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Sound patterns of snapping shrimp, fish, and dolphins in an estuarine soundscape of the southeastern USA

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ABSTRACT: Soundscape ecology is a relatively new scientific field that uses sound to characterize ecosystems, which can be helpful in tracking species, estimating relative population sizes, and monitoring behavior and overall habitat quality. Estuarine soundscapes are acoustically rich, and sound patterns in these systems are understudied. Therefore, the goal of this study was to understand the soundscape of a deep tidal river estuary, the May River, South Carolina, USA. Acoustic recorders (DSG-Oceans) were deployed to collect sound samples for 2 min every 20 min at 6 stations from February to November 2014. Acoustic data revealed that sound pressure levels (i.e. broadband, low, and high frequency) varied spatially and temporally, exhibiting distinct rhythmic patterns. Acoustic detection rates and diversity of biophonic (e.g. snapping shrimp, fish, and bottlenose dolphins *Tursiops truncatus*) and anthrophonic sounds (e.g. boat noise) were higher near the river mouth and decreased towards the headwaters. The soundscape exhibited strong temporal patterns of snapping shrimp (genus *Alpheus* and *Synalpheus*) snaps, fish calls and choruses (e.g. silver perch *Bairdiella chrysoura*, black drum *Pogonias cromis*, oyster toadfish *Opsanus tau*, spotted seatrout *Cynoscion nebulosus*, and red drum *Sciaenops ocellatus*), bottlenose dolphin vocalizations, and vessel noise. Depending upon the species, certain variables (i.e. location, month, day length, lunar phase, day/night, tide, and temperature anomaly) influenced sound production. These data provide new tools and baseline measurements to better understand how soundscapes can be used to gauge habitat quality and impacts of stormwater runoff, climate change, and noise pollution.

KEY WORDS: Estuarine soundscapes · Tidal river · Snapping shrimp · Fish sounds · Bottlenose dolphin echolocation · Anthropogenic noise

1. INTRODUCTION

Understanding the temporal rhythms and spatial patterns of underwater soundscapes is an emerging field in marine ecology. Soundscapes are composed of acoustic signals of biological origin (biophony), naturally occurring non-biological sounds (geophony), and human-made sounds (anthrophony) (Pijanowski et al. 2011). Recent studies have described the acoustic habitat of coral reefs (e.g. Simpson et al. 2004, Radford at al. 2008, Kennedy et al. 2010, Staaterman et al. 2017), oyster reefs and soft bottom habitats (e.g. Lillis et al. 2013, 2014a,b, Ricci et al. 2016), shallow intertidal estuaries (Lillis et al. 2014a,

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Ricci et al. 2016), and ocean shelves (Mann & Grothues 2009, Wall et al. 2013). It has been shown that sound is necessary for many biological processes such as fish reproduction (e.g. Guest & Lasswell 1978, Lowerre-Barbieri et al. 2008, Montie et al. 2016, 2017), larval settlement (e.g. Shanks 1995, Simpson et al. 2004, Lillis et al. 2013, 2014b), and predator–prey interactions (Barros & Odell 1995, Luczkovich et al. 2000, Gannon et al. 2005, Remage-Healey et al. 2006). Current passive acoustic monitoring allows precise and long-term assessment of marine soundscapes, which can provide instrumental information on biological diversity, the behavior of marine organisms over various temporal scales, and insight into habitat quality.

Significant contributors to marine soundscapes are of biological origin. Snapping shrimp (genus *Alpheus* and *Synalpheus*) are one of the main contributors to soundscapes and are found in habitats that include oyster reefs, coral reefs, and rocky substrates (Williams 1984). Adult snapping shrimp possess a claw that can grow to half the size of their entire body (Johnson et al. 1947). When this claw is closed rapidly, it creates a cavitation bubble which collapses and produces a loud snap (Versluis et al. 2000). The snap signatures are short in duration (<0.1 s) and broadband (i.e. 0–200 kHz) with peak source levels of 190 dB re 1 µPa at a standard reference distance of 1 m (Johnson et al. 1947). Studies have shown that the snaps are used in territorial interactions, communication, and foraging (MacGinitie 1937, Hazlett & Winn 1962, Knowlton & Moulton 1963).

In addition to snapping shrimp, major sound producing species in estuaries of the southeastern USA are typically fish belonging to the family Batrachoididae, such as oyster toadfish *Opsanus tau*, and to the family Sciaenidae, such as Atlantic croaker *Micropogonias undulatus*, silver perch *Bairdiella chrysoura*, black drum *Pogonias cromis*, spotted seatrout *Cynoscion nebulosus*, and red drum *Sciaenops ocellatus*. These fish produce calls by rapidly moving a pair of sonic muscles against their swim bladder (Winn 1964, Ramcharitar et al. 2006). The frequency ranges of the produced calls are species-specific, and the calls are associated mainly with courtship and spawning (e.g. Guest & Lasswell 1978, Luczkovich et al. 2008, Montie et al. 2016, 2017).

Estuaries in the southeastern USA are also foraging grounds for apex predators like bottlenose dolphins *Tursiops truncatus.* Bottlenose dolphins produce 3 types of sounds, which include whistles and burst pulse sounds used for communication, and echolocation used for navigating and locating prey (e.g. Herman & Tavolga 1980, Schultz et al. 1995, Janik et al. 2006). Whistles are frequency modulated tonal sounds with fundamental frequencies ranging between 2 and 20 kHz (Caldwell & Caldwell 1965), whereas burst pulse sounds are highly variable in structure and length (Blomqvist & Amundin 2004, Luís et al. 2016). Echolocation clicks are short (8–72 µs) broadband pulses with a frequency range between 40 and 130 kHz and inter-click intervals between 3 and 10 ms (Au et al. 1974, Wahlberg et al. 2011).

Another component of soundscapes are non-biological sounds associated with natural physical processes such as wind, rain, and waves (i.e. geophony or physical sounds) and human activities (i.e. anthrophony or anthropogenic noise). Coastal waters contain noise generated by recreational boats, commercial ships and vessels, pile-driving, dredging operations, and offshore windfarms (Madsen et al. 2006, Bailey et al. 2010, Bittencourt et al. 2014). Over the last century, noise pollution has become a rising problem in the marine environment and has been shown to impact marine organisms (e.g. McDonald et al. 2006, Bittencourt et al. 2014, Merchant et al. 2014, Pirotta et al. 2015, van Ginkel et al. 2018).

Recent work by Ricci et al. (2016) has shown distinct temporal patterns in the soundscape of a shallow estuary in North Carolina, USA (i.e. Middle Marsh within the Rachel Carson Estuarine Research Reserve [RCERR]). In a previous study, we illustrated how season, lunar phase, day/night, and temperature anomalies affected fish calling in the May River, South Carolina, USA, which is a deeper estuary that experiences stronger semi-diurnal tides than RCERR (Monczak et al. 2017). To further understand estuarine soundscapes, we deployed an array of 6 acoustic recorders that spanned the entire length of the May River estuary for a 9 mo period in 2014. The specific objectives were to: (1) determine the spatial and temporal patterns in broadband, low, and high frequency sound pressure levels (SPLs); (2) determine the biological and anthropogenic sources, spatial differences, and temporal rhythms of the sounds recorded; and (3) determine how certain factors (e.g. location, month, day length, lunar phase, day/night, tidal phase, and water temperature anomaly) influence snapping shrimp sounds, fish calling and chorusing, bottlenose dolphin vocalizations, and anthropogenic noise. These data provide a foundation for future studies that are investigating how soundscapes can be used to gauge habitat quality and impacts of stormwater runoff, climate change, and noise pollution.

2. MATERIALS AND METHODS

2.1. Study area

We performed passive acoustic monitoring at 6 locations (i.e. 4M, 9M, 14M, 19M, 34M, and 37M) in the May River (32° 12′ 49″ N, 80° 52′ 23″ W), South Carolina, USA, from 26 February to 21 November, 2014 (Fig. 1). The May River is a subtidal river that is ~22.10 km long, ~0.01 km wide near the headwaters, and ~1.02 km wide at the mouth. The river has a complicated topography with several creeks (e.g. Savage, Bull, and Bass Creeks), meanders, sand bars, and extensive patches of smooth cordgrass *Spartina alterniflora* and oyster reefs (i.e. eastern oyster *Crassostrea virginica*). Water depth ranges from ~0.5 to ~9.9 m and increases from the headwaters to the mouth (i.e. mean depths ± SD at Stns 4M, 9M, 14M, 19M, 34M, and 37M were 2.77 ± 3.42, 4.76 ± 2.71, 4.94 ± 3.00, 5.28 ± 1.85, 5.70 ± 2.29, and 6.69 ± 2.13, respectively). Given its location in the South Atlantic Bight, the May River exhibits large semidiurnal tides (~2.5 to 3.1 m) that influence salinity variability by pushing large amounts of ocean water into the estuary twice a day.

