency, DUR = Duration, BW = Bandwidth, MF = Median Frequency, 1.FQ = 1st Frequency Quartile (the frequency at which 25% of the total energy of the sound occurs), PF = Peak Frequency. Frequency parameters are in units of Hertz (Hz), time parameters in units of milliseconds (ms), and SNR in units of decibels (dB).

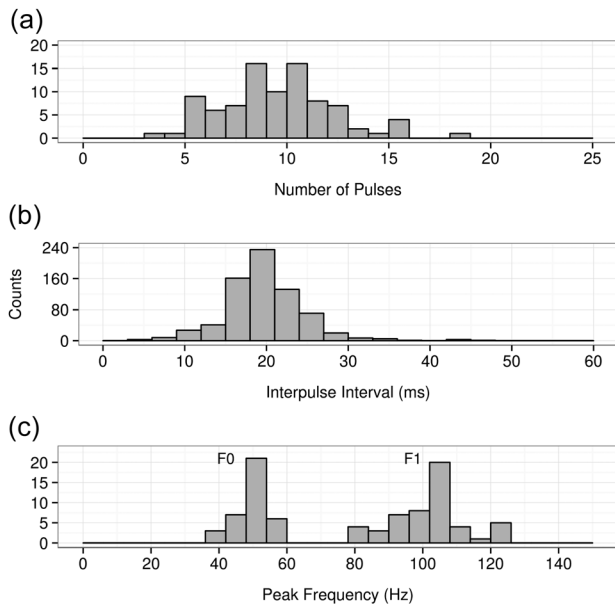


Figure 5. Histograms of Atlantic cod (*Gadus morhua*) grunt characteristics recorded in the Spring Cod Conservation Zone (SCCZ), Massachusetts Bay, Western Atlantic: a) number of pulses counted in each grunt ($n = 89$, binwidth = 1), b) interpulse interval (IPI), in ms ($n = 715$ [89 grunts], binwidth = 3 ms), and c) distribution of peak frequencies (Hz) when the first (F0) and second (F1) harmonics of each grunt were measured together ($n = 89$, binwidth = 6 Hz).

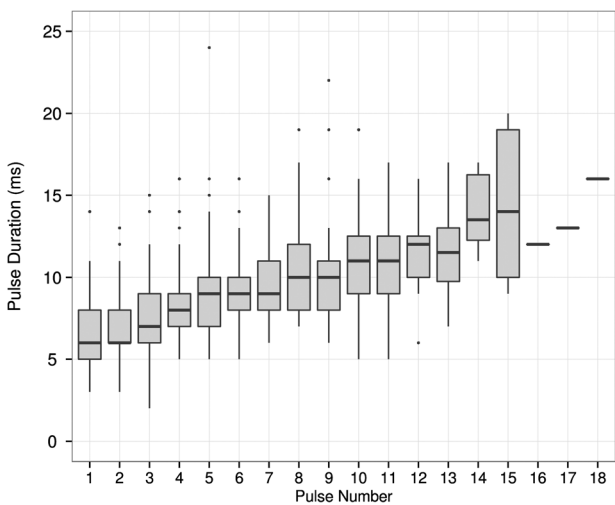


Figure 6. Box-and-whisker plot of Atlantic cod (*Gadus morhua*) pulse durations from grunts recorded in the Spring Cod Conservation Zone (SCCZ), Massachusetts Bay, Western Atlantic. Measurements are ordered sequentially by pulse occurrence within a grunt ($n = 805$ [89 grunts]). Lower and upper bounds of boxes represent lower and upper quartiles, respectively. Solid lines represent medians. Whiskers represent the furthest data points within 1.56 interquartile range (IQR) of the lower and higher quartile, respectively. Dots are outliers.

attributed to the few dominant males in the aggregation. Also, if dominant males are dispersed over a wide area, it is possible that males defending territories further away from the MARU are near the edge, or out, of recording range of the unit, and their

grunts would not be represented in the recordings. Future deployments of multiple MARUs over a larger geographical area will help to determine the spatial extent of the SCCZ spawning aggregation, while deployment of underwater cameras could provide insight into the social structure of the aggregation.

Additional sound types attributed to cod in captivity were not recorded during this deployment. We would not have expected to record clicks, as the frequency (5.95 ± 2.2 kHz, Vester *et al.*, 2004) is above the range of sounds recorded by the MARU at the set sampling rate. While it may have been possible to record hums, the association between the production of this sound with ventral mounts (Rowe and Hutchings, 2006) could explain why they did not appear in the recordings. The ventral mount, when the act of spawning and gamete release occurs in a mating pair, has been observed primarily in the water column based on tank studies (e.g. Brawn, 1961b; Rowe and Hutchings, 2006). However, since these behaviours have yet to be observed *in situ*, we cannot be sure to what depth in the water column a mating pair travels when participating in courtship and spawning. If mating occurs higher in the water column, hums could be out of range of our receivers, which were just 2 m above the seafloor. Longer-term recordings over multiple seasons with a higher bandwidth could potentially confirm the full vocal repertoire of cod.

