Received: 3 April 2020 | Accepted: 10 February 2021

DOI: 10.1111/mms.12800

ARTICLE

Marine Mammal Science

Long-term passive acoustics to assess spatial and temporal vocalization patterns of Atlantic common bottlenose dolphins (*Tursiops truncatus*) in the May River estuary, South Carolina

Alyssa D. Marian[1,2†] | Agnieszka Monczak[2,3] | Brian C. Balmer[1,4] | Leslie B. Hart[1,5] | Jamileh Soueidan[2,6] | Eric W. Montie[1,2†]

[1]Graduate Program in Marine Biology, College of Charleston of Charleston, Charleston, South Carolina

[2]Department of Natural Sciences, University of South Carolina Beaufort, Bluffton, South Carolina

[3]Institute of Biological and Environmental Sciences, University of Aberdeen, Aberdeen, UK

[4]National Marine Mammal Foundation, San Diego, California

[5]Department of Health and Human Performance, College of Charleston of Charleston, Charleston, South Carolina

[6]Graduate Program in Environmental and Sustainability Studies, College of Charleston of Charleston, Charleston, South Carolina

Correspondence
Eric W. Montie, One University Boulevard, Bluffton, SC 29909.
Email: emontie@uscb.edu

Funding information
Community Foundation of the Lowcountry; Palmetto Bluff Conservancy; Port Royal Sound Foundation; SC EPSCoR/IDeA Program, Grant/Award Number: #17-RE02; South Carolina Aquarium; South Carolina Sea Grant Consortium and S.C. Space Grant Consortium; Southeast Coastal Ocean Observing Regional Association, Grant/Award Number: NOAA NA16NOS0120028; Spring Island Trust; Town of Bluffton / Beaufort County; USC ASPIRE programs; USC RISE grants; USCB Sea Islands Institute; NOAA Integrated Ocean Observing System (IOOS)

Abstract

Passive acoustics has been used extensively to study bottlenose dolphins; yet very few studies have examined the spatial, temporal, and environmental influences on vocalization types (echolocation, burst pulse sounds, and whistles), and few are long-term and provide high temporal resolution over multiple years. We used data from 2013 to 2018 to establish baseline acoustic patterns for bottlenose dolphins in the May River estuary, South Carolina. We deployed acoustic recorders at six stations during 2013–2014 and three stations during 2015–2018, with locations spanning the entire estuary (headwaters to the mouth). We discovered that acoustic detection of dolphins varied not only spatially, but also yearly, monthly, and tidally. Higher numbers of echolocation bouts, burst pulse sounds, and whistles were detected at the mouth as compared to the headwaters. At the mouth, vocalization detections were greatest in fall and winter for multiple years, and

† These authors contributed equally to this manuscript.

echolocation detection was greatest during falling and low tides. This study provides an example of another tool, long-term passive acoustics monitoring, to better understand spatial and temporal distribution of dolphins in a typical salt marsh estuary, that can be applied to other ecosystems throughout the southeastern United States and globally.

KEYWORDS
bioacoustics, bottlenose dolphin, burst pulse sounds, cetacean, echolocation, marine mammal, *Tursiops truncatus*, vocalizations, whistles

1 | INTRODUCTION

Common bottlenose dolphins (*Tursiops truncatus*, henceforth referred to as bottlenose dolphins) are long-lived, with many individuals within the western Atlantic Ocean having high site fidelity to bays, sounds, and estuaries of the southeastern United States (e.g., Balmer et al., 2013; Hayes et al., 2019; Rosel et al., 2011). Thus, bottlenose dolphins serve as an important sentinel species for the health of marine ecosystems (Bossart, 2011; Wells et al., 2004). As top-level predators feeding on organisms at multiple trophic levels, dolphins are keystone species and play a critical role in responding to and maintaining the structure of an ecological community (e.g., Bossart, 2011; Heithaus et al., 2008; Ritchie & Johnson, 2009). Climate patterns and environmental gradients can impact their distribution, behavior, and foraging ecology. These same factors may also be influenced by anthropogenic activities such as boating, fishing, shoreline development, and dredging (e.g., Bejder et al., 2006; Jensen et al., 2009; Pirotta et al., 2015; Powell & Wells, 2011; Ross et al., 2011; Weilgart, 2007; Wells et al., 2008; Van Ginkel et al., 2017). Long-term monitoring of local dolphin stocks can help identify changes in health and abundance resulting from anthropogenic stressors, prey scarcity, or environmental contaminants (Schwacke et al., 2014; Wells et al., 2004).

In the southeastern United States, there is a complex mosaic of overlapping bay, sound, and estuarine (BSE) and coastal stocks of bottlenose dolphins (Hayes et al., 2019). BSE stocks exhibit localized movements and high site fidelity, while coastal stocks likely have extended movements and lower site fidelity to a given section of coastline (Balmer et al., 2018; Speakman et al., 2010; Zolman, 2002). In South Carolina, there are currently three BSE stocks (the Northern South Carolina Estuarine System Stock, the Charleston Estuarine System Stock, and the Northern Georgia/Southern South Carolina Estuarine System Stock) and two coastal stocks (the South Carolina/Georgia Coastal Stock and the Southern Migratory Coastal Stock) that have some degree of spatial and temporal overlap (Hayes et al., 2019). The Southern Migratory Coastal Stock is hypothesized to migrate along the coast between northern Florida and North Carolina during the spring and fall of each year (Hayes et al., 2019). The South Carolina/Georgia Coastal Stock has been identified to have some seasonal movements into BSE waters during summer (Speakman et al., 2010) and extended movements along the coast throughout the year (Balmer et al., 2018). In addition, some degree of overlap has been identified for adjacent BSE stocks in the South Carolina/Georgia coastal region (Silva et al., 2019).

Previous long-term, photographic-identification studies throughout the southeastern United States have provided some insight into site fidelity and seasonality for both BSE and coastal stocks. Many estuaries along the SC coast are known to have full time residents (e.g., Gubbins, 2002; Sloan, 2006; Speakman et al., 2010; Zolman, 2002). The Calibogue Sound, South Carolina, has been shown to have summer migrants, whereas areas closer to Charleston, South Carolina, have been shown to have fall and winter migrants (Speakman et al., 2010; Zolman, 2002). Methodologies to study distributions and habitat use of these stocks have focused on small vessel surveys and satellite telemetry, which are beneficial because they provide reliable identification, exact animal counts, and provide a good opportunity for recording surface behavior (Barlow & Taylor, 2005; Simard et al., 2015). However, visual survey methods can be labor intensive, logistically challenging, and lack high temporal resolution (Balmer et al., 2014). While the studies in the southeastern United States have been multi-year studies, visual surveys were mostly conducted monthly which provides only a snapshot of the spatial and temporal patterns within and between these stocks.

