Nocturnal patterns in fsh chorusing off the coasts of Georgia and eastern Florida

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research paper

Nocturnal patterns in fish chorusing off the coasts of Georgia and eastern Florida

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ABSTRACT.—Fish chorusing is a major component of the marine acoustic environment, and much of this chorusing activity happens at night. These nocturnal sounds are commonly associated with reproductive behavior. For many co-occurring taxa, increases in vocal activity may intensify acoustic competition within a constrained signaling environment; for nocturnal species, there is a limited time window for these critical behaviors, and competition to be heard by conspecifics likely increases. Using passive acoustic recording units deployed in the nearshore waters off Georgia and eastern Florida, we evaluated the nocturnal acoustic habits of fishes and examined how the sounds from nocturnal fish chorusing contribute to the overall soundscape. We examined long-term spectrograms for spatial and temporal patterns of fish calling. Black drum [*Pogonias cromis* (Linnaeus, 1766)] and toadfish (*Opsanus* sp.) dominated the nocturnal acoustic scene, but calls of other identified [e.g., red drum, *Sciaenops ocellatus* (Linnaeus, 1766); silver perch, *Bairdiella chrysoura* (Lacépède, 1802)] and unidentified calling species also occur. We examined the acoustic indices of entropy, acoustic diversity, and acoustic complexity to compare nocturnal and diurnal fish calling activity across the region. When sustained fish chorusing activity increases, entropy and acoustic diversity decrease, but acoustic complexity increases. With the acoustic differences in composition of nocturnally- and diurnally-active species groups, there is a different nocturnal soundscape than during the day. Passive acoustic surveys represent an exciting approach to understand the nocturnal reproductive activity of coastal fishes.

Fish sounds are a major component of the marine acoustic environment. An increasing number of long-term acoustic surveys have revealed the prevalence of fish calling activity in aquatic acoustic environments around the world (e.g., Cato 1976, 1978, 1992, D'Spain and Batchelor 2006, Locascio and Mann 2008, Parsons et al. 2013, Guan et al. 2015). These sounds are primarily produced in reproductive or agonistic behavioral contexts (Bass and Rice 2010). When three or more animals have calls that overlap or are produced in rapid succession, this pattern of vocalizing

is referred to as a chorus (Greenfield and Shaw 1983). Similar to choruses in other vertebrate and invertebrate taxa (Gerhardt and Huber 2002), the broader pattern of fish reproductive chorusing is often sustained in duration (over minutes to hours) as groups of males advertise to females and/or defend territories.

Many fish behaviors have strong diel cycles (Helfman 1986), and acoustic communication follows a similar trend (e.g., Ruppé et al. 2015). The exact reasons for diel behavioral partitioning is unclear, but has been hypothesized to be influenced by foraging opportunities or predator avoidance (Helfman 1986). As a result, fish acoustic communities may sort into diurnal, crepuscular, or nocturnal acoustic calling patterns, concentrating their calling during one particular time of day (Ruppé et al. 2015). These diurnal and nocturnal calling patterns thus create different soundscapes at different times of the day for the same location (Locascio and Mann 2011a, McIver et al. 2014, Staaterman et al. 2014).

Night is an important time period for reproductive activity for many fish species. Helfman (1986) suggested that nocturnal spawning in fishes may be quite common, but is often understudied, given how difficult it is to collect data through visual observations. As acoustic communication may play a critical role in mate attraction and reproductive success in many fish species (Bass and Rice 2010), passive acoustic recordings may serve as a useful observation method to understand the nocturnal acoustic and reproductive behaviors of fishes. Given the relatively limited amount of nocturnal behavioral and ecological data available for most fish species (such as feeding rates, movement, reproductive behavior, and habitat preferences), passive acoustic surveys offer the opportunity to explore how nocturnal reproductive behavior and chorusing varies geographically and seasonally.

For the present study, we conducted continuous, fixed-sensor passive acoustic surveys at five sites off Georgia and eastern Florida over an approximately 6-mo period to examine nocturnal patterns of fish sound production at seasonal and geographical scales. We used a combination of spectrographic analysis of the acoustic data combined with acoustic indices to explore diel trends in the marine acoustic environment. Black drum [*Pogonias cromis* (Linnaeus, 1766)] are a dominant acoustic fish species in this area (Soldevilla et al. 2014, Rice et al. 2016) and they call predominantly at night (Locascio and Mann 2011a); therefore, we predicted that their calling activity would strongly influence acoustic measurements across the entire region.

Methods

Acoustic data were collected and analyzed from mid-November 2012 through mid-April 2013 using marine autonomous recording units (MARUs; Calupca et al. 2000) deployed at five locations off the Georgia and eastern Florida coasts at depths of 13.7–17.3 m (Fig. 1, Table 1). These data were collected as part of two independent, but temporally-overlapping, passive acoustic studies. The three Georgia units were part of a baseline assessment survey for whale and fish bioacoustic activity in a Bureau of Ocean Energy Management (BOEM) wind planning area (Hodge et al. 2015), and the two Florida units are part of an ongoing passive acoustic survey for North Atlantic right whales (Soldevilla et al. 2014). MARUs were programmed to continuously record at a 2000 Hz sampling rate (providing a 0–1000 Hz frequency bandwidth in the recordings). Units were programmed with a 10 Hz high-pass filter to reduce electrical system noise, and an 800 Hz low-pass filter to reduce aliasing,
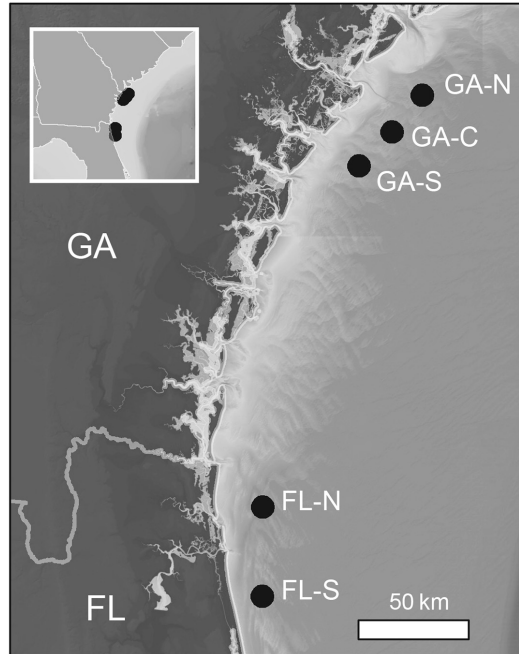
Figure 1. Map of recording locations showing positions of the marine autonomous recording units. Map inset shows recording unit locations in the context of the South Atlantic Bight.

with a roll-off of 22 dB per octave between 800–1000 Hz. The system sensitivity (mean and SE in parenthesis) for each unit was –152 (3) dB re: 1 V/μPa. Recording units were equipped with temperature-sensitive data loggers (Hobo Pro v2, Onset, Bourne, MA), which recorded temperature readings every 15 min. There were 140 d of concurrent recording effort available at each of the five sites (November 25, 2012– April 13, 2013). We evaluated two analytical methods to rapidly analyze diel patterns in the soundscape from this large data set: long-term spectrographic analysis and acoustic indices.

Long-term Spectrographic Analysis.—Most bioacoustic analysis relies on spectrograms (representation of the sound magnitude as frequency vs time) to detect individual calls that are typically on the order of seconds to minutes. Analyzing acoustic data from long-term surveys becomes very time consuming, often requires subsampling (Thomisch et al. 2015), and fine-scale analysis of spectrograms or listening to the data are not the best approach for looking at large scale changes over extended deployments at multiple locations (Sueur et al. 2012). An alternative method is to examine long-term patterns of acoustic activity that represent many months

Table 1. Location and depth of marine autonomous recording units used in the present study.