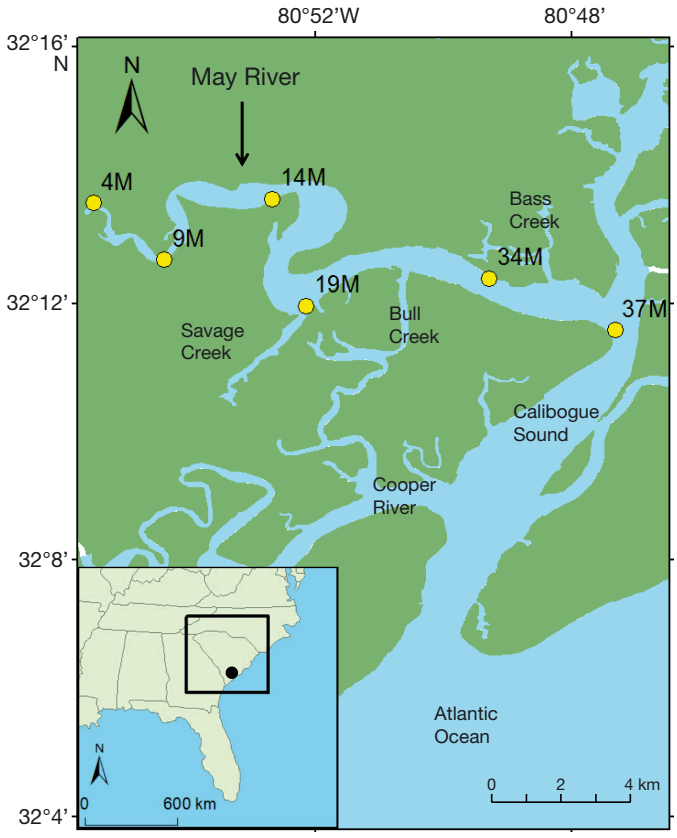

Fig. 1. May River depicting locations of Stns 4M, 9M, 14M, 19M, 34M, and 37M that were acoustically monitored from 26 February to 21 November, 2014. Stn 4M was located near the headwaters and Stn 37M at the mouth of the deep tidal river. (Inset) Location of the May River, South Carolina (black circle) in reference to the USA coast

2.2. Acoustic data collection

Following methods and results previously described (Monczak et al. 2017), we deployed DSG-Ocean recorders (Loggerhead Instruments) at Stns 4M, 9M, 14M, 19M, 34M, and 37M. DSG-Ocean recorders were scheduled to record sound for 2 min every 20 min at a sampling rate of 80 kHz and were mounted in custom-built frames (Mooring Systems). Instrument frames and recorders were painted with antifouling paint (Trilux 33). The frames were then deployed on the bottom (i.e. hydrophones were ~20 cm above the sediment surface) approximately 10 m from the shore (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m609p049_supp.pdf). To allow easy deployment and retrieval, we attached 7 m galvanized chain to the frame which was then attached to a line and auger along the side of the shore. Recorders were serviced roughly every 90 d for a total of 3 deployments. At the end of each deployment, DSG files were downloaded and batch converted into .wav files using DSG2wav© software (Loggerhead Instruments).

2.3. Environmental data collection

Water level and temperature loggers (HOBO 100-Foot Depth Water Level Data Logger U20-001-02-Ti and HOBO Water Temperature Pro v2 U22-001, Onset Computer Corporation) were placed in PVC housing and attached to the instrument frame with zip ties (Fig. S1). Depth measurements at Stns 4M, 14M, and 37M were determined from bottom pressure and atmospheric pressure readings (HOBO 100-Foot Barometric Pressure Level Data Logger U20-001-02-Ti, Onset Computer Corporation) using formulas provided by Onset Computer Corporation. Water depth measurements were scheduled to record every 10 min, while water temperature loggers were scheduled every hour. HOBO logger data were downloaded using HOBOware® Pro software (Onset Computer Corporation). We plotted continuous depth data versus date and time at Stn 37M. For stations without HOBO depth loggers, we determined depths using a hand held sonar (Vexilar Inc. Minneapolis, MN, USA). Additional environmental

parameters (i.e. salinity, pH, and dissolved oxygen) were recorded with a YSI 556 Handheld Multiparameter Instrument (YSI Inc./Xylem Inc.) twice a month at the 6 acoustic stations. For each parameter, means, standard deviations, maximum, and minimum values were reported. Depth, salinity, pH, and dissolved oxygen were not included in the statistical analysis because these parameters were not recorded continuously.

2.3. Sound pressure level analysis

For each 2 min .wav file (i.e. a total of 103 248 files), we determined the root mean square (rms) SPL for broadband (i.e. 1–40 000 Hz), low (i.e. 50–1200 Hz), and high (i.e. 7000–40 000 Hz) frequencies using custom scripts created in MATLAB R2014a (MathWorks). Broadband analysis included all sounds detected of biological, anthropogenic, and physical origin. Low frequency SPLs included fish calls, the lower bandwidth of snapping shrimp snaps, bottlenose dolphin vocalizations, and sounds of anthropogenic and physical origin, while high frequency SPLs included snapping shrimp calls, high frequency vocalizations of bottlenose dolphins, and sounds of anthropogenic and physical origin. Low and high frequency ranges were chosen based on power spectral density (PSD) analysis from previous studies which examined ranges and peaks in frequency of oyster toadfish, silver perch, black drum, spotted seatrout, red drum, and snapping shrimp calls (Monczak et al. 2017). For each station, we calculated the mean and standard deviation for broadband, high, and low frequency SPLs over the entire deployment period. To illustrate temporal rhythms in sound levels, we created heat maps of SPLs versus date and hour of day at the 6 stations.

2.4. Identification and quantification of sound sources

From 6 acoustic stations (i.e. 4M, 9M, 14M, 19M, 34M, and 37M), we manually reviewed files recorded at 4 stations (i.e. 4M, 9M, 14M, and 37M) using Adobe Audition CS5.5 software (Adobe Systems). These stations were chosen based on previous studies that indicated a high prevalence of fish calling and chorusing (Montie et al. 2015, Monczak et al. 2017). Files recorded at Stns 19M and 34M were not manually analyzed to simplify analysis; however randomly reviewing files of these stations revealed the presence of similar biological, physical, and anthropogenic sounds.

To understand the acoustic activity of snapping shrimp, we designed a signal detector in MATLAB R2017b to count the number of snaps in each 2 min .wav file. The signal detection involved a process that first identified a representative 3D feature for snapping shrimp calls (i.e. referred to A in Eq. 1) (Fig. S2). This approach has been utilized in 3D facial recognition and 3D facial landmark detection (e.g. Maes et al. 2010, Gilani et al. 2015). The next step of the signal detector algorithm was to reorganize each 2 min .wav file into a matrix of data frames using a predefined frame window (i.e. B in Eq. 1) and then compare the existing 3D feature $A_{m\times n}$ matrix to all possible $B_{m\times n}$ matrices within the 2 min acoustic file. We used parameter C to quantify the detection process of matching instances:

$$C = \frac{\sum_{m,n}\left[\left(A_{m\times n} - \bar{A}\right)\times\left(B_{m\times n} - \bar{B}\right)\right]}{\sqrt{\sum_{m,n}\left(A_{m\times n} - \bar{A}\right)^2 \sum_{m,n}\left(B_{m\times n} - \bar{B}\right)^2}} \quad (1)$$

where $\bar{A}$ and $\bar{B}$ are averages of matrix elements. Detection efficiency was controlled by a threshold level, which was set to 0.9 in this study; this means that all counted snaps were at least 90% similar to the representative 3D feature. In order to minimize false detections from soniferous fish species, we focused the snap frequency range between 7000 and 40 000 Hz (i.e. the snap was counted if 90% of the snap appeared between 7000 and 40 000 Hz) (Fig. S3). We used the same frequency filter (i.e. 7000 to 40 000 Hz) during high frequency sound pressure analysis. Based on this approach, we 'scanned' all the 2 min acoustic files and reported the 'C' value for each file (Fig. S3). We verified the accuracy of the detector by manually counting snaps in 100 random files recorded at Stn 4M and correlating these results with snap counts obtained from automatic detection. Pearson's correlation was high and significant ($r = 0.99$; $p < 0.001$; Fig. S4). We used Stn 4M as a reference since this station had the smallest acoustic space and shallowest depth. We applied the automatic detection process to all files recorded at Stns 9M, 14M, and 37M that had greater acoustic space and depth, without changing the threshold. Acoustic files that contained loud boat or rain noise were removed from snap rate analysis to avoid false negatives and/or positives, since broadband boat or rain sounds can mask or mimic snapping shrimp snaps. To illustrate the spatial and temporal patterns of snapping shrimp sound production, we created heat maps of snap rate versus date and hour of day

with corresponding water temperature and hours of daylight.

To identify and quantify fish calls, bottlenose dolphin vocalizations, physical sounds, and boat noise, we manually reviewed 68 832 .wav files from Stns 4M, 9M, 14M, and 37M. Spectrograms were visualized using a spectral resolution of 2048 and a 10 s time window. We identified sounds by comparing recordings to spectrograms published in previous studies (Tavolga 1958, dos Santos et al. 1995, Blomqvist & Amundin 2004, Montie et al. 2015, Monczak et al. 2017). For each 2 min .wav file, the intensity score of fish calling was determined based on 4 categories (i.e. 0 = no calls; 1 = 1 call detected; 2 = multiple calls; 3 = overlapping calls or chorusing) following similar methods described previously (Luczkovich et al. 2008, Monczak et al. 2017). Dolphin vocalizations (i.e. echolocation bouts, burst pulse sounds, and whistles) were individually counted in each 2 min file. Boat noise and physical sounds were scored based on 2 categories (i.e. 0 = no sound and 1 = sound present). For each station, we tallied the total number of files that contained fish calls, dolphin vocalizations, unknown biological sounds, boat noise, and physical sounds. Fish calls were dominant during the evening and night; thus, we summed intensity scores per night (from 12:00 to 11:40 h the next day), while dolphin vocalizations and boat sounds were summed per day (from 00:00 to 23:40 h). We plotted these sums (i.e. fish and dolphin sounds) with corresponding water temperature, hours of day light, and lunar cycle versus the date. Additionally, for spotted seatrout, we created heat maps of calling intensity versus date and hour of day with corresponding lunar cycle.

2.5. Statistical analyses

Statistical analyses were performed using SPSS Statistics 24 (IBM Corporation). We used a general linear model (GLM) to test which variables (i.e. location, month, day length, lunar phase, day/night, temperature anomaly, and tidal phase) significantly influenced broadband, high, and low frequency SPLs at all 6 stations. We used separate models to investigate how these factors influenced snap rates and dolphin vocalizations at 4 stations (i.e. 4M, 9M, 14M, and 37M). For snap rate, we included interactive factors (i.e. month × day/night and lunar phase × tidal phase). For dolphin vocalizations, we included an interactive factor between month and location. Because fish calls were scored using 4 categories and were summed per night, we did not include day/night and tide as factors in the GLM. To understand what variables influenced boat noise, we performed GLM analysis including station, month, season, week day, and day length as factors.