Passive acoustics can be utilized as an additional method to provide fine spatial and temporal scale (i.e., 24 hr/day, 7 days/week) approximations of distribution, habitat use, and potential declines of a local population (Marques et al., 2013; Mellinger et al., 2007). Since passive acoustic recorders have high temporal resolution, this approach may be particularly useful in identifying the arrival or departure of migratory, seasonal stocks. This approach allows us to collect long-term, continuous data that is not possible with other techniques. Passive acoustic monitoring can continue at night, regardless of weather and other conditions that inhibit visual observations, can operate year-round at relatively low costs, and is particularly useful in areas where there is low water visibility (Mellinger et al., 2007). Additionally, acoustic recordings can be reanalyzed, which is beneficial for verifying unexpected results or for testing a new analytical method (Simard et al., 2015).

By identifying baseline patterns in acoustic behavior, we can detect and monitor shifts associated with natural variability, changes in climate, or anthropogenic activities. Evidence from previous studies suggest that vocalization patterns can be influenced by vessel presence, stress, underwater noise, group size, prey activity, and season in study areas across the world (e.g., Buckstaff, 2004; Castellote et al., 2015; Esch et al., 2009; Jacobs et al., 1993; Marley et al., 2017; Nuuttila et al., 2017; Quick & Janik, 2008; Tellechea et al., 2014). However, there are virtually no studies examining spatial, temporal, and environmental influences on multiple vocalization types (echolocation, burst pulse sounds, and whistles) for one species, and few are long-term studies that provide extensive temporal coverage over multiple years.

In the present study, we monitored the estuarine soundscape from 2013 to 2018 in the May River estuary, South Carolina, to understand vocalization patterns (the abundances of echolocation, burst pulse sounds, and whistles) of bottlenose dolphins. The May River is a large, tidal river estuary that is characterized as having low volume in the headwaters and increasing volume towards the mouth. This tidal river estuary exhibits similar geographic characteristics to many other estuaries within the southeastern United States (e.g., Dalrymple et al., 1991; Meade, 1969). This geography leads to strong physical and chemical gradients (e.g., depth, salinity, pH, and dissolved oxygen) from the headwaters to the mouth that change seasonally and tidally, which may affect the abundance and distribution of prey and subsequently dolphins (Dalrymple et al., 1991; Ingram & Rogan, 2002). Dolphins within this estuary are considered part of the Northern Georgia/Southern South Carolina Estuarine System (NGSSCES) stock but may have some degree of overlap from the South Carolina-Georgia Coastal stock that inhabits the coastal waters adjacent to this region as is true of those nearby in Calibogue Sound (Gubbins, 2002; Hayes et al., 2019). The geography and stock structure of the May River estuary could serve as a model for understanding the spatial and temporal patterns of dolphin vocalizations in other tidal river estuaries that exhibit similar geographical, physical, and chemical gradients. Our hypotheses were: (1) echolocation would be the most common vocalization in the repertoire of estuarine dolphins; (2) the abundance of echolocation bouts, burst pulse sounds, and whistles would vary spatially with the highest detections near the mouth of the estuary; (3) vocalizations would vary seasonally with more detections in the spring and summer following the arrival of migrants; and (4) vocalizations would vary across multiple temporal scales including tidal, diel, and lunar rhythms.

2 | MATERIALS AND METHODS

2.1 | Study area

The May River is a tidal river estuary (32°12′49″N, 80°52′23″W) that is approximately 22 km in length and the width ranging from 0.01 km near the source to 1 km at the mouth (Figure 1). This estuary opens to the Calibogue Sound,

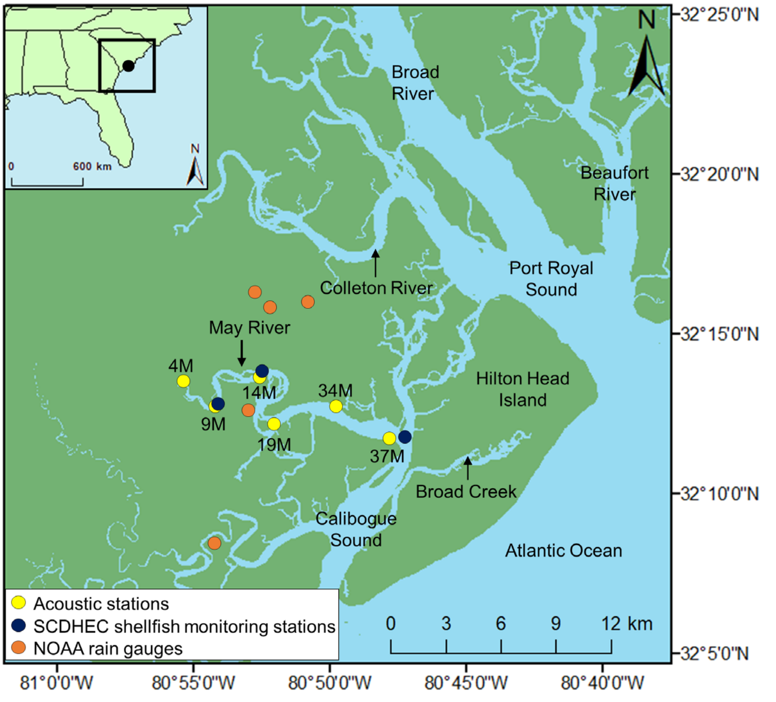

FIGURE 1 Map of the six passive acoustic recording stations in the May River estuary (yellow circles). Stations 4M, 9M, 14M, 19M, 34M, and 37M were used during 2013–2014. Stations 9M, 14M, and 37M were used from 2013 to 2018. Monthly water temperature, salinity, pH, and dissolved oxygen were measured at all six stations from 2016 to 2018. SCDHEC shellfish monitoring stations 19-19B (near 9M), 19–16 (near 14M), and 20–05 (near 37M) (blue circles) and locations of NOAA rain gauges (orange circles) are also included. (Inset) May River estuary (black circle) in reference to the east coast of the United States.

which is semiprotected by Hilton Head Island. Water depth ranges from approximately 3–25 m with shallower depths towards the headwaters. The May River estuary is associated with large areas of salt marsh and oyster reefs and is influenced by a 2.5–3.0 m semidiurnal tidal cycle. Previous research conducted from 2015 to 2017 showed that environmental variables vary spatially from the headwaters to the mouth. Temperature ranges from 19.93°C to 25.42°C, salinity from 7.76‰ to 29.23‰, dissolved oxygen from 2.64 to 11.44 mg/L, and pH from 6.52 to 8.97 (Monczak et al., 2017, 2019, 2020; Montie et al., 2015). Salinity, dissolved oxygen, and pH tend to be lower and more variable in the headwaters as compared to the mouth.

2.2 | Passive acoustic data collection

Data collection followed methodologies previous described (Monczak et al., 2017, 2019). In 2013–2014, we collected passive acoustic data at six locations in the estuary (stations 4M, 9M, 14M, 19M, 34M, and 37M), and in 2015–2018, we collected passive acoustic data at three of the six stations (stations 9M, 14M, and 37M; Figure 1). Station 4M was located closest to the headwaters, followed by stations 9M and 14M. Stations 19M, 14M, and 37M were closest to the mouth with station 37M near the mouth of the river closest to Calibogue Sound. Water depth increases from the headwaters to the mouth with stations 4M, 9M, 14M, 19M, 34M, and 37M having mean depths of 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 m, respectively (Monczak et al., 2019). All stations are characterized as having a mud bottom with nearby sand bars and intermittent oyster reefs. Stations were selected based on the abundance of prey activity (calling and chorusing of fish species associated with spawning) and position along the estuary that followed specific environmental gradients (near the headwaters, middle of the estuary, and near the mouth; Monczak et al., 2017). During 2013–2014, recorders were not deployed during winter. Recorders were deployed year-round beginning March 2015 through 2018.