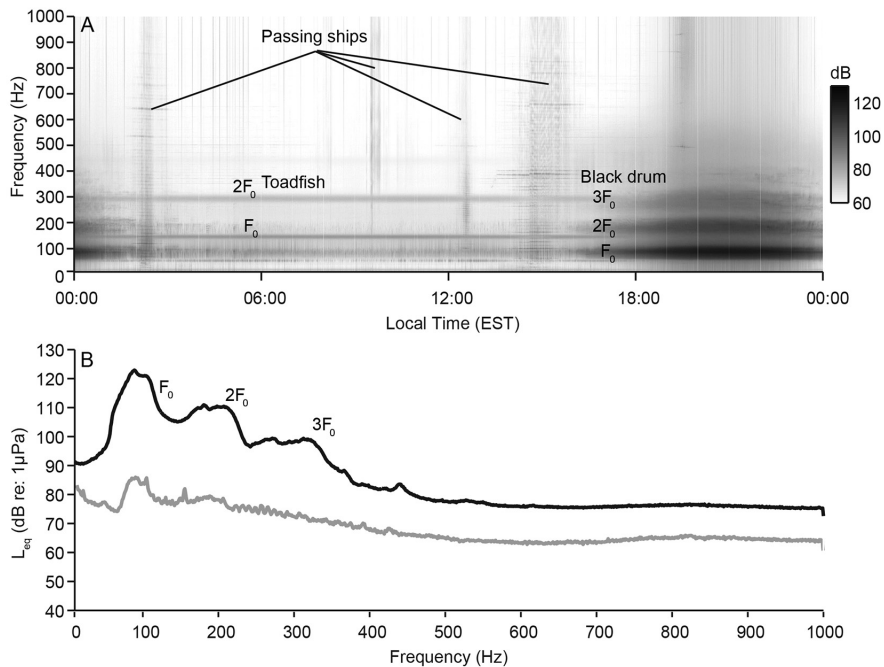| Unit	Latitude (°)	Longitude (°)	Depth (m)
Georgia North (GA-N)	31.992°N	80.597°W	14.9
Georgia Central (GA-C)	31.864°N	80.721°W	14.0
Georgia South (GA-S)	31.746°N	80.854°W	13.7
Florida North (FL-N)	30.553°N	81.247°W	15.8
Florida South (FL-S)	30.239°N	81.250°W	17.3

Figure 2. (A) A 24-hr spectrogram from 7 April on FL-N. The black drum and toadfish choruses are clearly visible. The fundamental frequency, and upper harmonics are labeled (F_0, $2F_0$, $3F_0$, respectively). The scale bar indicates the sound level in dB (re: 1 μPa). (B) Equivalent sound levels (L_{eq}) from day (gray, 10:00–15:00 hrs) and night (black, 18:00–24:00 hrs) periods from 24-hr spectrogram in (A) showing nocturnal differences in sound level. The black drum harmonic peaks from (corresponding to panel A) are labeled, but the toadfish harmonics are not readily visible.

of sound in a single image. These long-term spectrograms (or long-term spectral averages, LTSAs) are created by integrating slices of a specified time interval throughout the recording and they show diel or seasonal patterns of acoustic activity that often cannot be seen at finer time scales. Using the SEDNA and Triton software packages for MATLAB (Wiggins et al. 2010, Dugan et al. 2011), we created LTSAs encompassing the entire survey period for each site to evaluate the occurrence of fish chorusing activity. Spectrograms were created with the *pwelch* algorithm in 1 Hz bins and 10.24 s time slices, a Fast Fourier Transform (FFT) size of 512 points and a 1-hr integration time. With these representations, it is possible to see diel and seasonal trends in biological, anthropogenic and environmental acoustic activity at the ecosystem scale.

We evaluated the LTSAs to determine when energy increases in frequency bands were associated with different call types. Upon initial examination of the data, it became clear that the seasonal chorusing of black drum was one of the dominant sounds occurring on all sensors. Black drum produce a distinctive, low-frequency, high-amplitude call that can be heard in marine and estuarine habitats across the US Atlantic and Gulf of Mexico coasts (Mok and Gilmore 1983, Locascio and Mann 2011b, Tellechea et al. 2011), which has a fundamental frequency of approximately 70–90 Hz and a duration of approximately 0.2 s. Black drum form spawning aggregations and chorus for extended periods throughout the evening. In a LTSA, this

chorusing activity is evident as increased energy in the 60–100, 120–200, and 250–350 frequency bands (Fig. 2). The diel periodicity of chorusing can clearly be seen by identifying high acoustic energy periods in LTSAs that are 24 hrs or longer in duration (Fig. 2B). Similarly, it is possible to determine consistent diel patterns associated with other frequencies from unknown call types, many of which are likely produced by other sciaenids (Luczkovich et al. 2008). To visually confirm the daily patterns of chorusing activity, data were reviewed as 24-hr spectrograms in Raven Pro 1.5 software (Bioacoustics Research Program 2015).

Acoustic Indices.—To complement the spectrographic analysis, we also analyzed the data using several different acoustic indices, a relatively new approach to quantify changes in the acoustic environment over time and space (Pijanowski et al. 2011, Sueur et al. 2014). Acoustic indices attempt to represent highly complex acoustic data as a single value to examine different levels of biological or anthropogenic acoustic activity as a function of temporal or geographic variability (Sueur et al. 2014). These indices are conceptually similar to biodiversity indices, which quantitatively represent biodiversity measurements (e.g., species diversity or species richness) as univariate data (Sueur et al. 2008), and provide a way to distill large, complex data sets that vary over space and time. Currently, more than 30 acoustic indices have been developed (reviewed in Sueur et al. 2014), which represent various features of acoustic energy in time and frequency bins, and quantify them for regular time intervals across the entire recording. Acoustic indices have primarily been applied in terrestrial habitats (Sueur et al. 2008, Farina et al. 2011, Pijanowski et al. 2011, Farina and Pieretti 2014, Fuller et al. 2015), but are starting to be applied in marine environments (Parks et al. 2014, Kaplan et al. 2015, Harris et al. 2016). While many acoustic indices have been developed, only some indices are appropriate for a given data set (Sueur et al. 2014).

For our analysis, we used three different acoustic indices to explore trends in bioacoustic activity: Acoustic Entropy, the Acoustic Diversity Index, and the Acoustic Complexity Index. Acoustic Entropy (H; Sueur et al. 2008) measures the amount of entropy (noise) in the acoustic signal, where biological sounds have lower entropy (less noise), whereas environmental and anthropogenic noises have a higher level of entropy (more noise). The Acoustic Diversity Index (ADI; Pijanowski et al. 2011; Villanueva-Rivera et al. 2011) uses the Shannon Diversity Index (a statistical index often used in biodiversity surveys) to measure proportion of samples in 200-Hz wide frequency bins; the higher the diversity index, the greater variety of energy in frequency bands. The Acoustic Complexity Index (ACI; Pieretti et al. 2011) compares the sound levels in different, short-duration frequency bins, and biologically-relevant temporal and spectral scales. Several recent studies have examined the efficacy of these acoustic indices (McWilliam and Hawkins 2013, Lillis et al. 2014, Parks et al. 2014, Kaplan et al. 2015, Butler et al. 2016, Harris et al. 2016), but these studies did not explicitly examine diel changes in soundscape composition. Harris et al. (2016) found that ACI and H are more resilient against the influence of anthropogenic and wind-driven noise.

Acoustic indices were calculated using the soundecology 1.3.2 software package (Villanueva-Rivera and Pijanowski 2016) implemented in R (R Core Team 2016). To calculate H, calculations were made from 15-min bins using a 512 point FFT with 3.9 Hz and 0.256 s resolution, an amplitude threshold of –50 dB, 200-Hz frequency

bands, and the Hilbert transformation to measure the amplitude envelope. For ADI, calculations were made with a 200-Hz resolution, and −50 dB threshold, above which the proportion of samples in each frequency bin was calculated. The Shannon index and the Gini index were applied to these bin proportions to obtain ADI (e.g., Villanueva-Rivera et al. 2011). For ACI, calculations were made with an FFT of 512 points, and a cluster size of 60 s. The resulting values were divided by the number of minutes in the recording to reduce the effects of long-duration recordings (e.g., Villanueva-Rivera et al. 2011). Index results (one index measurement for every 15 min) were averaged for each hour of the day over the recording period for each sensor, yielding a total of 70,927 measurements for each index.

For each site and 15-min recording, sound files (n = 70,927) were classified by day, night, dawn, and dusk using daily location-specific astronomical data from the US Naval Observatory data portal (http://aa.usno.navy.mil/). "Dawn" was defined as the time interval between the start of civil twilight and sunrise; "day" was defined as the time interval between sunrise and sunset; "dusk" was defined as the time interval between sunset and the end of civil twilight; and "night" was defined as the time between the end of civil twilight on one day and the start of civil twilight on the next. Differences between index values and diel category for each site were analyzed with a two-way ANOVA with interaction, and a posteriori with a Tukey's HSD multiple comparisons test to examine differences between time of day and sites (JMP 12, SAS, Inc., Cary, NC).

Results

Long-term Spectrograms.—An examination of LTSAs spanning the entire survey period showed that all five recording locations exhibited considerable amount of diversity in their respective acoustic environments (Fig. 3). In many cases, intermittent broadband noise (appearing as short- and medium-duration vertical bands) was the result of passing ships and weather events. Weather events were typically multiple-hour long events and consistent across multiple sites, while ship noise was generally shorter in duration and not uniform across recording locations.

In addition to these abiotic and anthropogenic sources, numerous biological sound sources were apparent. Starting at the beginning of January in the FL-S unit (Fig. 3E), the seasonal chorus of black drum began, and continued through the nights over the remainder of the survey period, occasionally becoming more intense. The black drum chorus followed a regular nocturnal pattern, as the fish called for 4−8 hrs each night (Figs. 2B, 4A). These chorusing events were the dominant sound source in the 75−200 Hz frequency band, with the harmonic content visible in the upper three quartiles of acoustic energy within the spectrum (Fig. 4B). This geographical comparison of long-term spectrograms showed the temporal variation in the seasonal onset of reproductive activity for black drum populations.