Temperature anomalies were calculated by first performing a 30 d moving average on the data and then subtracting it from the observed water temperature. A positive anomaly indicated that the observed temperature was higher, while a negative anomaly indicated that the observed temperature was lower than the average. We used 4 categories to differentiate the lunar cycle: new moon (lunar days 27–4), first quarter (lunar days 5–11), full moon (lunar days 12–19), and third quarter (lunar days 20–26) (Eggleston et al. 1998). We used 4 categories to differentiate the tidal phase based on continuous depth data collected at 3 stations (i.e. 4M, 14M, and 37M): high tide (i.e. samples with the greatest depth within a tidal cycle), falling tide (samples between high and low tide), low tide (samples with the smallest depth), and rising tide (samples between low and high tide).

Normality of dependent variables was examined by investigating histograms, skewness, and kurtosis of the data. The absolute value of the skewness was <2 and of the kurtosis was <7, which indicated that the data were close to a normal distribution (Ghasemi & Zahediasl 2012, Nimon 2012, Kim 2013). If categorical variables significantly influenced sound counts, we performed additional tests to determine whether or not group means were significantly different. We used Tukey's honest significant difference (HSD) test if assumptions were not violated; otherwise we used Dunnett's C test. In addition, we performed a Pearson's correlation test between snap rate and high frequency SPLs (7000–40 000 Hz) of all 2 min files collected at Stns 4M, 9M, 14M, and 37M to better understand how these variables were correlated.

3. RESULTS

3.1. Spatial and temporal patterns of sound pressure levels

Comparisons of broadband (1–40 000 Hz), low (50–1200 Hz), and high (7000–40 000 Hz) frequency SPLs among all 6 stations in the May River revealed spatial differences (Fig. 2). Files recorded at Stn 14M had the highest SPL values, while files at Stn 4M (i.e. near the headwaters) had the lowest SPL values (Fig. 2). This variability may be attributed to the differences in water quality at these stations. The headwaters of

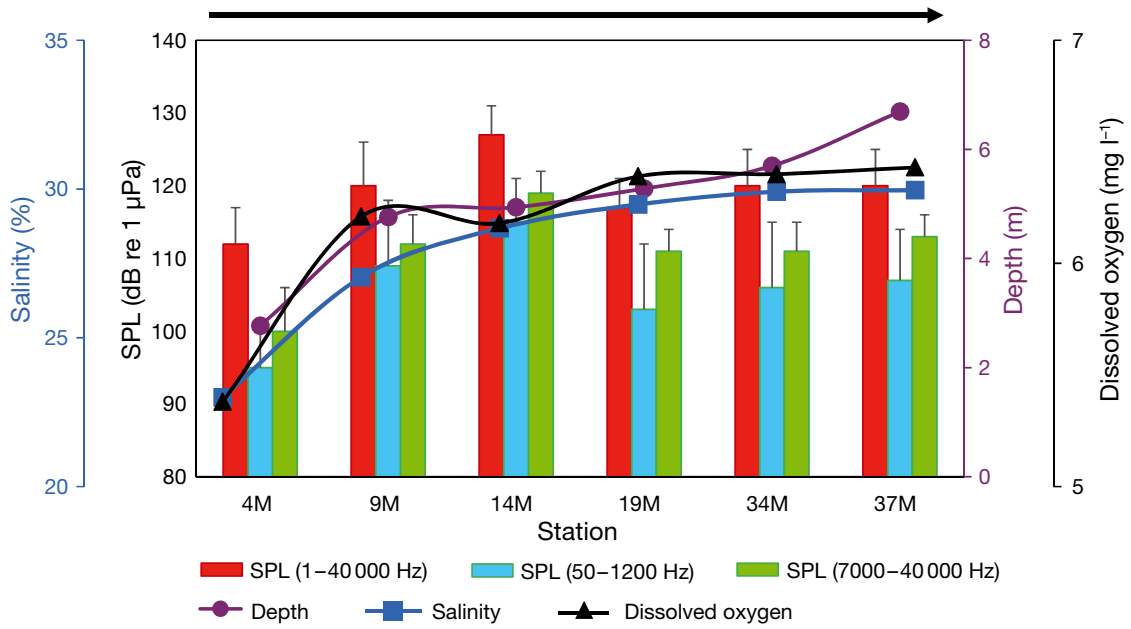

Fig. 2. Spatial patterns of broadband (1–40 000 Hz), low (50–1200 Hz), and high (7000–40 000 Hz) frequency sound pressure levels at Stns 4M, 9M, 14M, 19M, 34M, and 37M. Bars represent mean SPLs with standard errors. Also plotted are mean salinity, depth, and dissolved oxygen at each station. Black arrow on top of the graph indicates direction from the headwaters to the mouth of the May River

the May River experiences intense fluctuations in salinity (3.10–33.70‰) temperature (7.43–34.36°C), dissolved oxygen (2.90–8.80 mg l^{-1}), and pH (6.52–8.18) ranges, while the mouth of the river is less variable (Fig. 2). In addition, we observed distinct temporal patterns in SPLs that were influenced by day length, month, lunar phase, day/night, tidal phase, and temperature anomalies (Figs. 3 & 4; Fig. S5 & Table S1). Higher values of broadband, high, and low frequency SPLs were present in the summer months as compared to lower values in the early spring and late fall (Figs. 3 & 4; Fig. S5; $p < 0.001$). SPLs within the low frequency band were higher in the summer evenings and followed an oscillating pattern associated with the lunar phase (Figs. 3B & 4A–F; $p < 0.001$). SPLs within the low frequency band were also higher on the falling and low tide as compared to the values on the rising and high tide, as well as higher on the new moon compared to levels on the last quarter of the lunar phase (Figs. 3B & 4A–F; $p < 0.001$). Within the high frequency band, SPLs were substantially higher on the falling and low tide as compared to the values on the rising and high tide (Figs. 3C & 4G–L; $p < 0.001$). This tidal influence caused the striking diagonal pattern observed in the SPL heat maps. At all stations, positive temperature anomalies increased broadband, high, and low frequency SPLs (Table S1; $p < 0.001$). Patterns in the soundscape were consistent throughout the estuary (i.e. Stns 9M, 14M, 19M, 34M, and 37M), except for the headwaters (i.e. Stn 4M) (Fig. 4).

3.2. Species contribution to the soundscape of the May River

Through manual analyses of the acoustic files collected at 4 stations (i.e. 4M, 9M, 14M, and 37M), we detected the acoustic presence of snapping shrimp; 6 fish species including Atlantic croaker, black drum, silver perch, oyster toadfish, spotted seatrout, and red drum (Fig. S6); 3 unknown sounds of biological origin (Fig. S7); bottlenose dolphin vocalizations (Fig. S8); and boat noise (Fig. S9). Spatially, the highest species diversity was detected at the mouth of the May River (i.e. Stn 37M), where snapping shrimp, Atlantic croaker, black drum, oyster toadfish, silver perch, spotted seatrout, red drum, unknown sounds 1–3, and dolphin vocalizations were recorded; the lowest diversity was observed near the headwaters (i.e. Stn 4M) with a lower snapping rate and fewer calls of oyster toadfish, silver perch, spotted seatrout, unknown sounds 1 to 3, and dolphin vocalizations (Fig. 5A). Fish and dolphin sounds were detected most frequently at Stn 37M (25 599 files) and least frequent at Stn 4M (15 406 files) (Fig. 4A). Boat noise decreased from the mouth to the headwaters of the May River (i.e.