At each station, we deployed DSG-Ocean recorders (Loggerhead Instruments, Sarasota, FL) in custom-built instrument frames (Mooring Systems Inc., Cataumet, MA). Each frame had attachments for depth and temperature loggers (HOBO Water Temperature Pro v2 U22-001 and HOBO 100-Foot Depth Water Level Data Logger U20-001-02-Ti; Onset Computer Corporation, Bourne, MA). Water level was measured every 10 min and temperature was measured every hour. Each recorder had a High Tech hydrophone (sensitivity of −186 dBV μPa^{-1} and gain of 20 dB) and was powered by 24 D-cell alkaline batteries. Depth and temperature loggers were housed in PVC tubes and attached to the frames using zip ties. All frames, recorders, and PVC tubes were painted with antifouling paint. Each frame was equipped with 7 m of galvanized chain attached to a line. Instrument frames with recorders were then deployed on the bottom of the river, approximately 10 m from shore. The line was stretched along the bottom and attached to an auger on the shoreline. We scheduled acoustic recorders to collect sound data with a duty cycle of 2 min every 20 min at a sample rate of 80 kHz. All 2 min recordings were saved on a 128 GB SD card as a DSG file. DSG files were downloaded after each deployment and converted into WAV files. DSG-Ocean recorders were serviced approximately every 3 months. Recorders were tested for functionality before and after every deployment. To complete this task, we played tones at multiple frequencies (100, 200, 400, 800, 1,600, 3,200, 6,400, and 8,000 kHz) and calculated root mean square (rms) sound pressure levels (SPL) for each frequency.

Due to the complexity of sound propagation in water, the true detection range (the maximum distance a vocalizing dolphin can be detected from the recorder location) around each acoustic recorder is currently unknown. This range can be determined using cylindrical spreading models or through empirical measurement via playback experiments (e.g., Jensen et al., 2012; Simard et al., 2015). One study conducted in the West Florida Shelf that used DSG Ocean recorders (with similar hydrophone sensitivity of −186 dBV/μPa) found that the detection range of bottlenose dolphin whistles using a cylindrical spreading model was approximately 200–300 m (Simard et al., 2015). Our recording stations were greater than 3 km apart; therefore, it is unlikely that acoustic signals were recorded at multiple locations.

2.3 | Environmental data collection

From 2015 to 2018, we utilized six water quality stations throughout the river (4M, 9M, 14M, 19M, 34M, and 37M; Figure 1). Temperature, salinity, pH, and dissolved oxygen were measured monthly at all six stations using a YSI 556 Handheld Multiparameter Instrument (YSI Inc./Xylem Inc., Yellow Springs, OH) from 2016 to 2018. This data collection is ongoing; therefore, some 2019 data were presented to further highlight the variability throughout the estuary. We also compiled salinity data from the South Carolina Department of Health and Environmental Control (SCDHEC) Shellfish Monitoring Program for 2013–2018 in which salinity was measured monthly at multiple locations in the estuary. We used data from three SCDHEC locations closest to our acoustic stations (station 19-19B closest to station 9M, station 19–16 closest to station 14M, and station 20–05 closest to station 37M; Figure 1). To supplement these salinity data, we also used rainfall data provided by the National Oceanic and Atmospheric Administration (NOAA) rain gauges that were located within the May River watershed.

2.4 | Acoustic file review

We manually reviewed 2 min WAV files collected on the hour using Adobe Audition CS5.5 software (Adobe Inc., San Jose, CA). Spectrograms were reviewed using a 10 s time window, a spectral resolution of 2,048 set in Adobe

Audition, 50% window overlap, and no filter with frequency ranging from 0 to 40 kHz. In each file, we identified and counted individual bottlenose dolphin whistles, burst pulse sounds, and echolocation bouts by comparing each vocalization to example spectrograms published in previous studies (Herzing, 1996; Tyack, 1986; Figure 2). For our purposes, we only identified echolocation click bouts and did not analyze individual clicks. Echolocation bouts (click trains) were defined by the first and last visible click, each having durations of approximately 50–80 μs (Au, 1997;