While black drum were the most obvious acoustic sound sources at this temporal scale, there were other fish (both identified and unidentified species) calling at these locations. Toadfish (*Opsanus* sp.) choruses were visible (as near-horizontal lines, with a fundamental frequency of approximately 200 Hz). The toadfish chorus began in early/mid-March on FL-N (Figs. 3D, 5A) and early April on GA-N (Figs. 3A, 5A). Chorusing sounds from red drum [*Sciaenops ocellatus* (Linnaeus, 1766)] were
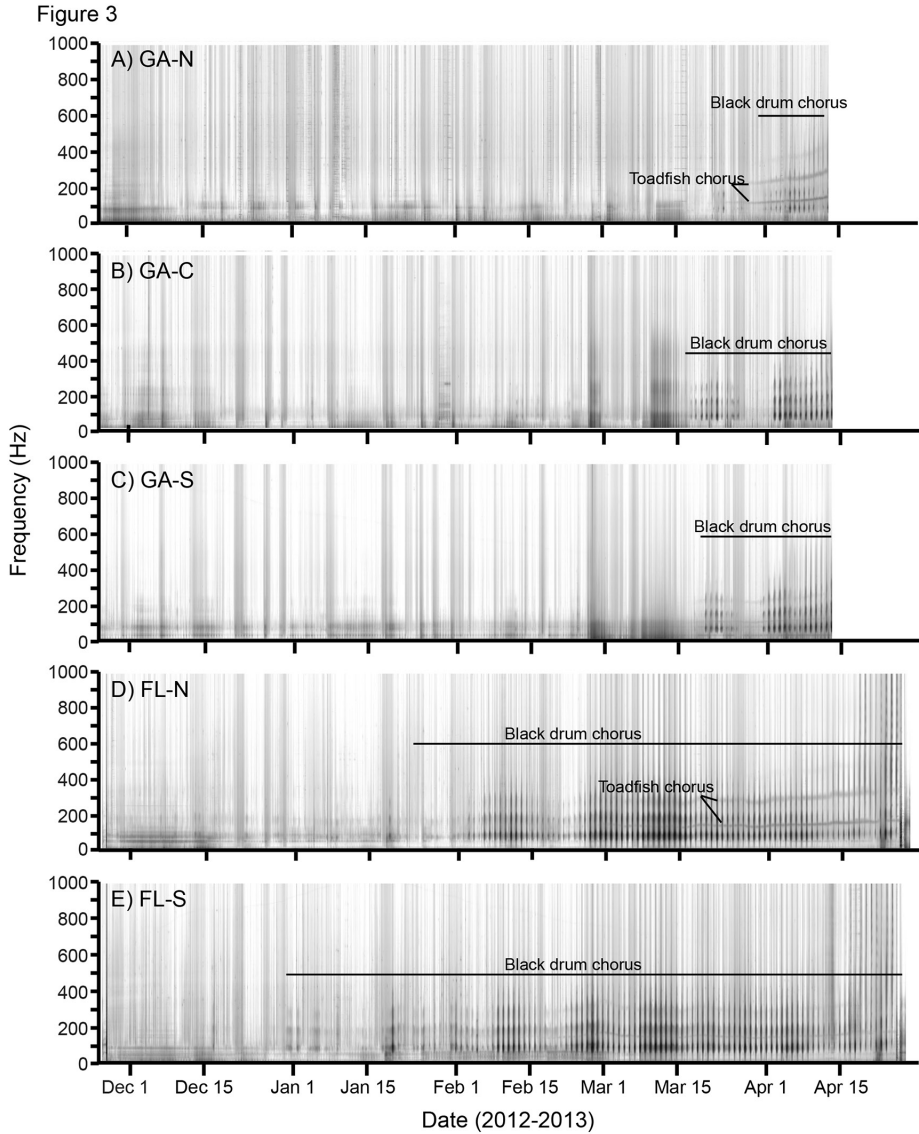
Figure 3

Figure 3. Spectrograms from passive acoustic survey at five locations in the South Atlantic Bight, recorded between November 2012 and April 2013: (A) GA-N, (B) GA-C, (C) GA-S, (D) FL-N, (E) FL-S. Where present, black drum and toadfish choruses are labeled on the spectrograms.

evident in short-term spectrograms during January and February at the FL sites (Fig. 6), but were not apparent in long-term spectrograms (Fig. 3).

Black drum aggregations started chorusing at FL-N first, starting on November 28, 2012, with intermittent breaks through January and February, then called through the remainder of the survey until April 15, 2013 (Fig. 5A). Drum at FL-S chorused for a single day on 16 December, 2012, and then started their seasonal calling on 30 December, 2012 (with a few gaps in the first half of January), through 15 April, 2013. The three Georgia sites were more similar in their chorusing timeline with a start in mid-March (GA-N: March 21, GA-C: March 18, GA-S: March 19). Drum at the three GA sites stopped their chorusing between March 26 and March 31, and
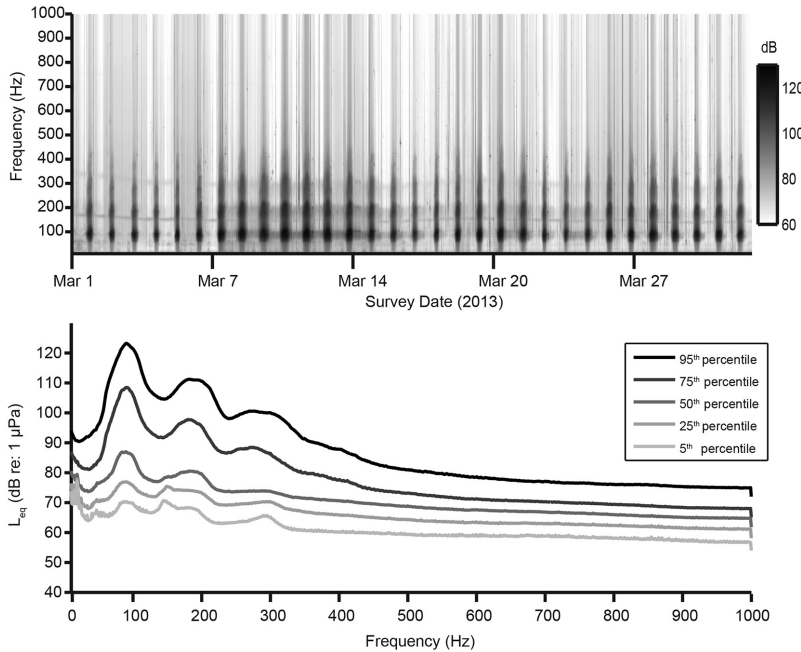
Figure 4. (A) Long-term averaged spectrogram of acoustic data from March 1 to 30, recorded at FL-S, showing nocturnal chorusing of black drum. (B) Corresponding equivalent sound levels (L_{eq}) showing the distribution acoustic energy as statistical percentiles (indicated in legend).
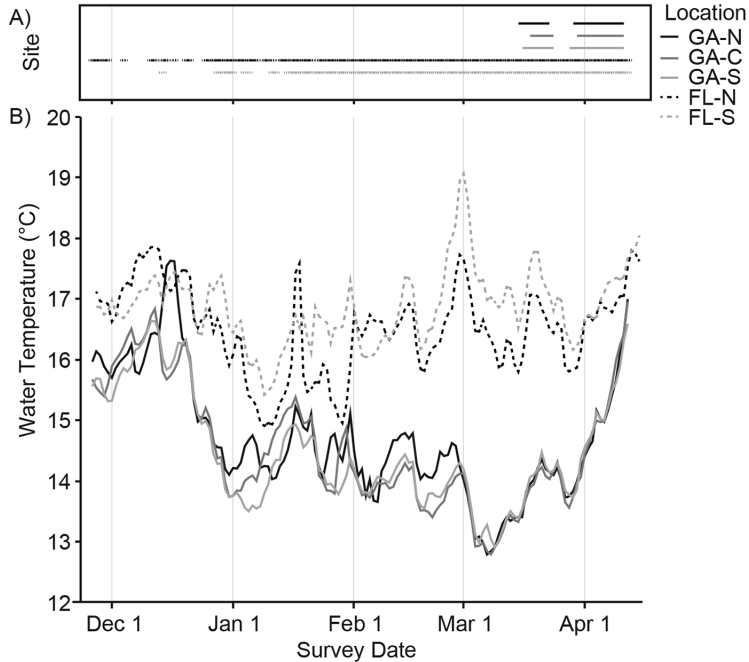