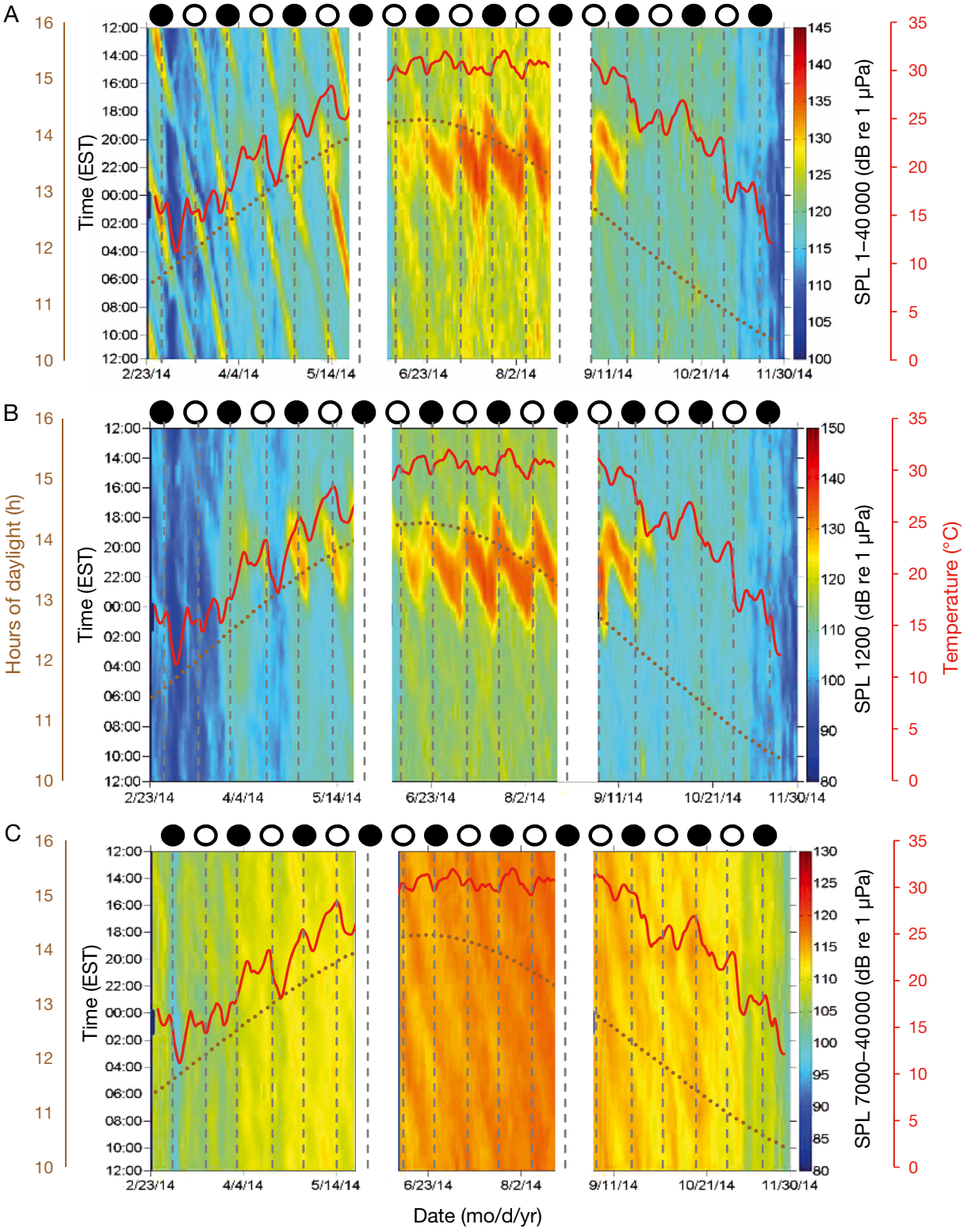

Fig. 3. Example of temporal patterns of (A) broadband (1–40 000 Hz); (B) low (50–1200 Hz); and (C) high (7000–40 000 Hz) frequency sound pressure levels at Stn 9M with corresponding hours of daylight (brown dotted line), temperature (red line), and lunar phase. Winter = February–March; spring = April–May; summer = June–September; and fall = October–November. Black and white circles correspond to new and full moon, respectively. Time is shown between noon and noon of the next day (EST: Eastern Standard Time). Two gaps in data (23 May–4 June and 16–29 August 2014) correspond to breaks between deployments due to maintenance of equipment

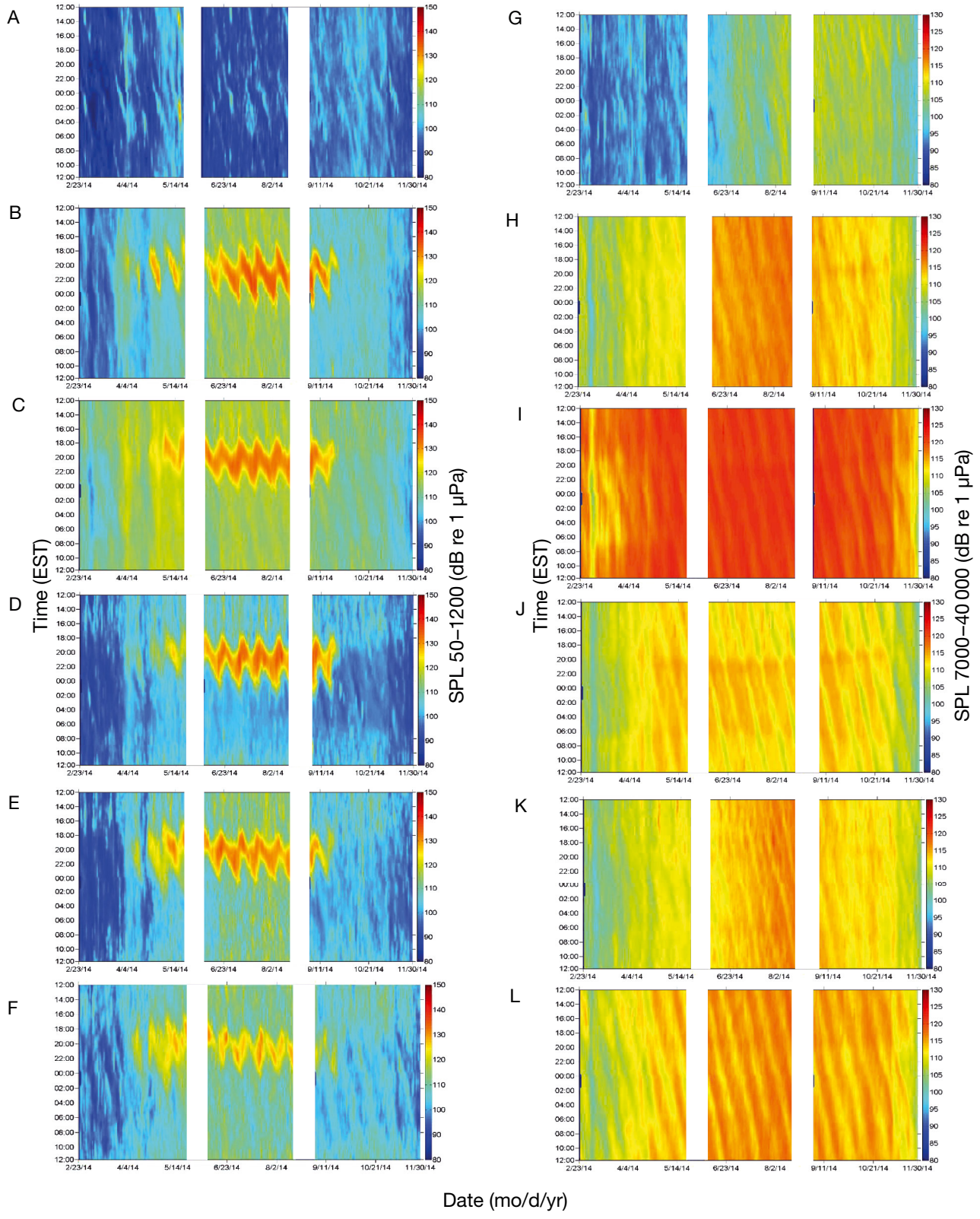

Fig. 4. Spatial and temporal patterns of low (50–1200 Hz) frequency sound pressure levels (SPLs) at Stns (A) 4M; (B) 9M; (C) 14M; (D) 19M; (E) 34M; and (F) 37M and high frequency (7000–40 000 Hz) SPLs at Stns (G) 4M; (H) 9M; (I) 14M; (J) 19M; (K) 34M; and (L) 37M. Time is shown between noon and noon of the next day (EST: Eastern Standard Time). Two gaps in data (23 May–4 June and 16–29 August 2014) correspond to breaks between deployments due to maintenance of equipment

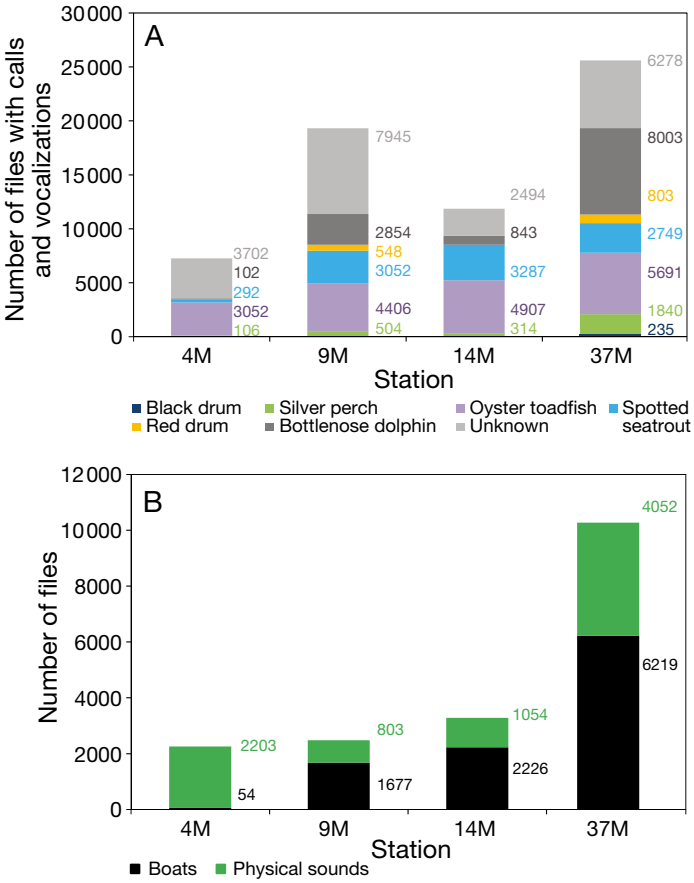

Fig. 5. Number of acoustic files with (A) biological sounds (i.e. fish calls, bottlenose dolphin vocalizations, and unknown sounds); and (B) physical sounds (i.e. rain, wind, and water flow) and boat noise in the May River

37M = 36.2%; 14M = 12.9%; 9M = 10.3%; 4M = 0.3% of files analysed) (Fig. 5B). Other sounds present in the recordings were physical sounds (i.e. rain, wind, and water flow) (Fig. 5B).

We found a positive correlation between snap rate and high frequency SPL values ($p < 0.001$), although the correlation was weaker than expected with high frequency SPL reaching an asymptote even though snap rate increased (Fig. S10). Therefore, we further investigated the spatial and temporal patterns of snap rate and detected distinct temporal patterns that resembled the SPL patterns within the high frequency band (Figs. 3C, 4G–L & 6). Factors that significantly influenced snap rate were location, month, day length, lunar phase, day/night, tidal phase, temperature anomaly, as well as interactive factors (i.e. month × day/night and tidal phase × lunar phase) (Table S2). The highest snap rate was detected at Stn 14M (875.99 ± 1.22) (mean ± SE), then at 9M (660.72 ± 1.24), followed by 37M (583.92 ± 1.23) and the lowest at Stn 4M (186.78 ± 1.32) (Fig. 6; Fig. S11A). Snaps were detected more frequently during the spring and summer (April to September) as compared to the winter (February to March) and fall (October to November) (Fig. 6; $p < 0.001$). The most striking finding was the cyclical pattern of elevated snap rates that followed the tidal cycle, which was similar to the diagonal pattern observed in the SPL heat maps within the high frequency band and depth (Figs. 3C, 4G–L, 6 & 7). Snap rate was higher during low tide as compared to high tide (Figs. 6 & 7; Fig. S11B; $p < 0.001$). Snap rates were higher during the daytime in the winter, spring, and fall (i.e. March, April to May, and October to November, respectively) but higher in the nighttime in the summer (i.e. June to September) (Fig. S12; $p < 0.001$). Temperature anomalies influenced the snap rate ($p < 0.001$). Higher snap rates were associated with positive temperature anomalies.