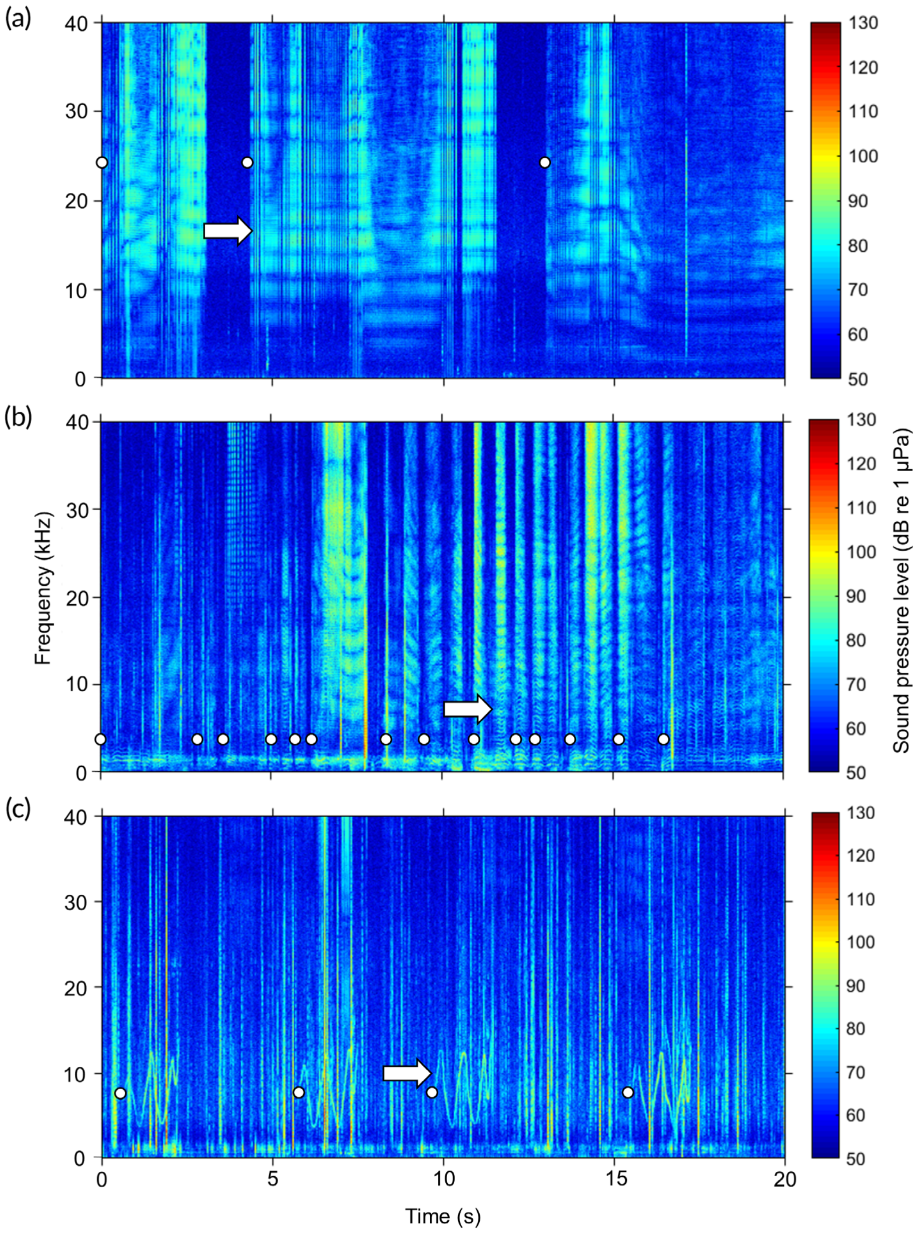

FIGURE 2 Spectrograms highlighting examples of bottlenose dolphin (a) echolocation bouts (b) burst pulse sounds (c) and whistles detected in the May River estuary (white arrows). Each example was recorded using a DSG Ocean recorder during this study. White dots indicate the onset of each vocalization that was counted: (a) three echolocation bouts, (b) fourteen burst pulse sounds, and (c) four whistles.

Hendry, 2004). To be considered a separate echolocation bout, the interbout interval was two times greater than the preceding inter-click interval (Simard et al., 2010). Individual burst pulse sounds were defined by the start and end of clearly defined harmonic bands with high repetition (pulse intervals of 25–175 ms; Au, 1997; Watkins, 1968). Burst pulse sounds were not separated by subtype (e.g., feeding buzzes and squawks). Individual whistles were tonal signals identified by the onset and termination of a single band with a duration >0.1 s that may have one or more frequency modulations (or inflection points; Gridley et al., 2017; Janik & Slater, 1999; Janik et al., 2013). While rare, overlapping whistles were counted only once for consistency. Any vocalizations not clearly defined were not included in our analysis.

2.5 | Data and statistical analysis

We performed statistical analysis using R software version 3.6.1. We used generalized linear models to investigate factors (location, year, month, lunar phase, tidal phase, day/night cycle, and temperature) that influenced acoustic detections for the 2013–2014 (included stations 4M, 9M, 14M, 19M, 34M, and 37M) and 2013–2018 (included stations 9M, 14M, and 37M) data sets. To account for gaps in data due to servicing equipment or equipment failure, we used data from the same date ranges each year in our models. First, we attempted to use a Gaussian general linear model followed by a Poisson generalized linear model, both of which did not fit our data. Our data contained a large number of zeros and were not normally distributed. To account for this over-dispersion, a negative binomial distribution was used for analysis. Lunar phase was categorized as new moon, first quarter, full moon, or last quarter following Eggleston et al. (1998). Tidal phase was categorized as high tide, falling tide, low tide, or rising tide based on depth data collected at each station. Samples with the greatest depth in a tidal cycle were categorized as high tide, while samples with the smallest depth were categorized as low tide. Samples that fell between high and low tide were categorized as falling tide and samples that fell between low and high tide were categorized as rising tide. We used a separate model for each type of dolphin vocalization (echolocation, burst pulse sounds, and whistles). These models were sequential nested models and model selection was based on a forward stepwise selection process and relied upon Akaike information criterion (AIC). For the selected models, we performed a likelihood-ratio chi-square test for each factor to compare the goodness of fit of the model with and without the factor. This approach assisted in understanding the effect size of each factor in our models. Dissolved oxygen, pH, and salinity were not included in our statistical models because they were measured only once a month from 2016 to 2018. Dunnett's post hoc comparisons were conducted for each selected model to understand differences between group means within each factor.

3 | RESULTS

3.1 | Acoustic detections

In the 2013–2014 data set, we reviewed 71,098 acoustic files collected at six stations (Table 1). Bottlenose dolphin vocalizations that we were able to identify included echolocation, burst pulse sounds, and whistles (Figure 2). For this 2-year data set, echolocation occurred in the most WAV files (20,409) as compared to the number of files with burst pulse sounds (3,043) and whistles (759). In addition, the total bouts of echolocation we detected was much higher than the numbers of individual burst pulse sounds and whistles (137,574, 12,482, and 3,840, respectively). For the 2013–2018 data set, we reviewed approximately 96,220 acoustic files from three stations (Tables 1 and 2). Relative numbers of echolocation bouts, burst pulse sounds, and whistles followed a similar pattern with echolocation occurring in the most WAV files (27,324) as compared to burst pulse sounds (4,954) and whistles (2,134). The total

TABLE 1 Bottlenose dolphin acoustic detections at six stations in the May River estuary, South Carolina, from 2013 to 2014.

	File detections				Total vocalizations		
	Total files	Echolocation (%)	Burst pulse sounds (%)	Whistles (%)	Echolocation (%)	Burst pulse sounds (%)	Whistles (%)
2013							
4 M	6,003	35 (0.58)	12 (0.20)	2 (0.03)	203 (75.20)	61 (22.60)	6 (2.22)
9 M	5,988	1,195 (19.97)	339 (5.66)	41 (0.68)	2,257 (77.70)	585 (20.10)	63 (2.17)
14 M	5,985	615 (10.28)	91 (1.52)	60 (1.00)	2,605 (75.00)	572 (16.50)	295 (8.50)
19 M	5,967	3,060 (51.28)	600 (10.05)	112 (1.88)	24,437 (90.10)	2,193 (8.08)	495 (1.82)
34 M	5,965	2,851 (47.80)	260 (4.36)	64 (1.07)	19,564 (94.30)	921 (4.44)	263 (4.27)
37 M	5,965	3,951 (66.24)	468 (7.85)	257 (4.31)	31,611 (88.40)	2,363 (6.61)	1769 (4.95)
2014							
4 M	5,869	15 (0.26)	14 (0.26)	1 (0.02)	84 (51.50)	78 (47.90)	1 (0.61)
9 M	5,868	756 (12.88)	186 (12.88)	7 (0.12)	4,530 (89.30)	510 (10.00)	35 (0.69)
14 M	5,870	223 (3.80)	73 (3.80)	2 (0.03)	940 (79.50)	240 (20.30)	2 (0.17)
19 M	5,875	2,442 (41.57)	428 (41.57)	87 (1.48)	19,451 (89.20)	1,930 (8.85)	429 (7.97)
34 M	5,872	2,828 (48.16)	371 (48.16)	78 (1.33)	20,577 (92.00)	1,543 (6.90)	244 (1.09)
37 M	5,871	2,438 (41.53)	201 (41.53)	48 (0.82)	11,315 (86.80)	1,486 (11.40)	238 (1.83)

Note. File detections = the number of files in which each vocalization type was detected; % = number of detections divided by the number of files analyzed, multiplied by 100%. Total vocalizations = the sum of all detections that were counted in WAV files for each vocalization type; % = the summed detections of each vocalization type divided by the sum of all vocalization types, multiplied by 100%.

number of echolocation bouts detected was higher than the number of burst pulse sounds and whistles (213,430, 25,440, and 15,664, respectively).