Figure 5. Seasonal site-specific variation in black drum nocturnal chorusing activity and water temperature. (A) Nightly occurrence of black drum chorusing events, and (B) mean sea-floor daily water temperature (°C) recorded on the MARU. Gray vertical lines in both panels indicate beginning of each month of data collection.
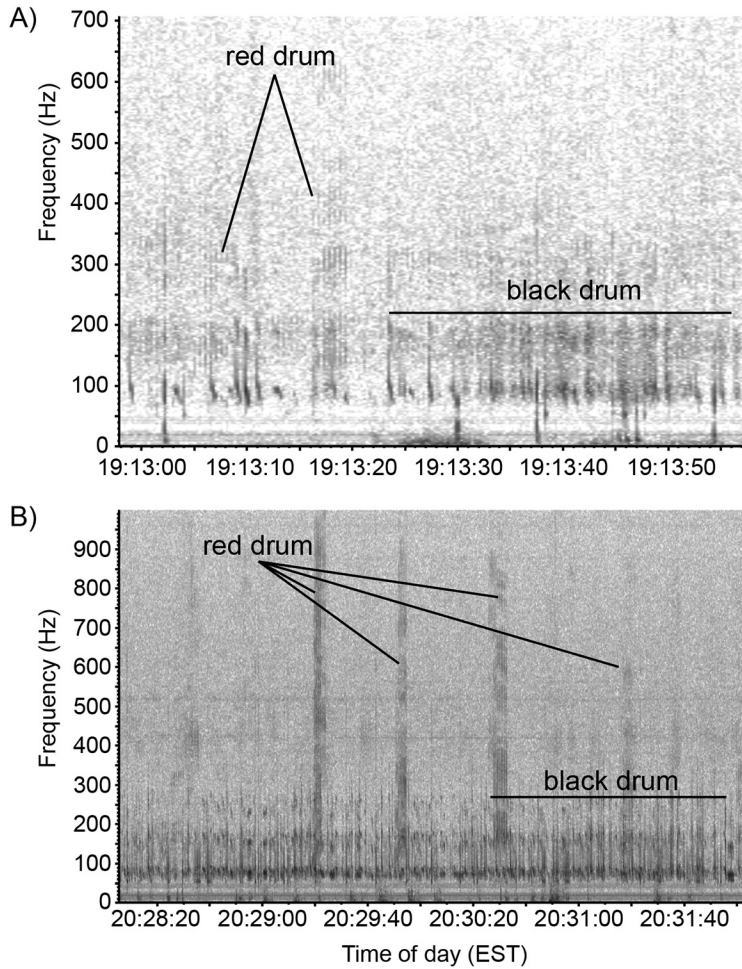
Figure 6. Spectrograms showing examples of red drum chorus overlapping with black drum chorus, from the FN-N site: (A) recorded December 22, 2012, at 19:13 EST; (B) recorded January 20, 2012, at 20:28 EST. Spectrograms were created in Raven Pro 1.5, with a Fast Fourier Transform (FFT) size = 1024 points and 75% overlap. Note different frequency and time scales between panels (A) and (B).

then resumed from April 1 to 12. Water temperature was consistently higher at the Florida sites compared to Georgia throughout this winter (Fig. 5B). There was a statistically significant association between the occurrence of drum chorusing and water temperature across all five sites (binary logistic regression: df = 1, χ^2 = 202.5633, $P < 0.0001$). The gap in chorusing for the Georgia units in late March (Fig. 5A) coincided with a cold-water pulse during that same time period (Fig. 5B).

ACOUSTIC INDICES.—The acoustic indices all showed diel variability, with varying degrees of diel change at the different locations. Acoustic Entropy (H) values were highest at the GA-C and FL-N sites, and lowest at the GA-S and FL-S sites (Fig. 7). The strongest decrease in entropy at night occurred at the FL-N site (between 16:00 and 4:00 hrs), while GA-C showed a less dramatic decrease in entropy at night than during the day. GA-S showed an increase in entropy between 00:00 and 07:00
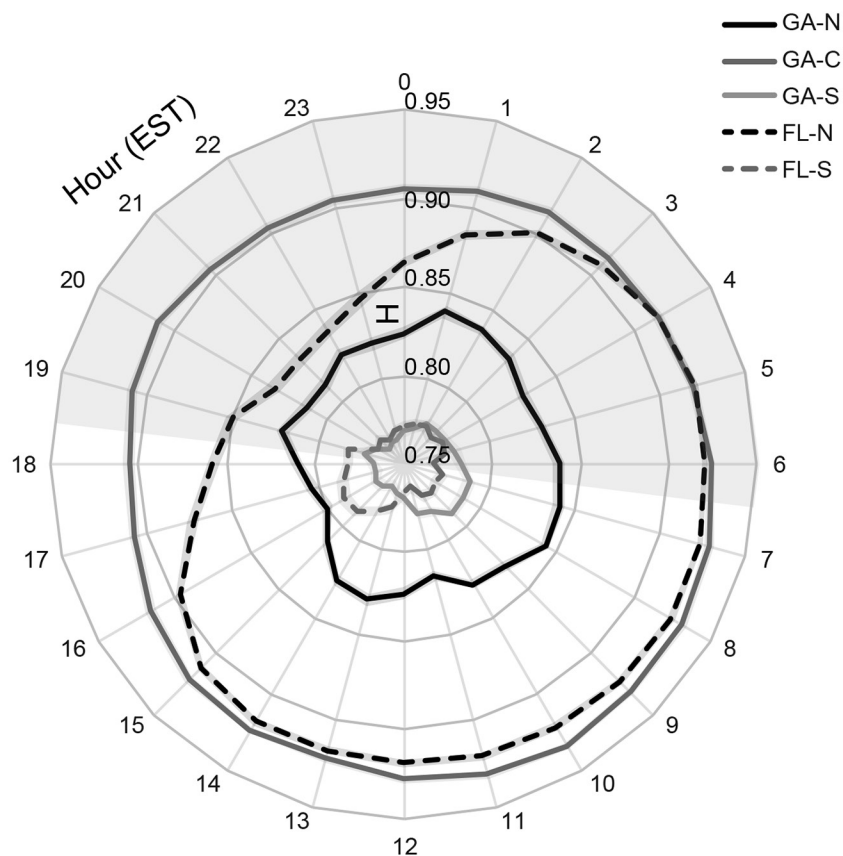
Figure 7. Circular graph of Acoustic Entropy (H) (mean ± SE) vs hour of the day for each of the recording site over the entire survey period. Radial axis represents H, and circumference axis represents time. Gray shading in background indicates the night time period across the survey.
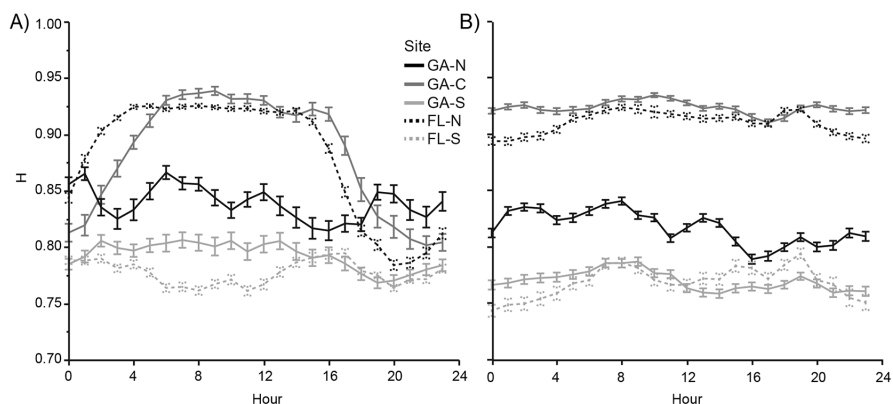

Figure 8. Acoustic Entropy (H) (mean and SE) vs hour of the day for time periods (A) with black drum chorusing and (B) no black drum chorusing at each of the recording sites.
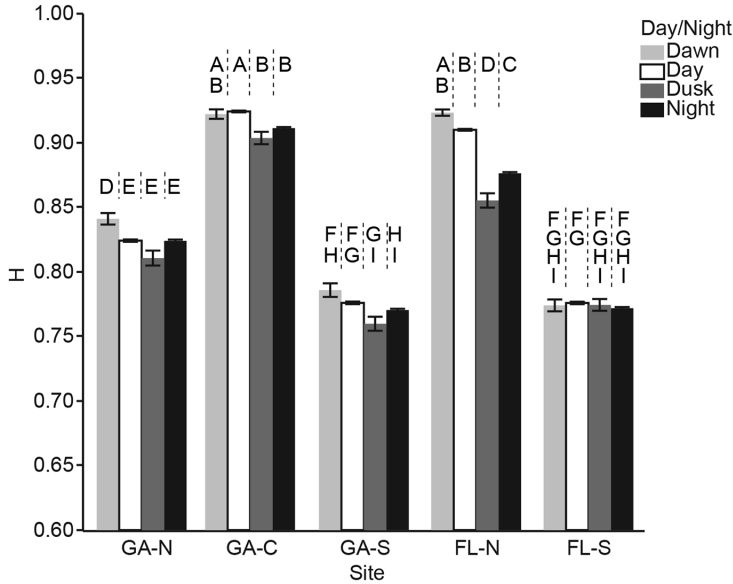
Figure 9. Acoustic Entropy (H) during day (gray) (mean and SE) versus night (black) for all sites. Letters above each bar indicate statistical differences between treatments (from two-way ANOVA and Tukey's HSD post hoc test); groups that do not share the same letter are significantly different from each other.

hrs, while entropy increased at FL-S from 12:00 to 20:00 hrs. A comparison of entropy values between the period with black drum chorusing (Fig. 8A) and without black drum chorusing (Fig. 8B) highlights this was likely the driving force behind the strong difference in diel patterns of entropy across sites, with low acoustic diversity when black drum chorusing dominated the soundscape. There were statistical differences in Acoustic Entropy (H) between sites and time of day (two-way ANOVA: df = 19,70807, F = 2417.7, P < 0.001; Fig. 9). All sites except FL-S had some statistical differences in entropy for different times of day; GA-C, GA-S, FL-N all differed significantly in entropy between day and night (Tukey's HSD test: α = 0.05, Q = 3.54394, Online Table S1).