Similar to the findings we described regarding soundscape data of the May River during 2013 (Monczak et al. 2017), we detected spatial and temporal patterns in the courtship calls of black drum, silver perch, oyster toadfish, spotted seatrout, and red drum (Table S3; Fig. 8). Location was a significant factor influencing diversity of fish species and amount of calling in this most recent study, with the highest number of species and calling detected at Stn 37M and the lowest at Stn 4M. For all fish species, temperature anomaly influenced the amount of calling (Table S3). Within the spawning season, drops in temperature (i.e. a negative anomaly) decreased fish calling, while rises in temperature (i.e. a positive anomaly) increased sound production. In addition to location and temperature anomaly, month was a factor that influenced silver perch calling (Table S3). Within the spawning season of silver perch, the highest amount of calling was recorded between March and May and the lowest rates in June and July (i.e. end of calling season) ($p < 0.001$). For oyster toadfish, additional factors that influenced calling included month, day length, and lunar phase (Table S3). Calling was positively correlated with day length and was more prevalent between March and June as compared to July through November ($p < 0.001$). More calls of oyster toadfish were recorded around the new moon and first quarter as compared to the full moon and last quarter of the lunar phase ($p < 0.001$). For spotted seatrout, additional factors that influenced calling included month, day length, and lunar phase (Table S3). Calling was positively correlated with day length and was more prevalent between May and September as compared to April

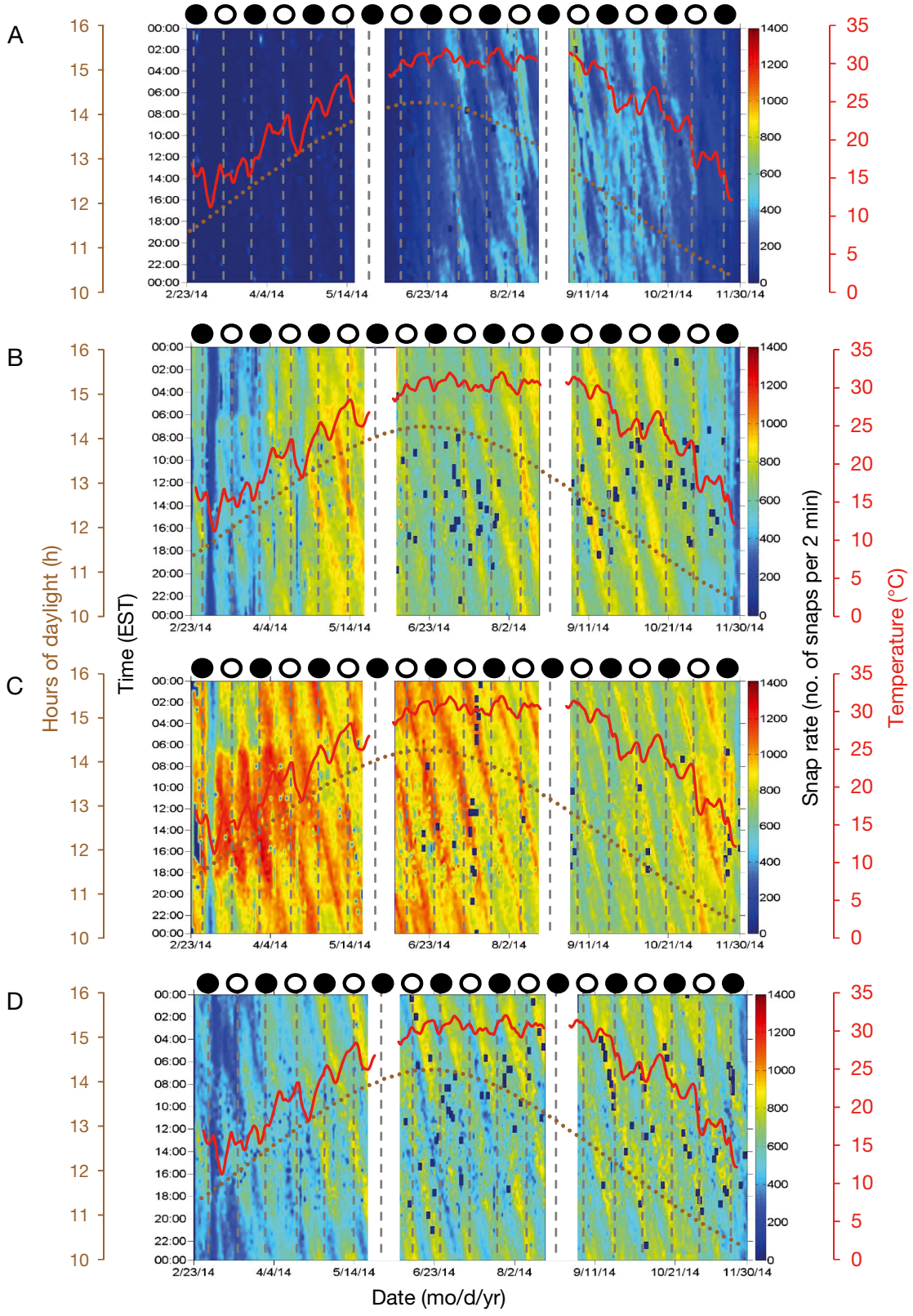

Fig. 6. Heat maps representing the number of snapping shrimp snaps in 2-minute files at Stns (A) 4M; (B) 9M; (C) 14M; and (D) 37M with corresponding hours of daylight (brown dotted line), temperature (red line), and lunar phase. Winter = February–March; spring = April–May; summer = June–September; and fall = October–November. Black and white circles correspond to new and full moon, respectively. Time is shown between midnight and midnight of the next day (EST: Eastern Standard Time). Two gaps in data (23 May–4 June and 16–29 August 2014) correspond to breaks between deployments due to maintenance of equipment

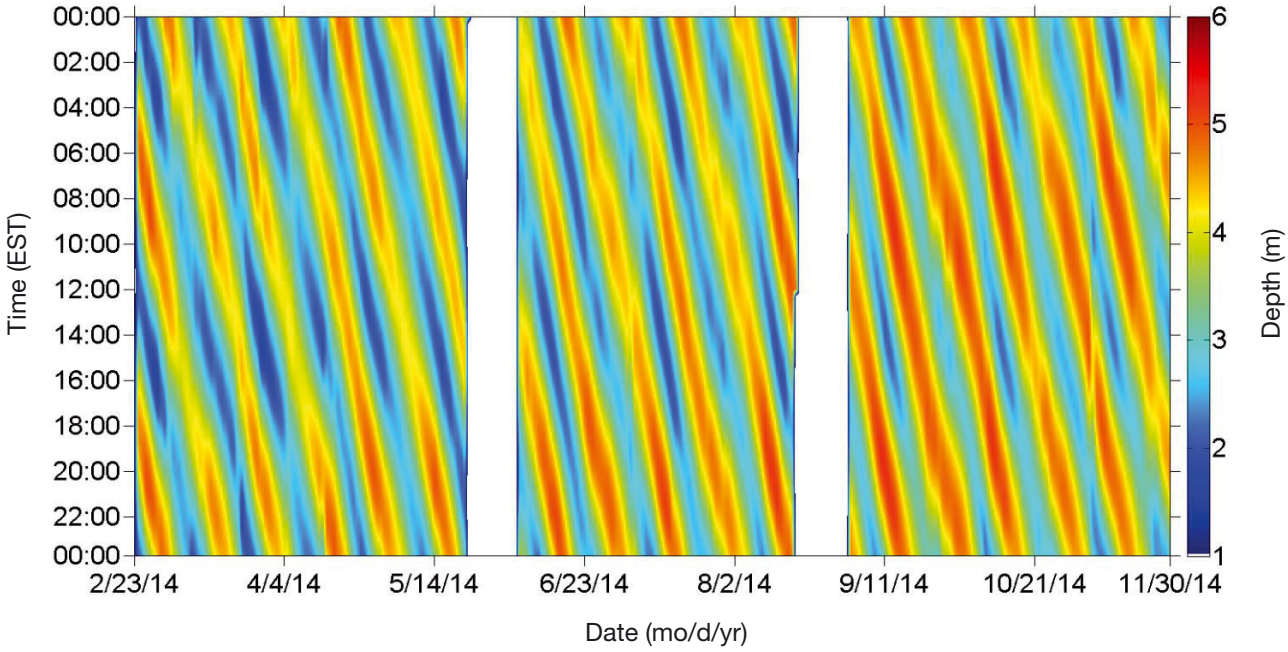

Fig. 7. Example of a heat map representing depth data collected at Stn 37M. Time is shown between midnight and midnight of the next day (EST: Eastern Standard Time). Two gaps in data (23 May–4 June and 16–29 August 2014) correspond to breaks between deployments due to maintenance of equipment. Depth data collected at Stns 4M and 14M revealed similar patterns

(i.e. beginning of calling season) and October (i.e. end of calling season) ($p < 0.001$). Longer nightly chorusing occurred on the first quarter of the lunar phase as compared to the new moon and on the last quarter compared to the full moon ($p < 0.001$). Heat maps revealed that spotted seatrout calling had similar cyclical patterns at Stns 9M, 14M, and 37M and that this pattern was similar to the low frequency SPL pattern observed at Stns 9M, 14M, 19M, 34M, and 37M (Figs. 4A–F & 9).

We detected spatial and temporal patterns of bottlenose dolphin vocalizations (Fig. 10; Table S4). Echolocation was the most prevalent type of sound recorded, followed by burst pulse sounds, then whistles (Fig. 10). Vocalizations occurred most frequently at Stn 37M, followed by 9M, then 14M, and then 4M (Fig. 10; $p < 0.001$). Month and day length influenced sound production, and we detected a strong seasonal pattern at Stn 37M (Fig. 10; Table S4). At this particular station, all 3 types of sounds were recorded more frequently during February and March (i.e. winter) and November (i.e. fall) than in the rest of the months ($p < 0.001$). We recorded more echolocation and burst pulse sounds on the first quarter and full moon as compared to the other lunar phases, as well as more echolocation and burst pulse vocalizations on the low tide versus high tide ($p < 0.001$). Day and night were significant factors influencing the amount of burst pulse sounds with an increase during the night ($p < 0.001$) (Table S4).