3.2 | Models

For the 2013–2014 data set, the best fitting model for echolocation, burst pulse sounds, and whistles included station, year, month, lunar phase, and day/night cycle as factors (Tables 3 and S1). These models also included a month × station interaction and year × station interaction. For the 2013–2018 data set, we found that the best model for echolocation and burst pulse sounds included station, year, month, lunar phase, day/night cycle, and tide as factors with month × station interaction, year × station interaction, and tide × station interaction (Tables 4 and S2). For whistles, the best model included station, year, month, and day/night cycle as factors with a month × station interaction and a year × station interaction.

3.3 | Spatial patterns

Both the 2013–2014 and 2013–2018 data sets were used to investigate spatial patterns in the May River estuary. Relative proportions of each vocalization type varied by location ($p < .001$; Tables 3 and 4). At the headwaters (stations 4M, 9M, and 14M), we detected the lowest number of echolocation bouts and observed the smallest percentage of echolocation (203 detections in 2013 and 84 in 2014; 75% and 51%, respectively; Table 1). Generally, the

TABLE 2 Bottlenose dolphin acoustic detections at three stations in the May River estuary, South Carolina, from 2015 to 2018.

	File detections				Total vocalizations		
	Total files	Echolocation (%)	Burst pulse sounds (%)	Whistles (%)	Echolocation (%)	Burst pulse sounds (%)	Whistles (%)
2015							
9 M	7,063	606 (8.58)	160 (2.27)	102 (1.44)	4,069 (67.00)	790 (13.00)	1210 (19.90)
14 M	7,065	184 (2.60)	18 (0.25)	3 (0.04)	668 (79.40)	42 (4.99)	131 (15.60)
37 M	7,062	2,792 (39.54)	194 (2.75)	198 (2.80)	20,209 (87.40)	1,287 (5.57)	1,618 (7.00)
2016							
9 M	8,758	865 (9.88)	256 (2.92)	62 (0.71)	5,776 (77.90)	985 (13.30)	656 (8.44)
14 M	8,757	322 (3.68)	29 (0.33)	6 (0.07)	1,760 (84.30)	268 (12.80)	61 (2.92)
37 M	8,749	3,237 (37.00)	306 (3.50)	237 (2.71)	24,627 (85.50)	2,039 (7.08)	2,127 (7.39)
2017							
9 M	8,733	1,029 (11.78)	493 (5.65)	89 (1.02)	7,075 (66.10)	2,662 (24.88)	962 (8.99)
14 M	8,734	387 (4.43)	37 (0.42)	9 (0.10)	2,258 (92.30)	102 (4.17)	87 (3.56)
37 M	7,028	3,144 (44.74)	758 (10.79)	313 (4.45)	38,241 (87.00)	3,782 (8.60)	1,939 (4.41)
2018							
9 M	6,866	650 (9.47)	254 (3.70)	44 (0.64)	4,574 (77.20)	938 (15.80)	412 (6.95)
14 M	8,702	451 (5.18)	49 (0.56)	12 (0.14)	2,670 (90.80)	129 (4.86)	143 (4.86)
37 M	8,703	4,479 (51.47)	1,042 (11.97)	644 (7.40)	48,245 (82.00)	6,660 (6.66)	3,916 (6.66)

Note. File detections = the number of files in which each vocalization type was detected; % = number of detections divided by the total number of files analyzed, multiplied by 100%. Total vocalizations = the sum of all detections that were counted in WAV files for each vocalization type; % = the summed detections of each vocalization type divided by the sum of all vocalization types, multiplied by 100%.

number of echolocation bouts detected, and the percentage of total detections increased towards the mouth (Table 1; Figure S1). The opposite was true for burst pulse sounds with larger percentages of total vocalizations detected near the headwaters (stations 4M, 9M, and 14M; Table 1; Figure S1). However, the number of file detections of burst pule sounds were generally higher towards the mouth similarly to echolocation. Interestingly, at station 9M, we generally observed more file detections of echolocation bouts and burst pulse sounds relative to stations 4M and 14M. The number of whistles detected was greatest at station 37M, while the fewest were detected at station 4M (Table 1).

Overall, total vocalizations detected (including echolocation, burst pulse sounds, and whistles) increased from the headwaters to the mouth. For the 2013–2014 data set, stations 4M, 9M, and 14M (closer to the headwaters) had significantly lower detections compared to stations 19M, 34M, and 37M (closer to the mouth of the estuary; Dunnett's post hoc test, $p < .001$; Figures 3 and S2). Similarly, in the 2013–2018 data set, detections were lower at stations 9M and 14M (i.e., closer to the headwaters) as compared to station 37M (at the mouth of the estuary; Dunnett's post hoc test, $p < .001$; Figure 4). Additionally, we observed notable variability in environmental parameters among stations. From 2016 to 2018, we measured the lowest salinity, pH, and dissolved oxygen at the headwaters (station 4M; Figure 5). This station also had the largest overall variability in salinity and dissolved oxygen as compared to stations closer to the mouth (stations 34M and 37M).

TABLE 3 Results of the best generalized linear models that investigated the influence of various factors on bottlenose dolphin vocalizations in the May River estuary, South Carolina in 2013–2014.

Model	Likelihood ratio chi-square	*p*
Echolocation		
Station	18,678.96	**<.001**
Month	2,008.51	**<.001**
Month*Station	1,798.66	**<.001**
Year	1,344.27	**<.001**
Year*Station	1,075.60	**<.001**
Lunar phase	12.55	**.006**
Day/Night	0.32	.574
Burst pulse sounds		
Station	2,013.46	**<.001**
Month	1,221.97	**<.001**
Month*Station	777.21	**<.001**
Year	67.10	**<.001**
Year*Station	65.61	**<.001**
Lunar phase	24.71	**<.001**
Day/Night	14.47	**<.001**
Whistles		
Station	851.10	**<.001**
Month	321.18	**<.001**
Month*Station	223.78	**<.001**
Year	139.28	**<.001**
Year*Station	68.15	**<.001**
Lunar phase	19.39	**<.001**
Day/Night	0.56	.455

Note: Likelihood ratio tests comparing factor effects for 2013–2018. Factors are arranged according to effect size. Bold values indicate significant parameters in the negative binomial model ($p < .05$).

3.4 | Temporal patterns

In the 2013–2018 data set, we observed high levels of variability in acoustic detections over multiple temporal scales. Detections of echolocation, burst pulse sounds, and whistles were significantly influenced by year ($p < .001$; Table 4). For stations 14M and 37M (stations closest to the mouth), we detected the most echolocation in 2013, 2017, and 2018 (Dunnett's post hoc test, $p < .001$; Figure S3). This same pattern was observed for burst pulse sounds and whistles at station 37M (Dunnett's post hoc test, $p < .001$; Figure S3). We investigated whether average yearly salinity and rainfall levels influenced yearly dolphin vocalizations but did not find any clear patterns (Figure S3). In addition to year, acoustic detections were significantly influenced by month ($p < .001$; Table 4). The most prominent acoustic pattern we observed was at station 37M, which had the most echolocation, burst pulse sounds, and whistles during November, followed by December, January, and then February, with detections decreasing in the spring and summer months (Dunnett's post hoc test, $p < .001$; Figure 6). In June and July, we observed the lowest overall detections (Dunnett's post hoc test, $p < .001$).