Acoustic Diversity Index (ADI) values were lowest at GA-S, but the other sites were only slightly higher (Fig. 10). With the exception of GA-N and GA-S, all sites showed peak acoustic diversity at mid-day, and a decrease in acoustic diversity at night. There were statistical differences in ADI between sites and time of day (two-way ANOVA: df = 19,70907, F = 208.8915, P < 0.0001; Fig. 11), with statistical differences between night and day at GA-N, FL-N, and FL-S, but not GA-C or GA-S (Tukey's HSD test: α = 0.05, Q = 3.54394, Online Table S2).

Acoustic Complexity Index (ACI) values increased in all locations at dusk and at night compared to dawn and day (Fig. 12). There were significant statistical differences in ACI between sites and time of day (two-way ANOVA: df = 19,68654, F = 259.4887, P < 0.0001; Fig. 13) with statistical differences between night and day at GA-N, FL-N, and FL-S, but not GA-C or GA-S (Tukey's HSD test: α = 0.05, Q = 3.54394, Online Table S3). All sites except GA-N showed significant differences in ACI between night and day, whereas dawn and dusk often statistically overlapped with night and/or day (Fig. 13). The post hoc analysis revealed three different statistical groupings of
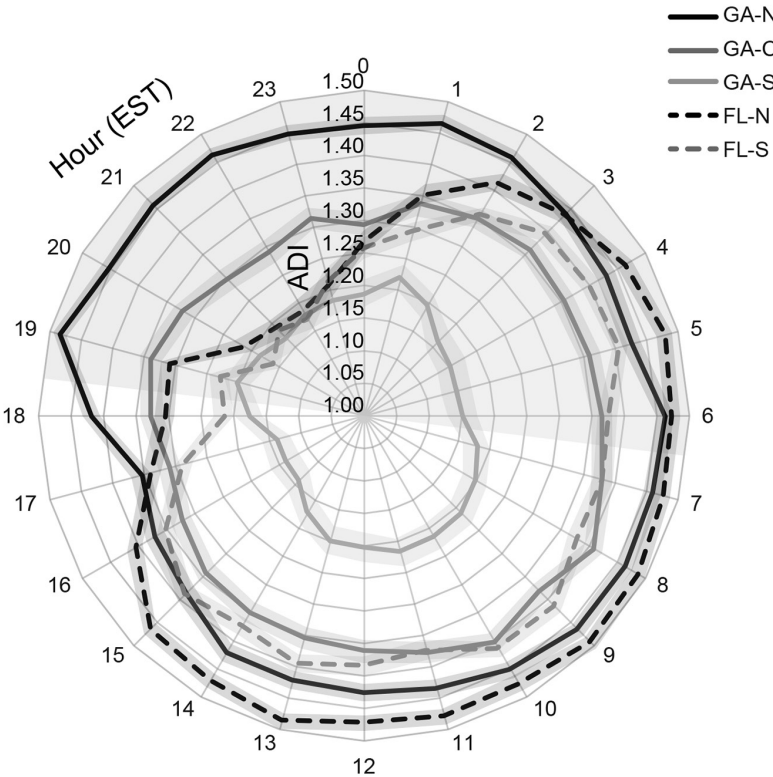
Figure 10. Circular graph of Acoustic Diversity Index (ADI) (mean and SE) vs hour of the day for each of the recording site over the entire survey period. Radial axis represents ADI, and circumference axis represents time. Gray shading in background indicates the night time period across the survey.
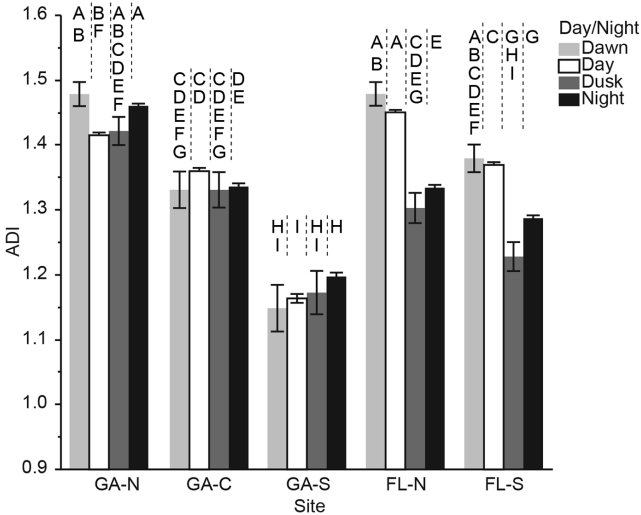

Figure 11. Acoustic Diversity Index (AD) (mean and SE) at dawn, day, dusk, and night for all sites. Letters (oriented vertically) above each bar indicate statistical differences between treatments (from two-way ANOVA and Tukey's HSD post hoc test); groups that do not share the same letter are significantly different from each other.
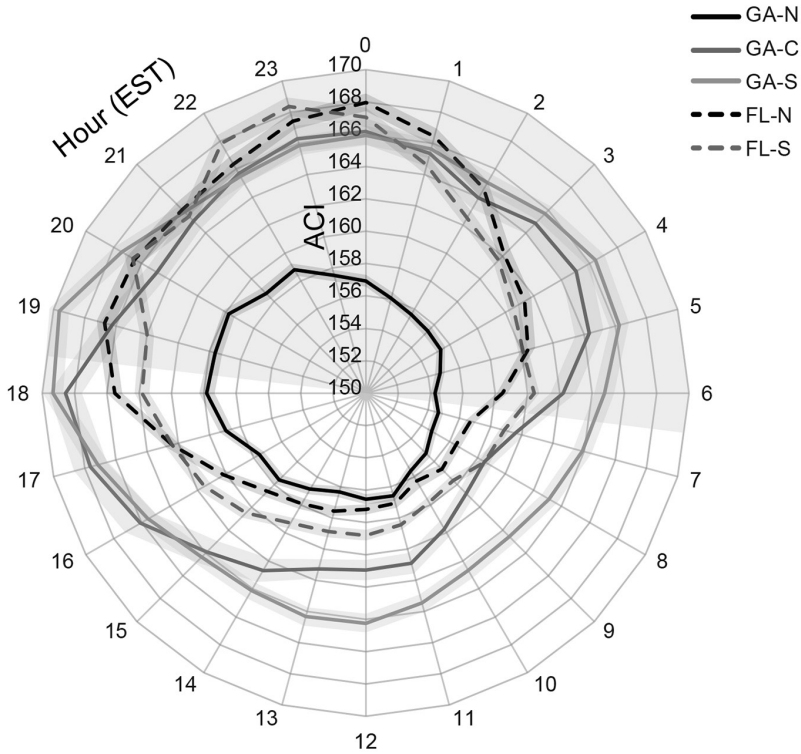
Figure 12. Circular graph of Acoustic Complexity Index (ACI) (mean and SE) vs hour of the day for each of the recording site over the entire survey period. Radial axis represents ACI, and circumference axis represents time. Gray shading in background indicates the night time period across the survey.

nocturnal ACI values: G-N and G-S differed significantly from each other, and the three other sites (GA-C, FL-N, FL-S).

Discussion

The nearshore marine habitats off of Georgia and Florida are dynamic acoustic environments, with significant diel variation in acoustic activity. The nocturnal chorus of black drum is the dominant sound source (including biological, environmental, and anthropogenic sounds), across diel periods, seasons, and locations. Both the LTSA and acoustic index data showed the consistent seasonal nocturnal trends in acoustic scenes that are strongly driven by black drum chorusing.