Location, season, month, and weekday influenced boat noise patterns (Table S5). Boat noise occurred the most at Stn 37M and the least at Stn 4M (Fig. 11; $p < 0.001$). Boat noise was most prevalent in the summer followed by spring, then fall, and the lowest in the winter. Boat noise was detected more frequently on Friday, Saturday, and Sunday as compared to other days of the week ($p < 0.001$). The highest number of boat sounds was detected on July 4, 2014 (Independence Day) at Stn 37M (i.e. 47 files with boat noise; 65% of files for that day) and on August 31, 2014 (Labour Day weekend) at Stns 14M (i.e. 31 files with boat noise; 43% of files for that day) and 9M (i.e. 22 files with boat noise; 31% of files for that day).

4. DISCUSSION

The spatial and temporal patterns of biological sounds in the May River exemplify the complex, rhythmic patterns of soundscapes in tidal river estuaries. Sound pressure levels in the low frequency (i.e. indicative of fish calling and the lower portion of snapping shrimp snaps) and high frequency bands (i.e. associated with snapping shrimp acoustic detections) were lower in the headwaters of the May River

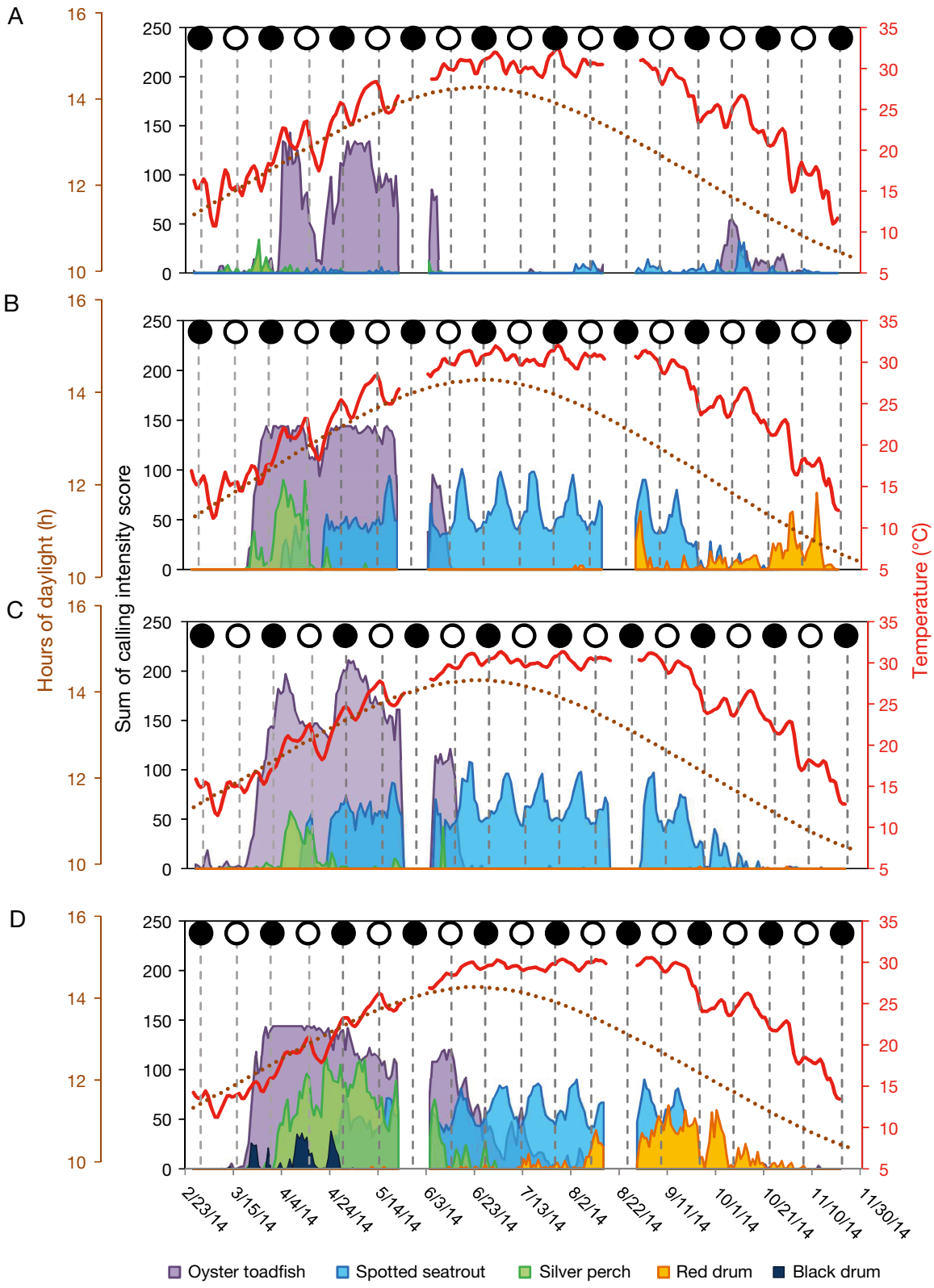

Fig. 8. Seasonal and spatial patterns of fish sound production in the May River. Sum of calling intensity scores from noon to noon of the next day at Stns (A) 4M; (B) 9M; (C) 14M; and (D) 37M. Also shown are hours of daylight (brown dotted line), water temperature (red line), and new (dark circles) and full (white circles) moon phases. Winter = February–March; spring = April–May; summer = June–September; and fall = October–November. Two gaps in data (23 May–4 June and 16–29 August 2014) correspond to breaks between deployments due to maintenance of equipment

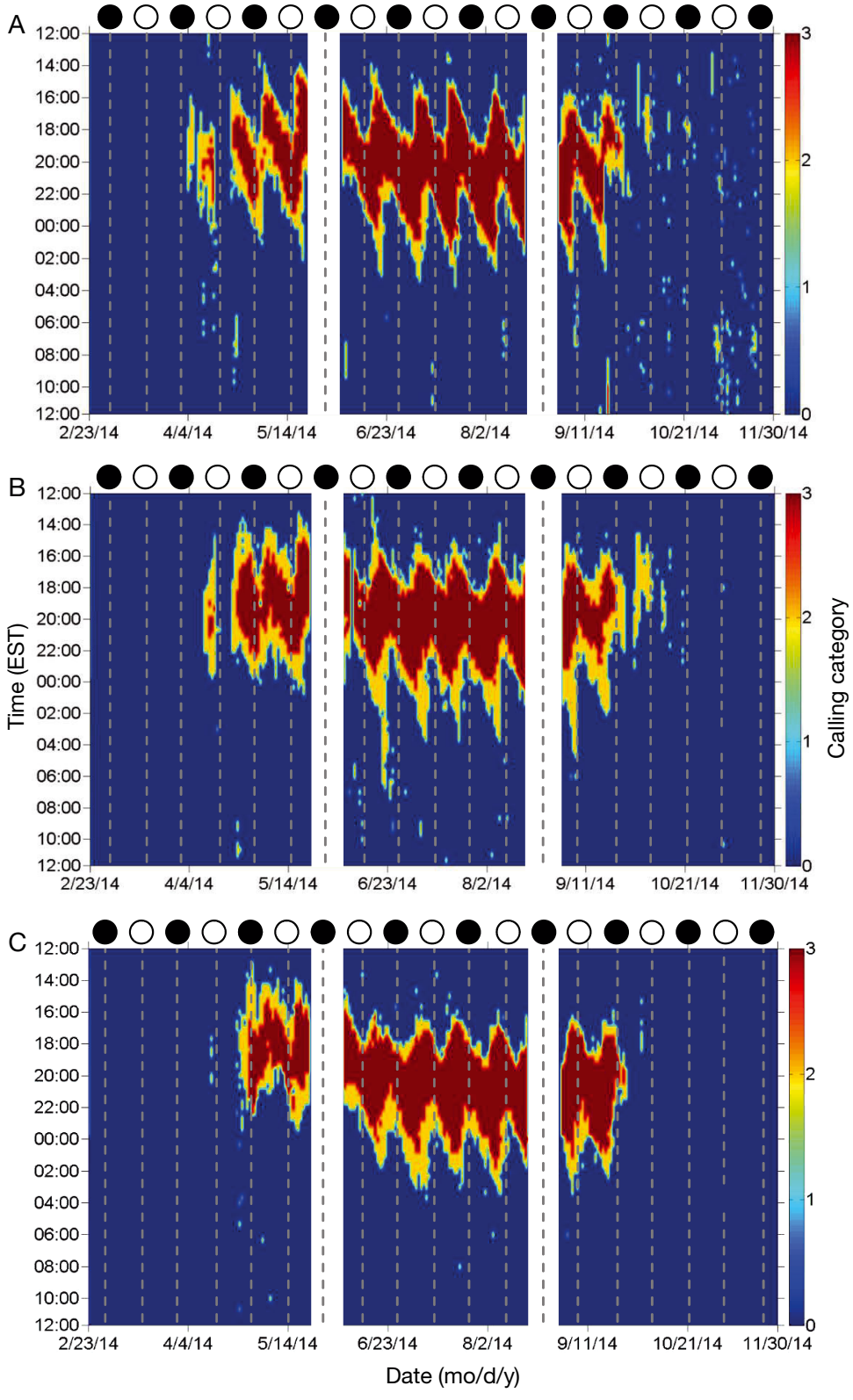

Fig. 9. Heat maps representing calling intensity scores of spotted seatrout *Cynoscion nebulosus* at Stns (A) 9M; (B) 14M; and (C) 37M. Time is shown between noon and noon of the next day (EST: Eastern Standard Time). Dark and white circles correspond to new and full moon, respectively. Two gaps in data (23 May–4 June and 16–29 August 2014) correspond to breaks between deployments due to maintenance of equipment