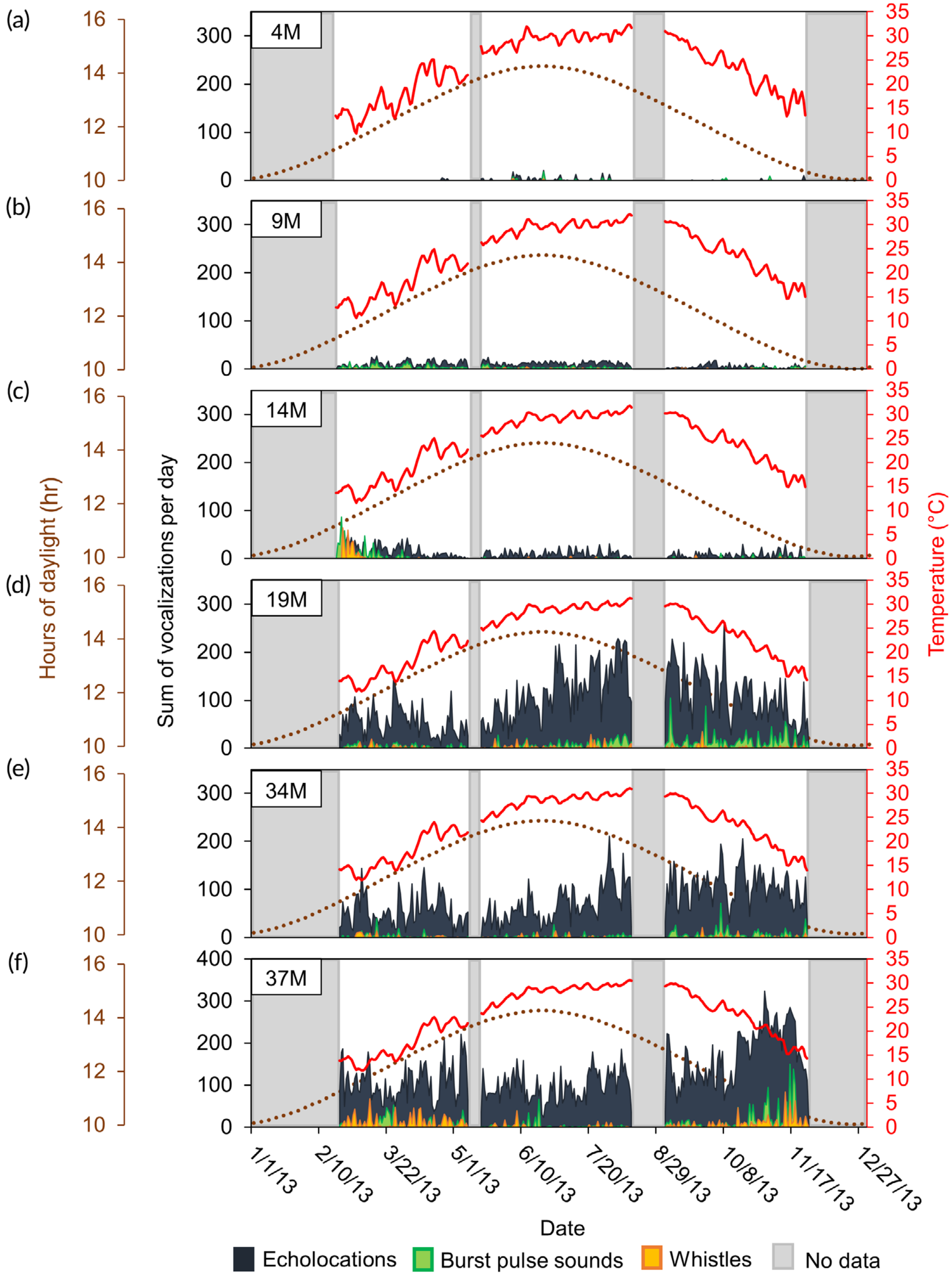

FIGURE 3 Total vocalizations for bottlenose dolphins by station in the May River estuary during 2013 ordered from the headwaters (top) to the mouth (bottom). Sum of vocalizations per day, average daily temperature (red line), and hours of daylight (brown dotted line) for all six stations. Gaps in data (gray boxes) were due to breaks in deployments. Similar patterns were observed during 2014.

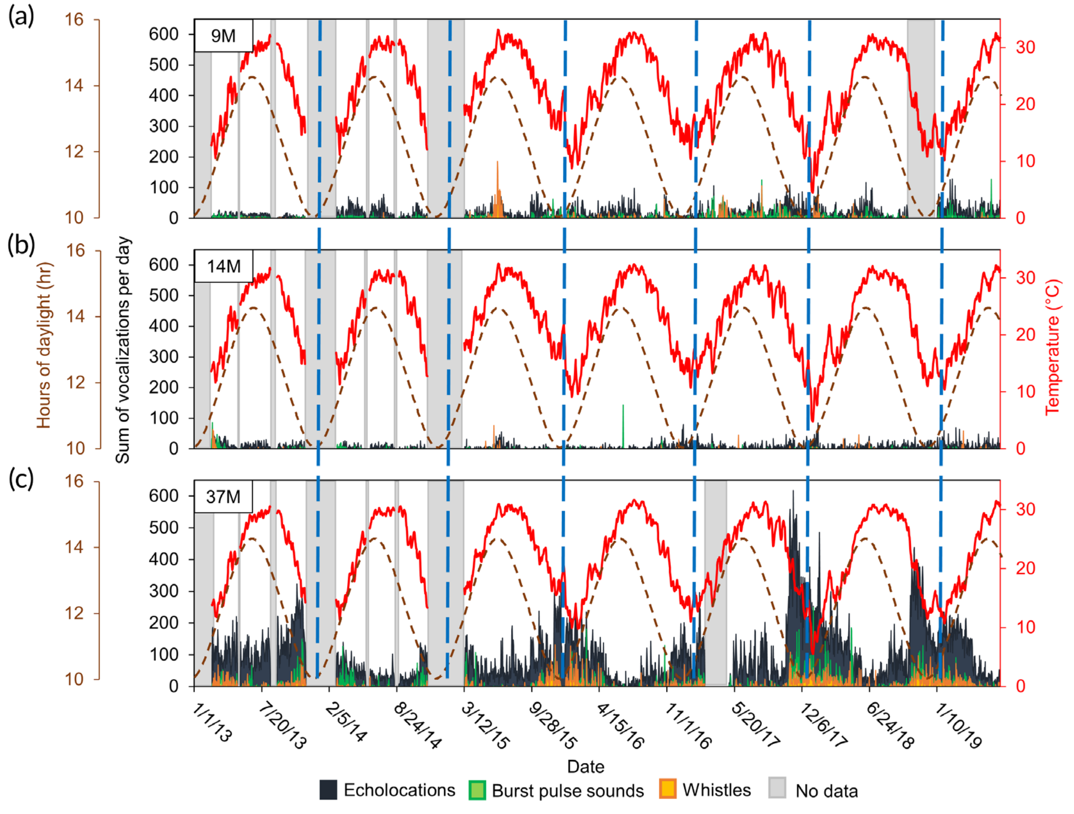

FIGURE 4 Total vocalizations for bottlenose dolphins for three stations in the May River estuary from 2013 to 2018 ordered from the headwaters (top) to the mouth (bottom). While not included in results and statistical analysis, the beginning of 2019 was included here to help illustrate acoustic patterns observed at station 37M during the winter–spring of 2019. Sum of vocalizations per day, average daily temperature (red line), and hours of daylight (brown dotted line) for three stations. Dashed blue lines indicate the end/onset of each year. Gaps in data (gray boxes) were due to breaks in deployments or equipment failure.