Measurements of cod grunts are consistent with values reported in the literature. The first measurements of cod grunts reported a peak frequency of 50 Hz and a duration of around 200 ms (Brawn, 1961c). Finstad and Nordeide (2004) measured grunts from wild-caught cod near Norway with a mean frequency of 49.7 Hz and a mean duration of 215 ms. In comparison, cod grunts recorded in the SCCZ in this study had a peak fundamental frequency of 49.7 Hz and a duration of 167.6 ms. When the fundamental and second harmonics were measured together, a bimodal distribution of peak frequencies was apparent (Figure 5c) such that in some cases the peak was the fundamental frequency, while in other cases it was the second harmonic (Figure 5c). A similar trend was observed in the “boatwhistle” calls of Lusitanian toadfish in Portugal, where the second and fourth harmonics were the dominant frequencies of the call (Amorim *et al.*, 2006). Another interesting aspect of the grunt measurements was the increase in pulse duration over the length of the grunt. Hawkins and Rasmussen (1978) reported “degradation” in the grunt from captive cod in the UK, and similar findings were reported by Finstad and Nordeide (2004) for cod recorded in Norway. Locascio and Mann (2011) observed a similar occurrence with the sounds of black drum (*Pogonias cromis*) in Florida. They attributed this to fatigue of the muscles responsible for sound production. Further studies of the sound production mechanism in cod could provide insight into the source of this acoustic feature.

Cod grunts are likely to be masked by anthropogenic sound sources, especially in coastal areas with high human use, such as the SCCZ and surrounding waters. Studies of cod hearing, both in the laboratory and in the field indicate that cod can detect sounds with frequencies up to 500 Hz (e.g. Chapman and Hawkins, 1973; Sand and Karlsen, 1986; Astrup and Møhl, 1993). As cod grunts fall within the same frequency range as many anthropogenic sound sources, it is likely that communication between conspecifics will be hindered in areas of high background noise (Hawkins and Chapman, 1975; Hatch *et al.*, 2008). Since it is believed that the grunts can function as both a reproductive advertisement to females and an aggressive display towards competitors (e.g. Brawn, 1961a; Rowe and Hutchings,

2004), the loss of the ability to detect sound, even if it is for a temporary period of time, could greatly disrupt cod spawning behaviour and reproductive success. In the future, it would be valuable to determine the source level (SL) of the cod grunt to accurately determine its vulnerability to acoustic masking from background noise. Furthermore, knowledge of grunt SL would allow the estimation of a detection radius of autonomous recorders for this species-specific signal and enable further PAM efforts to be conducted at scales that are meaningful to this species.

Future efforts to study the acoustic behaviour of fish *in situ* could utilize and improve upon the methods described in this paper to inform management and conservation. One of the benefits of using passive acoustic monitoring to study marine vertebrates is the acquisition of large datasets; however, these large datasets are difficult to analyse efficiently without automated detectors (Van Parijs *et al.*, 2009). Future studies would benefit from the development of automated detectors to more efficiently subsample data for analysis. Another improvement to the methodologies presented in this study would be to expand the scope of the recordings in terms of location, duration and sampling rate of the recorders. As mentioned elsewhere in the paper, expanding the recordings over a longer time frame and wider area would provide additional insight into the extent of the cod spawning ground, and how long cod remain in the area. Increasing the sampling rate of the recorders would also allow additional sounds in the cod repertoire to be recorded if they were present. To apply the findings of studies such as this to the management and conservation of fish stocks, it is necessary to use calling rates as a proxy to estimate abundance in spawning grounds. Recent approaches focus on deriving estimates of abundance from terrestrial animals and marine mammal calls (Marques *et al.*, 2012). These methods need to be applied to calling fish to evaluate their potential for deriving abundance estimates for a given stock. Abundance estimates derived from passive acoustic data could then be used in tandem with or as a supplement to traditional stock estimates for fish species such as Atlantic cod.

In conclusion, this study has shown that PAM is a feasible method for studying cod spawning aggregations *in situ*. The next step for PAM is three-fold: to further explore the spatial extent and persistence of known aggregations, to prospect existing PAM data in Massachusetts waters and the greater Gulf of Maine area to locate additional spawning aggregations, and to investigate whether grunt rate can be used to formulate an index of relative cod abundance.

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