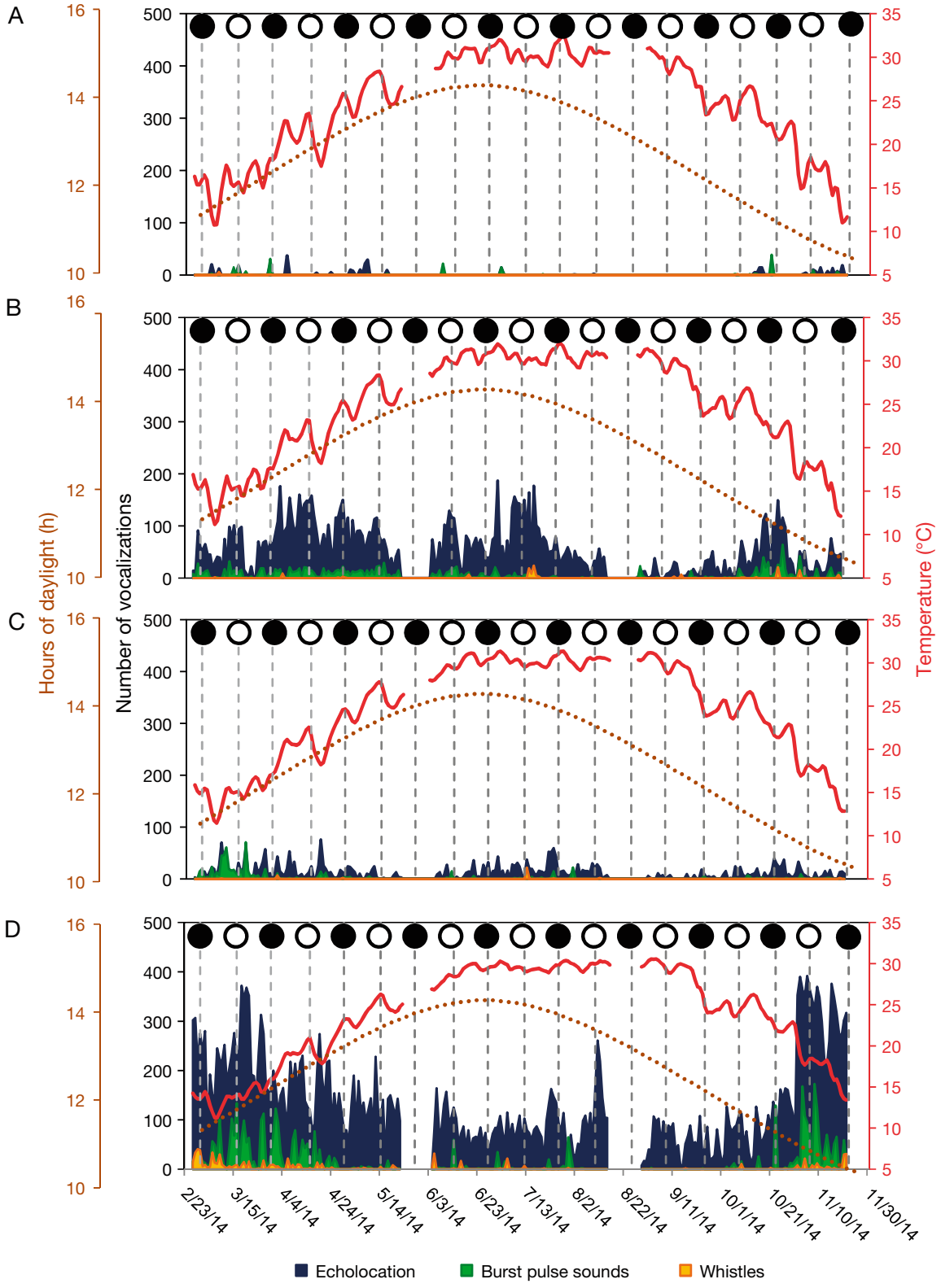

Fig. 10. Seasonal and spatial patterns of bottlenose dolphin *Tursiops truncatus* vocalizations in the May River. Sum of echolocation bouts, whistles, and burst pulse sounds per day at Stns (A) 4M; (B) 9M; (C) 14M; and (D) 37M. Also shown are hours of daylight (brown dotted line),water temperature (red line), new (dark circles), and full (white circles) moon phases. Winter = February–March; spring = April–May; summer = June–September; and fall = October–November. Two gaps in data (23 May–4 June and 16–29 August 2014) correspond to breaks between deployments due to maintenance of equipment

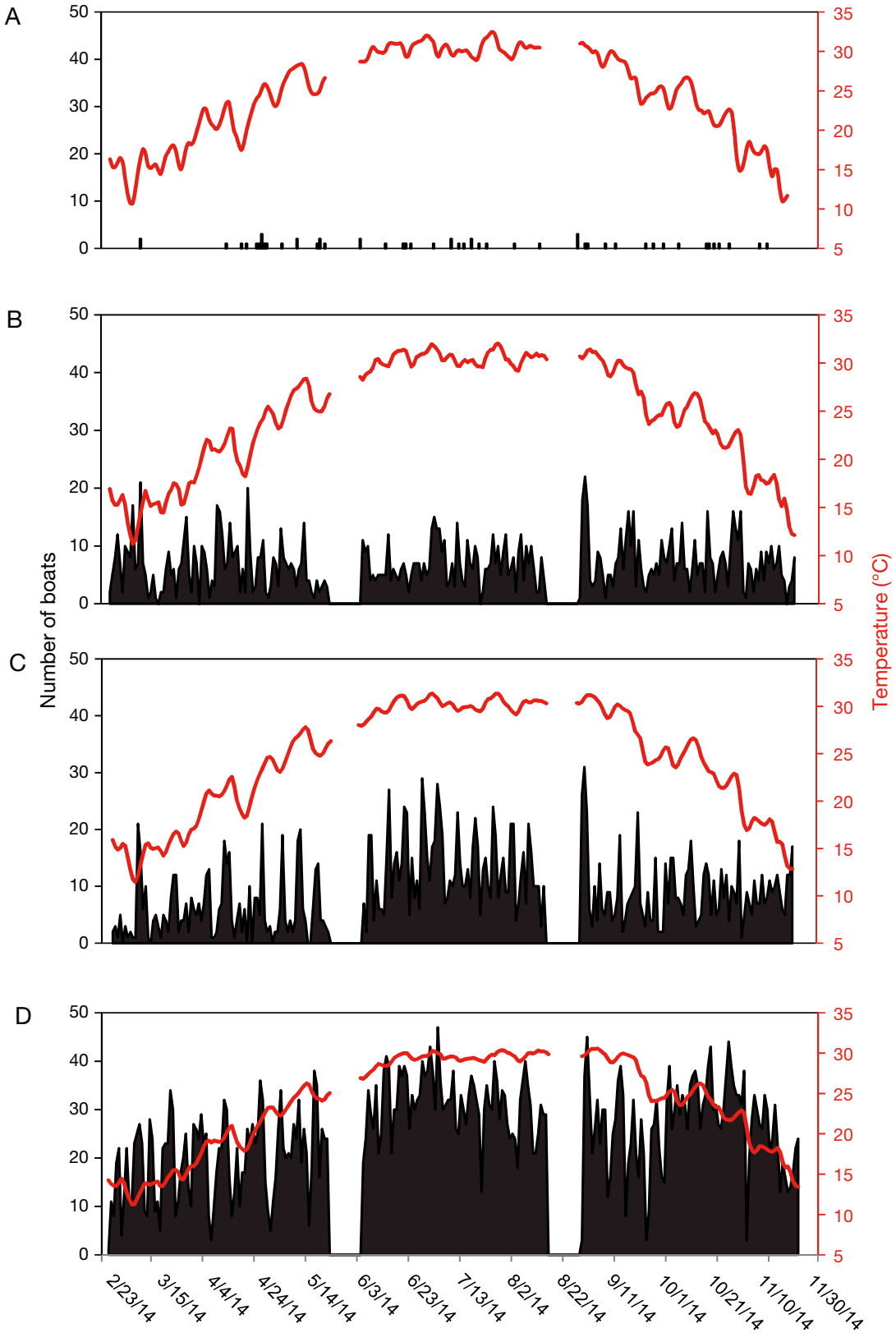

Fig. 11. Seasonal and spatial patterns of boat noise in the May River. Total number of boats detected per day at Stns (A) 4M; (B) 9M; (C) 14M; (D) 37M with corresponding water temperature (red line). Two gaps in data (23 May–4 June and 16–29 August 2014) correspond to breaks between deployments due to maintenance of equipment

and much higher at deeper locations towards the mouth. These sound pressure levels varied over seasonal, monthly, lunar, daily, and tidal scales. The most striking patterns were the oscillating peaks in low frequency SPLs driven by spotted seatrout chorusing that followed a circadian and lunar phase rhythm in calling, as well as the diagonal peaks in high frequency SPLs driven by snapping shrimp snaps that followed the tide. Understanding these patterns of biological sounds is an absolute necessity in order to determine how organisms use acoustic cues for larval settlement and recruitment, and how soundscapes may respond to noise pollution, degradation in habitat quality, and climate change.

4.1. Spatial patterns in sound pressure levels and biological sounds

In many studies, high frequency SPLs are considered to be a close representative of snapping shrimp acoustic activity (Lillis et al. 2014b, Staaterman et al. 2014, Ricci et al. 2016). Our study, however, showed that this correlation was weaker than expected, with high frequency SPLs reaching an asymptote despite a continued increase in snap rate. Signal detectors for snapping shrimp calls have been used in the past, and our observations confirm that this quantitative method is more accurate in investigating patterns of acoustic activity (Radford et al. 2008, Bohnenstiehl et al. 2016). We found differences in snap rates among stations, with the highest amount of snaps detected at Stn 14M and the least at Stn 4M. At Stn 14M, the recorder was situated close to a small island that was surrounded by mud banks and oyster reefs, while Stn 4M was located at the shallow headwaters with minimal oyster reefs present. Studies have shown that snapping shrimp are typically found in waters less than 55 m deep and are associated with structures like oysters, rocks, and corals that provide interstices in which shrimp thrive (Everest et al. 1948, Lillis et al. 2014b, Butler et al. 2016). Studies conducted in Pamlico Sound, NC revealed that oyster reef habitats display more snapping shrimp calls than soft bottom habitats (Lillis et al. 2014a, 2018).