Furthermore, we identified distinct patterns for echolocation and burst pulse sounds that followed the day/night, lunar, and tidal cycles. We detected significantly more echolocation and burst pulse sounds during the night, particularly during winter as compared to summer (Dunnett's post hoc test, $p < .001$; Figure 7). Lastly, we observed a very distinct pattern in echolocation at the estuary mouth (station 37M) that followed the tidal cycle. We detected significantly more echolocation during the falling and low tide as compared to the rising and high tide (Dunnett's post hoc test, $p < .001$; Figures 8–10).

4 | DISCUSSION

4.1 | Acoustic repertoire

Bottlenose dolphins produce a variety of detectable vocal signals (e.g., echolocation clicks, burst pulse sounds, and whistles) as a way to respond to and interact with conspecifics and their environment (e.g., Caldwell & Caldwell, 1968; Cook et al., 2004). As expected, in the May River estuary, bottlenose dolphins primarily utilize echolocation, but burst pulse sounds and whistles are also included in their repertoire. Echolocation click trains and

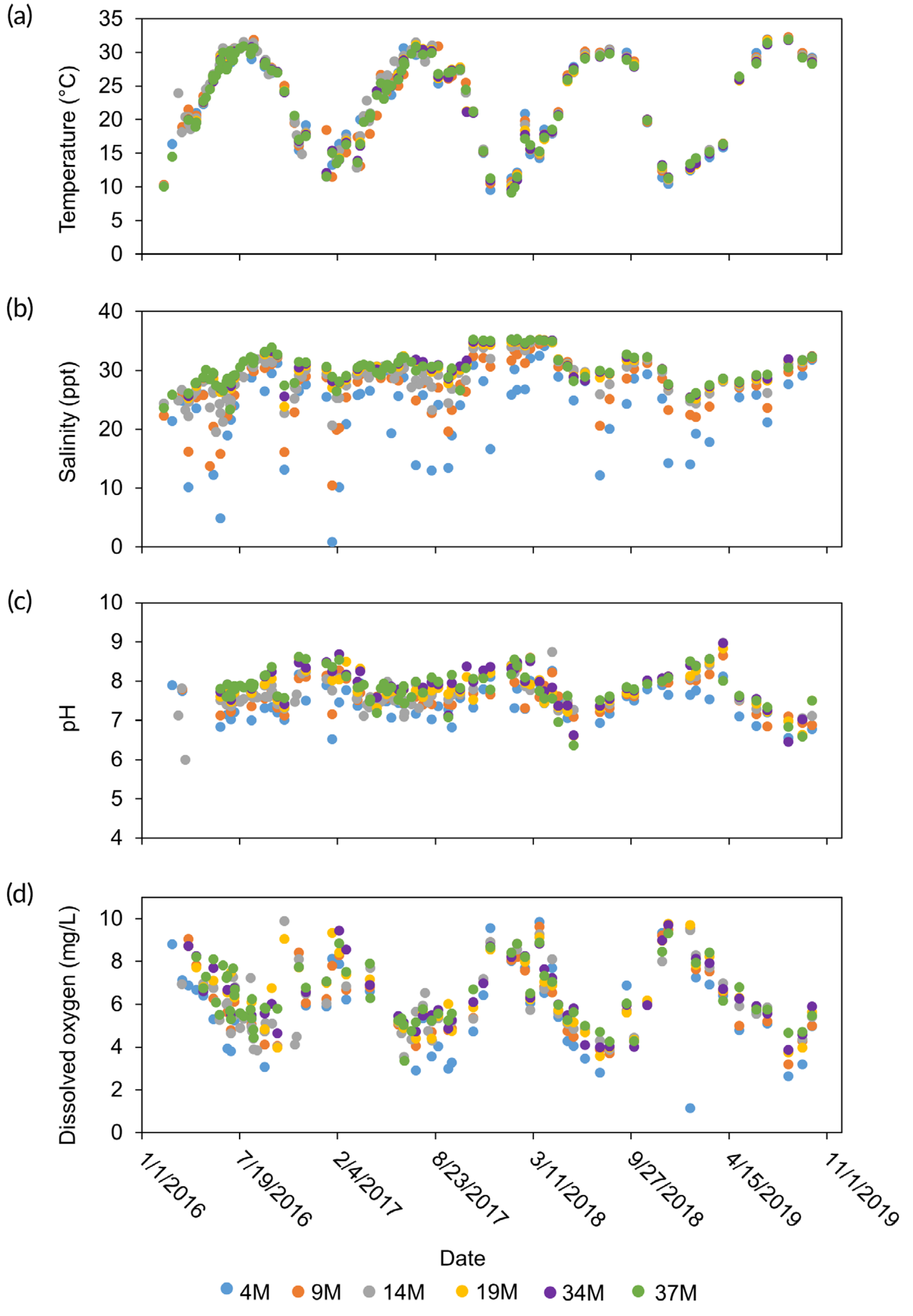

FIGURE 5 Comparisons of environmental parameters observed in the May River estuary from 2016 to 2019 at all six stations. Data from 2019 were included here to further highlight the variability throughout the May River estuary.

buzzes are directional, high frequency vocalizations that are used for navigation and foraging (Herzing, 1996, 2014; Janik, 2000). In the May River estuary, echolocation accounted for approximately 51%–89% of the total vocalizations near the headwaters (i.e., stations 4M, 9M, and 14M) and accounted for approximately 87%–94% near the mouth (i.e., stations 19M, 34M, and 37M).