There was considerable geographic variation in the seasonality of nocturnal black drum chorusing behavior. Both the Florida locations showed that drum chorusing started 2 mo before the Georgia locations (Fig. 5A). While the Florida locations had warmer water temperatures earlier in the season than did Georgia (Fig. 5B), absolute temperature (or a temperature threshold) may not explain all geographical differences, since the water temperature at the Georgia locations did not reach that of the Florida sites until after Georgia black drum chorusing has ended. Several other factors may contribute to these differences. For example, analysis of bottom habitat
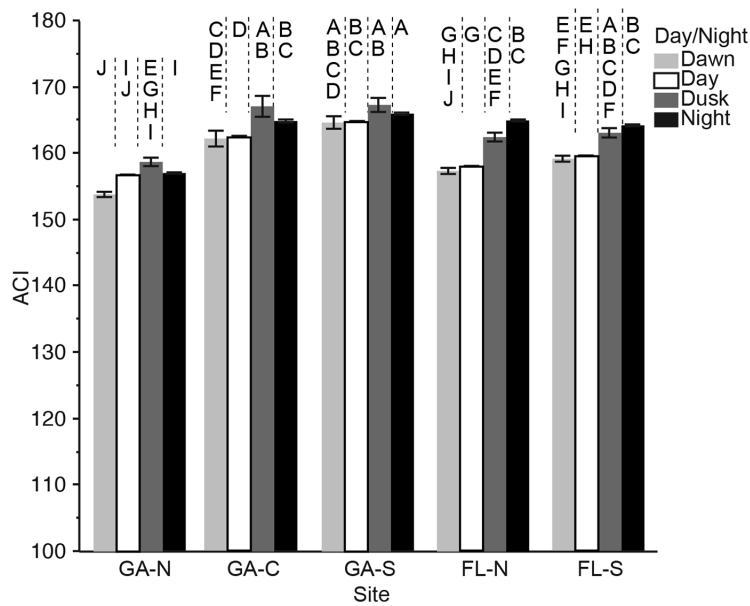
Figure 13. Acoustic Complexity Index (ACI) (mean and SE) at dawn, day, dusk, and night for all sites. Letters (oriented vertically) above each bar indicate statistical differences between treatments (from two-way ANOVA and Tukey's HSD post hoc test); groups that do not share the same letter are significantly different from each other.
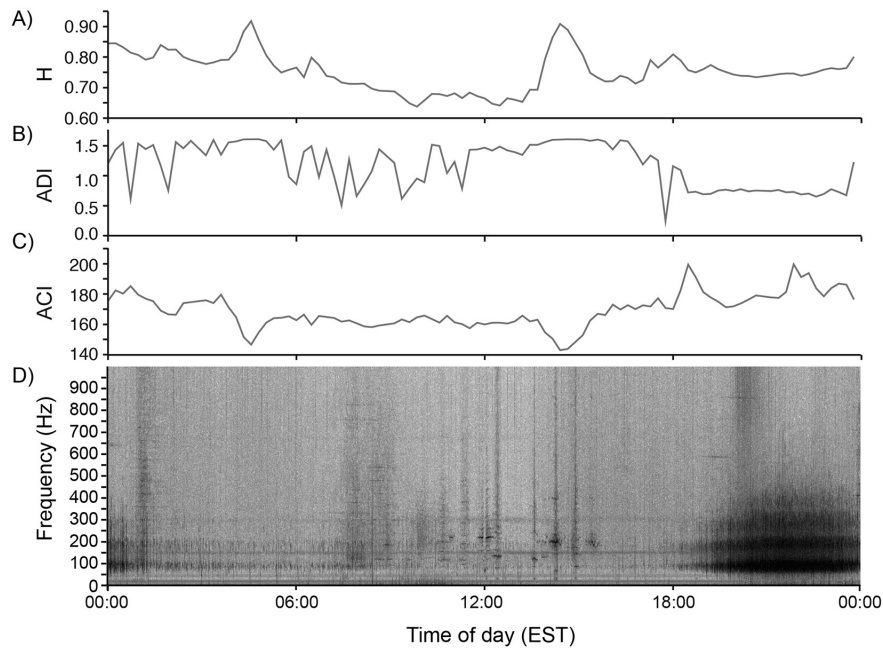

Figure 14. Acoustic indices and spectrogram for the same 24-hr time period at FL-S. Data were recorded on March 16, 2013. (A) Acoustic Entropy (H), (B) Acoustic Diversity Index (ADI), (C) Acoustic Complexity Index (ACI), and (D) 24-hr spectrogram. The spectrogram was created in Raven Pro 1.5, with a Fast Fourier Transform (FFT) size = 1024 points and 75% overlap.

structure at these sampling locations showed a variation in hard and soft bottom cover across the region (Conley et al. 2015). Additionally, differences in population size within the chorus or spatial movement of the aggregation may contribute to regional differences in sound levels. There is some degree of genetic connectivity between black drum in Georgia and Florida (Leidig et al. 2015), so it is possible that some individuals chorusing in Florida earlier in the season may move into Georgia later in the spring.

Though black drum were the most prevalent fish sounds, they were certainly not the only vocalizing fish. There were crepuscular and nocturnal choruses of red drum visible at several sites (Fig. 6). Red drum appeared to start their seasonal chorusing earlier in the late winter/early spring, and for a shorter period of time than black drum. There was also occasional temporal overlap between red drum and black drum chorusing events. Toadfish (*Opsanus* sp.) were also visible in LTSAs and 24-hr spectrogram data, though they started chorusing later in the season. We also observed putative fish calls of unknown origin, both in individual, repeated, and chorus-like behavior. Ongoing efforts to identify which species produce particular calls can further help reveal the diel and seasonal dynamics of fish acoustic communication within these communities.

While our data and analyses revealed several trends in the bioacoustic phenology at these locations, there are several known acoustic sources that were not included in our data analysis, either because of sampling rate or analytical methods. While the vast majority of fish hear and communicate within the low frequency band that we sampled (0–1000 Hz) (Bass and Liu 2007), there are known examples of taxa that play a significant role in the acoustic community above this frequency range. Snapping shrimp (family Alpheidae) are one of the dominant biological sound sources in oceans around the world (Johnson et al. 1947, McWilliam and Hawkins 2013, Kaplan et al. 2015), but their sounds occur at frequencies above 2 kHz and thus were not recorded as part of our survey. Other species of sciaenids produce extended calls at night that extend above 1000 Hz (Luczkovich et al. 1999, 2008). The analytical focus on long-term calling patterns caused a bias toward longer-duration chorusing activity, causing us to miss shorter duration individual calls produced by many fish and invertebrate species. Incorporating automated detection approaches (e.g., Van Parijs et al. 2009, Potamitis 2014, Kottege et al. 2015, Urazghildiiev and Van Parijs 2016) alongside long-term acoustic analysis could help clarify the diel and seasonal dynamics of short duration, isolated calls. However, this approach may not be readily scalable in terms of species-specific resolution, accuracy, or precision for the effort required.

Acoustic Indices.—The use of acoustic indices to characterize the structure or dynamics of acoustic communities is early in its application phase, but our index data suggest promise for exploring diel or seasonal patterns in sound production. Indices showed consistent, but complex statistical differences between times of day and locations (Figs. 9, 11, 13), with consistent statistical differences between night and day (Online Tables S1–S3). Dawn and dusk often overlapped with either night and/or day, suggesting that these crepuscular time periods are transitional rather than distinct for acoustic behaviors.

One of the principal challenges in using acoustic indices to explore large data sets is ability to discern how specific acoustic events contribute to a particular index

value over a given period of time. An intuitive and immediate concern is the degree to which ship noise or other environmental/anthropogenic sounds contribute to index values. A direct comparison of a 24-hr spectrogram with the corresponding acoustic index values (Fig. 14) showed that the ship sounds (visible as narrow vertical bands in the spectrogram between 12:00 and 18:00 hrs, Fig. 14D) corresponded to increases in H, ADI, or ACI (Fig. 14A–C), while the sustained black drum chorus resulted only in a moderate increase in ACI and H, but not ADI. It is possible that the resolution of our acoustic indices may be constrained by our relatively low sampling rate (2 kHz), and are better suited for analysis of data with audio sampling rates, as used in other studies (e.g., Lillis et al. 2014, Butler et al. 2016). The short-term changes in index values are likely due to shorter duration events not visible at longer times scale in the spectrogram.

There are both advantages and disadvantages of using acoustic indices at this scale of acoustic data (Sueur et al. 2014). As with any data-intensive method, there is a temptation to accept quantitative results without extensive validation of their accuracy. While acoustic indices have been applied and validated in many terrestrial studies (e.g., Sueur et al. 2008, 2014, Farina et al. 2011, Pijanowski et al. 2011, Villanueva-Rivera et al. 2011, Farina and Pieretti 2014), their application to the marine environment is relatively recent (McWilliam and Hawkins 2013, Lillis et al. 2014, Parks et al. 2014, Staaterman et al. 2014, Kaplan et al. 2015, Butler et al. 2016), and the field is still in the process of understanding how the composition and temporal patterns of acoustic activity correspond to resulting index values. It is also unclear how differences in sampling rate, bit depth, and spectral resolution impact the performance of the indices. Acoustic indices are theoretically well suited to address diel changes in soundscape composition, as diel changes in acoustic activity are widespread in marine and terrestrial ecosystems. Acoustic indices may provide a way to evaluate these daily changes. For example, Fuller et al. (2015) describe a nocturnal increase of H and ADI in a subtropical Australian forest. However, most of the applications has been either on spatial (McWilliam and Hawkins 2013, Lillis et al. 2014, Parks et al. 2014, Butler et al. 2016) or seasonal (Lillis et al. 2014) variation. Using acoustic indices to describe diel variation may hold significant promise, but still require further validation and understanding of how the algorithms behave under different recording and analytical approaches.