We also observed similar spatial patterns in fish and bottlenose dolphin sound production with the headwaters having lower abundance in fish calling and dolphin vocalizations than the mouth of the May River. These findings are consistent with previous fish acoustics work conducted in this area, which collectively provides evidence of persistent spatial patterns in fish courtship sounds that are present year after year (Montie et al. 2015, Monczak et al. 2017). Of the 5 fish species recorded, 4 belonged to Sciaenidae, a family of fish that is considered a primary diet of bottlenose dolphins in the southeastern USA (Gannon & Waples 2004, Pate & McFee 2012). Thus, the higher echolocation abundance at the mouth of the May River may be associated with the higher amount and diversity of fish calls at this location.

The spatial differences in species contribution to the soundscape among the various stations may be a representation of habitat quality. The headwaters of the May River experiences larger fluctuations in temperature, salinity, pH, and dissolved oxygen than locations further towards the mouth. These fluctuations in environmental parameters are more challenging for marine organisms and may explain why we detect fewer snapping shrimp snaps, fish calls, and bottlenose dolphin vocalizations in the headwaters (Lenihan & Peterson 1998, Tolley et al. 2006). An alternative explanation may be that the headwaters are lower in volume than locations further downriver. The widening and deepening of the tidal river estuary downriver increases the acoustic space, which allows the recorders to detect more snaps, fish calls, and dolphin vocalizations.

4.2. Processes underlying temporal patterns of sound in the May River estuary

4.2.1. Seasonal changes

High frequency SPLs varied with seasons, ranging from ~80 dB re 1 µPa in the winter to ~130 dB in the summer. These sound level patterns followed the warming and cooling patterns of the estuary and were similar to patterns described in the West Bay Marine Reserve estuary (WBMR), North Carolina (Bohnenstiehl et al. 2016). Seasonal patterns of snap rates were also similar to the findings from the WBMR (Bohnenstiehl et al. 2016). In the present study, the highest number of snaps increased in the spring and summer (i.e. April to September), as water temperature and hours of daylight increased. As the fall (i.e. October to November) approached, the number of snaps decreased, following decreasing hours of daylight and the cooling patterns of the estuary.

These data also provide details on temporal patterns of sound production for a community of soniferous fishes that were similar to the patterns observed previously in this area (Monczak et al. 2017). The calling season of black drum was observed between February and March, silver perch between February

and June, oyster toadfish between February and June with some calling to November, spotted seatrout between May and September, and red drum between September and October (Montie et al. 2015, Monczak et al. 2017). Of the 5 soniferous fish species detected in the May River, spotted seatrout chorusing contributed most significantly to the oscillating pattern of low frequency sound levels. The repeated patterns from one year to the next (i.e. 2013 and 2014) show that passive acoustic monitoring could be used to track annual changes in fish courtship sounds.

At the mouth of the May River (i.e. Stn 37M), we detected peaks in dolphin vocalizations in the early spring and fall, which were most likely associated with higher abundance of bottlenose dolphins in that area during that time. However, we did not observe this seasonal pattern at other locations. Prior photo ID studies within southeastern USA estuaries have demonstrated seasonal immigration and emigration of dolphins, as well as the presence of resident and transient animals (Gubbins 2002, Mattson et al. 2005, Speakman et al. 2006). It is possible that the southern migratory stock passes and feeds near the mouth of the May River (i.e. Stn 37M) on their northward spring migration to North Carolina between February and April and on their southward fall migration to northern Florida between October and December (Zolman 2002, Speakman et al. 2006). The presence of residents and transients may increase the levels of detected vocalizations at the mouth and not deeper into the May River because of the higher diversity and abundance of prey at the mouth as compared to the headwaters (i.e. as suggested by the greater diversity and the increased acoustic detections of fish at Stn 37M).

4.2.2. Lunar phase

A few studies have observed differences in SPL patterns that followed the astronomical lunar cycle (Radford et al. 2008, Staaterman et al. 2014). Our findings support these observations, suggesting that the lunar phase significantly influences biological sound levels in an estuary. The lunar cycle was a significant factor that influenced the acoustic activity of snapping shrimp, with more snaps detected during the new moon. These findings are different from the results previously reported in estuaries of North Carolina, USA (i.e. Middle Marsh within the RCERR) by Ricci et al. (2016), who observed no significant difference in the high frequency SPLs among the different lunar phases. Our findings do align with research conducted on coral reefs in northeastern New Zealand and the Florida Keys, where the number of snaps were higher on the new moon (Radford et al. 2008, Butler et al. 2016). The same studies reported higher number of snaps during nighttime suggesting a correlation between the amount of light and snapping activity. This correlation might explain why snap rates were highest during the new moon, when light from the moon is minimal. Both the May River and the RCERR have higher turbidity than coral reef systems and this difference in lunar phase effect (i.e. May River vs. RCERR) on snap rates is surprising and might suggest an interaction between lunar phase and tide (see discussion below).

The lunar phase significantly influenced calling intensity of oyster toadfish and spotted seatrout. We recorded longer calling episodes of oyster toadfish around the new moon and first quarter in comparison to the full moon and last quarter of the lunar phase. Longer chorusing episodes of spotted seatrout with earlier start times occurred on the first and last quarter phases as reported by Monczak et al. (2017). These persistent patterns in sound production are important and may indicate preferable times of spawning (McMichael & Peter 1989, Saucier & Baltz 1993).

4.2.3. Tidal phase

We recorded differences in high and low frequency SPLs over the tidal cycle with higher levels occurring on the low tide. Snap rates followed the same tidal pattern. In addition, the highest snap rate was detected on the low tide during the new moon when the average tidal ranges are larger. These findings differ from the studies conducted on oyster reefs in the RCERR that recorded no significant differences in high frequency SPL throughout a tidal cycle (Ricci et al. 2016). Ecological and tidal differences exist between our study site and RCERR, which may explain the different patterns. First, the recorders in the May River were located at deeper depths (0.5 to 9.9 m) than the recorders at the RCERR (0.1 to 1.5 m). Secondly, the May River is influenced by larger semidiurnal tides (2.5 to 3.1 m) as compared to the RCERR tides (1.0 to 1.5 m). Lastly, in the May River, the oyster reefs are intertidal, while in the RCERR, the oyster reefs are subtidal (Eggleston et al. 1999, Ricci et al. 2016). These tidal and ecological differences may explain the discrepancy in the lunar and tidal effects on these 2 estuarine soundscapes.

Due to the large tidal range in the southern portion of South Carolina, as the water drains during the low

tide, many of the intertidal creeks and marsh grasses are not accessible to marine animals, forcing them to retreat into the deeper portion of the river and closer to our recorders. This temporal pattern most likely explains why we detect higher numbers of snap rates, louder chorusing of spotted seatrout (i.e. as measured by low frequency SPLs), and increased acoustic presence of bottlenose dolphins on the low tide. The higher snap rates on the low tide could reflect increased foraging behavior of snapping shrimp (i.e. through detection of snaps) when small prey are forced out of the marsh grass into the deeper parts of the river (MacGinitie 1937, Hazlett & Winn 1962). Fish chorusing and spawning, particularly spotted seatrout, might also be associated with the tide, with individuals seeking prey in the marsh grass at high tide and then moving into the deeper open water to spawn at low tides (i.e. during the evening and night). In this way, the tide affects predator-prey interactions and may make it more efficient for bottlenose dolphin to forage actively on the low tide (i.e. as detected by increased echolocation rates) as opposed to the high tide when prey can easily disperse into the marsh grass (Hoese 1971).

4.2.4. Circadian rhythms

Interestingly, we detected daily fluctuations in high and low frequency SPLs that varied seasonally. Sound pressure levels peaked during the night in the summer, while levels peaked during the day in the winter. In the RCERR during the summer, sound levels in the low and high frequency bands were also higher at night (Ricci et al. 2016). Snap rates exhibited similar patterns to high frequency SPL and were elevated during the day in the winter, spring, and fall and during the night in the summer. The shifts between diurnal and nocturnal snapping activity occurred in June (diurnal to nocturnal) and November (nocturnal to diurnal). These findings confirm the circadian patterns of snapping shrimp acoustic activity first reported by Bohnenstiehl et al. (2016) in the WBMR. The reasoning for this shift is still not clear and could be driven by changes in water temperature, species composition, behavior, and/or foraging activity (Bohnenstiehl et al. 2016). Similar to studies conducted previously in the May River and in the RCERR, sciaenids were more active in the late afternoon and evening, elevating low frequency SPLs in the spring and summer shortly before sunset and into the evening (Montie et al. 2015, Ricci et al. 2016, Monczak et al. 2017).

4.3. Monitoring the health of an estuary through soundscape analysis

The spatial and temporal patterns in the soundscape of the May River illustrate the importance of this estuary as essential habitat for snapping shrimp, fish, and bottlenose dolphins. In the headwaters of the May River, there are minimal to no oyster reefs, less snapping shrimp snaps, no fish chorusing (which most likely indicates no spawning of sciaenids and oyster toadfish), and few dolphin vocalizations (which most likely indicates minimal presence and minimal foraging). As mentioned previously, this part of the river is shallower and experiences higher fluctuations in environmental parameters; therefore, it may not be suitable habitat for key ecosystem processes. In addition, due to increases in development, these volume sensitive headwaters have experienced a greater deterioration in water quality as compared to locations further towards the mouth (Van Dolah et al. 2008).

In this study, we showed that soundscape ecology is a powerful, noninvasive tool that can be used to investigate acoustic behavior and complex interactions between multiple trophic levels, from invertebrates to apex predators. Many behaviors in the estuary (e.g. foraging, socializing, defense, mating, and spawning) depend on acoustic communication. Recording underwater sounds allowed us to hone in on key behaviors at much finer temporal scales, which is not possible with traditional monitoring techniques. In this case, it allowed us to detect distinct temporal patterns in snapping shrimp acoustics, fish courtship, and foraging and communication patterns of bottlenose dolphins. These are key behaviors of marine organisms that can help with gauging the health of estuaries.

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