What Do Diel Patterns in Soundscapes Mean for Fishes?—Sounds at night are important in the behavior and ecology of many different fish species. Many nocturnal fish species vocalize in chorusing and individual calling contexts (Bright and Sartori 1972, Ruppé et al. 2015, McCauley and Cato 2016, van Oosterom et al. 2016). Several fish species—such as sciaenids, groupers, squirrelfish, and toadfish—exhibit most of their reproductive activity at night (Locascio and Mann 2008, 2011a, Luczkovich et al. 2008, Mann et al. 2008, McIver et al. 2014), and the sounds they produce play a critical role in this behavior. Additionally, many larval fishes often settle at night, and may use fish and other biological sounds as orientation cues during recruitment (e.g., Tolimieri et al. 2000, Simpson et al. 2004, Stanley et al. 2012, Bertucci et al. 2015).

The acoustic data at these large spatial and temporal scales show the reproductive behavior of black drum populations at the seasonal level. Fish behavior at night is often difficult to visually observe, particularly in remote field settings (Helfman 1986).

With these acoustic data, we can observe the daily and seasonal onset of breeding activity, and how this behavior changes at different locations. Gathering such data would be extremely difficult to do through other, more traditional methods, such as standard trawl surveys or visual observations. For fishes that engage in nocturnal spawning aggregations (Mann et al. 2008, 2010), acoustic surveys may be an effective approach for further investigation of reproductive phenology, as well as fisheries management (Wall et al. 2014).

Our acoustic survey data revealed that there are considerable changes in the acoustic environment and bioacoustic activity on both daily and seasonal levels off Georgia and Florida. This and other passive acoustic surveys in the marine environment increasingly highlight how frequent nocturnal acoustic behaviors are among fishes (Picciulin et al. 2013, McIver et al. 2014, Ruppé et al. 2015, van Oosterom et al. 2016), and the nighttime hours are a critical diel period in their life history.

Acknowledgments

Literature Cited

Bass AH, Liu Z. 2007. Neural and behavioral mechanisms of audition. *In:* Hara TJ, Zielinski BS, editors. Fish Physiology, Volume 25: Sensory Systems Neuroscience. San Diego: Academic Press. p. 377–410. http://dx.doi.org/10.1016/S1546-5098(06)25009-X

Bass AH, Rice AN. 2010. Vocal-acoustic communication in fishes: neuroethology. *In:* Breed MD, Moore J, editors. Encyclopedia of Animal Behavior. Oxford: Academic Press. p. 558–567. http://dx.doi.org/10.1016/B978-0-08-045337-8.00274-6

Bertucci F, Parmentier E, Berten L, Brooker RM, Lecchini D. 2015. Temporal and spatial comparisons of underwater sound signatures of different reef habitats in Moorea Island, French Polynesia. PLoS One. 10(9):e0135733. http://dx.doi.org/10.1371/journal.pone.0135733

Bioacoustics Research Program. 2015. Raven Pro 1.5: Interactive sound analysis software. Ithaca, NY: Cornell Lab of Ornithology. Available from: http://www.birds.cornell.edu/brp/raven/RavenOverview.html

Bright TJ, Sartori JD. 1972. Sound production by the reef fishes *Holocentrus coruscus, Holocentrus rufus* and *Myripristis jacobus,* family Holocentridae. Hydro-Lab J. 1:11–20.

Butler J, Stanley JA, Butler MJ. 2016. Underwater soundscapes in near-shore tropical habitats and the effects of environmental degradation and habitat restoration. J Exp Mar Biol Ecol. 479:89–96. http://dx.doi.org/10.1016/j.jembe.2016.03.006

Calupca TA, Fristrup KM, Clark CW. 2000. A compact digital recording system for autonomous bioacoustic monitoring. J Acoust Soc Am. 108(5):2582. http://dx.doi.org/10.1121/1.4743595

Cato DH. 1976. Ambient sea noise in waters near Australia. J Acoust Soc Am. 60(2):320–328. http://dx.doi.org/10.1121/1.381109

Cato DH. 1978. Marine biological choruses observed in tropical waters near Australia. J Acoust Soc Am. 64(3):736–743. http://dx.doi.org/10.1121/1.382038

Cato DH. 1992. The biological contribution to the ambient noise in waters near Australia. Acoust Aust. 20(3):76–80.

Conley MC, Anderson MG, Geselbracht L, Newton R, Weaver KJ, Barnett A, Prince J. 2015. The South Atlantic Bight Marine Assessment: species, habitats and ecosystems. Boston,

MA. The Nature Conservancy, Eastern US Division. Available from: http://nature.ly/marineSAtlanticBightERA

D'Spain GL, Batchelor HH. 2006. Observations of biological choruses in the Southern California Bight: a chorus at midfrequencies. J Acoust Soc Am. 120(4):1942–1955. http://dx.doi.org/10.1121/1.2338802

Dugan PJ, Ponirakis DW, Zollweg JA, Pitzrick MS, Morano JL, Warde AM, Rice AN, Clark CW, Van Parijs SM. 2011. SEDNA – bioacoustic analysis toolbox. IEEE OCEANS. 2011:1–10.

Farina A, Pieretti N. 2014. Sonic environment and vegetation structure: a methodological approach for a soundscape analysis of a Mediterranean maqui. Ecol Inform. 21:120–132. http://dx.doi.org/10.1016/j.ecoinf.2013.10.008

Farina A, Pieretti N, Piccioli L. 2011. The soundscape methodology for long-term bird monitoring: a Mediterranean Europe case-study. Ecol Inform. 6(6):354–363. http://dx.doi.org/10.1016/j.ecoinf.2011.07.004

Fuller S, Axel AC, Tucker D, Gage SH. 2015. Connecting soundscape to landscape: which acoustic index best describes landscape configuration? Ecol Indic. 58:207–215. http://dx.doi.org/10.1016/j.ecolind.2015.05.057

Gerhardt HC, Huber F. 2002. Acoustic communication in insects and anurans: common problems and diverse solutions. Chicago, IL: University of Chicago Press.

Greenfield MD, Shaw KC. 1983. Adaptive significance of chorusing with special reference to the Orthoptera. *In:* Gwynne DT, Morris GK, editors. Orthopteran mating systems: sexual competition in a diverse group of insects. Boulder, CO: Westview Press. p. 1–27.

Guan S, Lin T-H, Chou L-S, Vignola J, Judge J, Turo D. 2015. Dynamics of soundscape in a shallow water marine environment: a study of the habitat of the Indo-Pacific humpback dolphin. J Acoust Soc Am. 137(5):2939–2949. http://dx.doi.org/10.1121/1.4919312

Harris SA, Shears NT, Radford CA. 2016. Ecoacoustic indices as proxies for biodiversity on temperate reefs. Methods Ecol Evol. 7(6):713–724. http://dx.doi.org/10.1111/2041-210X.12527

Helfman G. 1986. Fish behaviour by day, night and twilight. *In:* Pitcher TJ, editor. The behaviour of teleost fishes. New York: Springer. p. 366–387. http://dx.doi.org/10.1007/978-1-4684-8261-4_14

Hodge KB, Muirhead CA, Morano JL, Clark CW, Rice AN. 2015. North Atlantic right whale occurrence in two wind planning areas along the mid-Atlantic US coast: implications for management. Endanger Species Res. 28(3):225–234. http://dx.doi.org/10.3354/esr00683

Johnson MW, Everest FA, Young RW. 1947. The role of snapping shrimp (*Crangon* and *Synalpheus*) in the production of underwater noise in the sea. Biol Bull. 93(2):122–138. http://dx.doi.org/10.2307/1538284

Kaplan MB, Mooney TA, Partan J, Solow AR. 2015. Coral reef species assemblages are associated with ambient soundscapes. Mar Ecol Prog Ser. 533:93–107. http://dx.doi.org/10.3354/meps11382

Kottege N, Jurdak R, Kroon F, Jones D. 2015. Automated detection of broadband clicks of freshwater fish using spectro-temporal features. J Acoust Soc Am. 137(5):2502–2511. http://dx.doi.org/10.1121/1.4919298

Leidig JM, Shervette VR, McDonough CJ, Darden TL. 2015. Genetic population structure of black drum in US waters. N Am J Fish Manage. 35(3):464–477. http://dx.doi.org/10.1080/02755947.2015.1017123

Lillis A, Eggleston DB, Bohnenstiehl DR. 2014. Estuarine soundscapes: distinct acoustic characteristics of oyster reefs compared to soft-bottom habitats. Mar Ecol Prog Ser. 505:1–17. http://dx.doi.org/10.3354/meps10805

Locascio JV, Mann DA. 2008. Diel periodicity of fish sound production in Charlotte Harbor, Florida. Trans Am Fish Soc. 137(2):606–615. http://dx.doi.org/10.1577/T06-069.1

Locascio JV, Mann DA. 2011a. Diel and seasonal timing of sound production by black drum (*Pogonias cromis*). Fish Bull. 109(3):327–338.

Locascio JV, Mann DA. 2011b. Localization and source level estimates of black drum (*Pogonias cromis*) calls. J Acoust Soc Am. 130(4):1868–1879. http://dx.doi.org/10.1121/1.3621514

Luczkovich JJ, Pullinger RC, Johnson SE, Sprague MW. 2008. Identifying sciaenid critical spawning habitats by the use of passive acoustics. Trans Am Fish Soc. 137(2):576–605. http://dx.doi.org/10.1577/T05-290.1

Luczkovich JJ, Sprague MW, Johnson SE, Pullinger RC. 1999. Delimiting spawning areas of weakfish, *Cynoscion regalis* (Family Sciaenidae) in Pamlico Sound, North Carolina using passive hydroacoustic surveys. Bioacoustics. 10(2–3):143–160. http://dx.doi.org/10.1080/09524622.1999.9753427

Mann DA, Locascio JV, Coleman FC, Koenig CC. 2008. Goliath grouper *Epinephelus itajara* sound production and movement patterns on aggregation sites. Endanger Species Res. 7(3):229–236. http://dx.doi.org/10.3354/esr00109

Mann DA, Locascio JV, Schärer M, Nemeth M, Appeldoorn R. 2010. Sound production by red hind *Epinephelus guttatus* in spatially segregated spawning aggregations. Aquat Biol. 10(2):149–154. http://dx.doi.org/10.3354/ab00272

McCauley RD, Cato DH. 2016. Evening choruses in the Perth Canyon and their potential link with Myctophidae fishes. J Acoust Soc Am. 140(4):2384–2398. http://dx.doi.org/10.1121/1.4964108

McIver EL, Marchaterre MA, Rice AN, Bass AH. 2014. Novel underwater soundscape: acoustic repertoire of plainfin midshipman fish. J Exp Biol. 217(13):2377–2389. http://dx.doi.org/10.1242/jeb.102772

McWilliam JN, Hawkins AD. 2013. A comparison of inshore marine soundscapes. J Exp Mar Biol Ecol. 446:166–176. http://dx.doi.org/10.1016/j.jembe.2013.05.012

Mok HK, Gilmore RG. 1983. Analysis of sound production in estuarine aggregations of *Pogonias cromis, Bairdiella chrysoura*, and *Cynoscion nebulosus* (Sciaenidae). Bull Inst Zool Acad Sin. 22(2):157–186.

Parks SE, Miksis-Olds JL, Denes SL. 2014. Assessing marine ecosystem acoustic diversity across ocean basins. Ecol Inform. 21:81–88. http://dx.doi.org/10.1016/j.ecoinf.2013.11.003

Parsons M, McCauley R, Thomas F. 2013. The sounds of fish off Cape Naturaliste, Western Australia. Acoust Aust. 41(1):58–64.

Picciulin M, Calcagno G, Sebastianutto L, Bonacito C, Codarin A, Costantini M, Ferrero EA. 2013. Diagnostics of nocturnal calls of *Sciaena umbra* (L., fam. Sciaenidae) in a nearshore Mediterranean marine reserve. Bioacoustics. 22(2):109–120. http://dx.doi.org/10.1080/09524622.2012.727277

Pieretti N, Farina A, Morri D. 2011. A new methodology to infer the singing activity of an avian community: the Acoustic Complexity Index (ACI). Ecol Indic. 11(3):868–873. http://dx.doi.org/10.1016/j.ecolind.2010.11.005

Pijanowski BC, Villanueva-Rivera LJ, Dumyahn SL, Farina A, Krause BL, Napoletano BM, Gage SH, Pieretti N. 2011. Soundscape ecology: the science of sound in the landscape. BioScience. 61(3):203–216. http://dx.doi.org/10.1525/bio.2011.61.3.6

Potamitis I. 2014. Automatic classification of a taxon-rich community recorded in the wild. PLoS One. 9(5):e96936. http://dx.doi.org/10.1371/journal.pone.0096936

R Core Team. 2016. R: a languange and environment for statistical computing. Vienna, Austria: R foundation for Statistical Computing. Available from: http://www.r-project.org/

Rice AN, Morano JL, Hodge KB, Muirhead CA. 2016. Spatial and temporal patterns of toadfish and black drum chorusing activity in the South Atlantic Bight. Environ Biol Fishes. 99(10):705–716. http://dx.doi.org/10.1007/s10641-016-0511-z

Ruppé L, Clément G, Herrel A, Ballesta L, Décamps T, Kéver L, Parmentier E. 2015. Environmental constraints drive the partitioning of the soundscape in fishes. Proc Natl Acad Sci USA. 112(19):6092–6097. http://dx.doi.org/10.1073/pnas.1424667112

Simpson SD, Meekan MG, McCauley RD, Jeffs A. 2004. Attraction of settlement-stage coral reef fishes to reef noise. Mar Ecol Prog Ser. 276:263–268. http://dx.doi.org/10.3354/meps276263

Soldevilla MS, Rice AN, Clark CW, Garrison LP. 2014. Passive acoustic monitoring on the North Atlantic right whale calving grounds. Endanger Species Res. 25(2):115–140. http://dx.doi.org/10.3354/esr00603

Staaterman E, Paris CB, DeFerrari HA, Mann DA, Rice AN, D'Alessandro EK. 2014. Celestial patterns in marine soundscapes. Mar Ecol Prog Ser. 508:17–32. http://dx.doi.org/10.3354/meps10911

Stanley JA, Radford CA, Jeffs AG. 2012. Location, location, location: finding a suitable home among the noise. Proc R Soc B. 279:3622–3631. http://dx.doi.org/10.1098/rspb.2012.0697

Sueur J, Farina A, Gasc A, Pieretti N, Pavoine S. 2014. Acoustic indices for biodiversity assessment and landscape investigation. Acta Acust united Ac. 100(4):772–781. http://dx.doi.org/10.3813/AAA.918757

Sueur J, Gasc A, Grandcolas P, Pavoine S. 2012. Global estimation of animal diversity using automatic acoustic sensors. *In:* Le Galliard JF, Guarini JM, Gaill F, editors. Sensors for ecology: towards integrated knowledge of ecosystems. Paris: CNRS. p. 101–119.

Sueur J, Pavoine S, Hamerlynck O, Duvail S. 2008. Rapid acoustic survey for biodiversity appraisal. PLoS One. 3(12):e4065. http://dx.doi.org/10.1371/journal.pone.0004065

Tellechea JS, Norbis W, Olsson D, Fine ML. 2011. Calls of the black drum (*Pogonias cromis*: Sciaenidae): geographical differences in sound production between northern and southern hemisphere populations. J Exp Zool. 315A(1):48. http://dx.doi.org/10.1002/jez.651

Thomisch K, Boebel O, Zitterbart DP, Samaran F, Van Parijs S, Van Opzeeland I. 2015. Effects of subsampling of passive acoustic recordings on acoustic metrics. J Acoust Soc Am. 138(1):267–278. http://dx.doi.org/10.1121/1.4922703

Tolimieri N, Jeffs A, Montgomery JC. 2000. Ambient sound as a cue for navigation by the pelagic larvae of reef fishes. Mar Ecol Prog Ser. 207:219–224. http://dx.doi.org/10.3354/meps207219

Urazghildiiev IR, Van Parijs SM. 2016. Automatic grunt detector and recognizer for Atlantic cod (*Gadus morhua*). J Acoust Soc Am. 139(5):2532–2540. http://dx.doi.org/10.1121/1.4948569

van Oosterom L, Montgomery JC, Jeffs AG, Radford CA. 2016. Evidence for contact calls in fish: conspecific vocalisations and ambient soundscape influence group cohesion in a nocturnal species. Sci Rep. 6: 19098. http://dx.doi.org/10.1038/srep19098

Van Parijs SM, Clark CW, Sousa-Lima RS, Parks SE, Rankin S, Risch D, Van Opzeeland IC. 2009. Management and research applications of real-time and archival passive acoustic sensors over varying temporal and spatial scales. Mar Ecol Prog Ser. 395:21–36. http://dx.doi.org/10.3354/meps08123

Villanueva-Rivera LJ, Pijanowski BC. 2016. soundecology 1.3.2: soundscape ecology. Available from: http://cran.r-project.org/package=soundecology

Villanueva-Rivera LJ, Pijanowski BC, Doucette J, Pekin B. 2011. A primer of acoustic analysis for landscape ecologists. Landsc Ecol. 26(9):1233–1246. http://dx.doi.org/10.1007/s10980-011-9636-9

Wall CC, Simard P, Lindemuth M, Lembke C, Naar DF, Hu C, Barnes BB, Muller-Karger FE, Mann DA. 2014. Temporal and spatial mapping of red grouper *Epinephelus morio* sound production. J Fish Biol. 85(5):1470–1488. http://dx.doi.org/10.1111/jfb.12500

Wiggins SM, Roch MA, Hildebrand JA. 2010. TRITON software package: analyzing large passive acoustic monitoring data sets using MATLAB. J Acoust Soc Am. 128(4):2299. http://dx.doi.org/10.1121/1.3508074