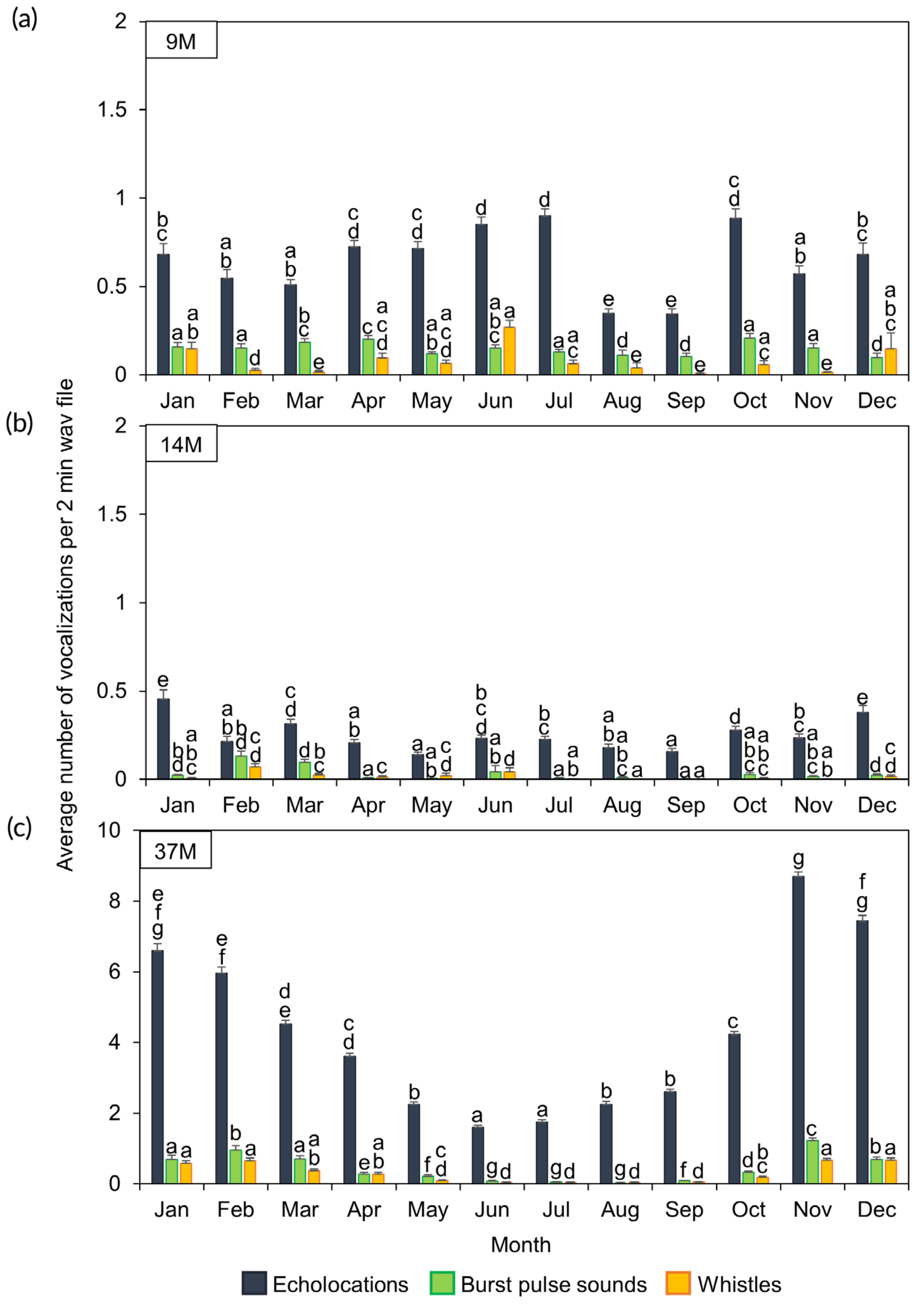

FIGURE 6 Monthly detections for bottlenose dolphin vocalizations at three stations in the May River estuary for 2013–2018 collectively. In order to see patterns at stations 9M and 14M, *y*-axes are not the same as 37M. Error bars indicate the standard error. Lettering above bars are based on Dunnett's post hoc tests. Different letters indicate significant differences in group means ($p < .05$).

Burst pulse sounds are more diverse and complex; these sounds are often referred to as barks, squawks, grunts, and screams that are used in a variety of social behaviors including aggression, discipline, courtship, and sexual activity (e.g., Herzing, 1996, 2014). Because of their complexity, they are the least studied vocalization type but there has

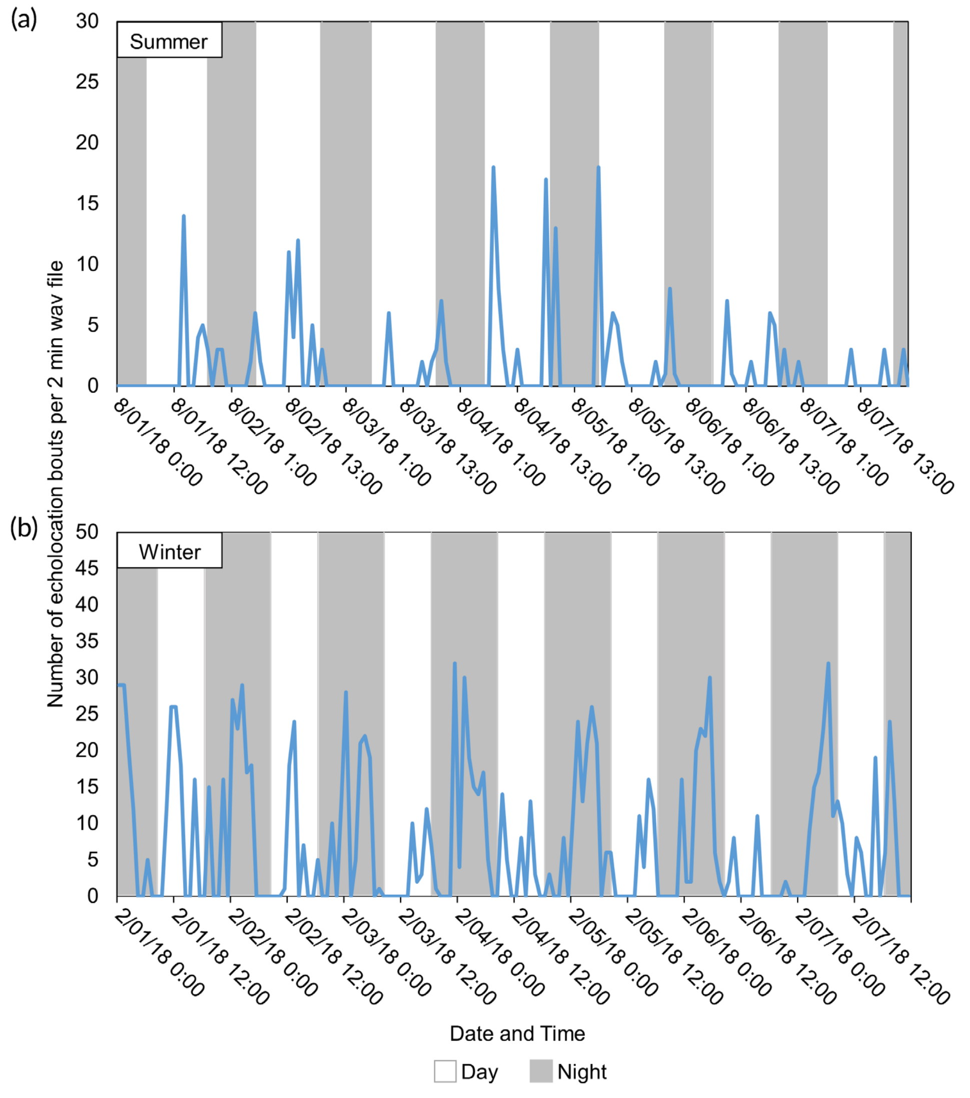

FIGURE 7 Detections of bottlenose dolphin echolocation collected on the hour at station 37M in the May River estuary for (a) one full week in summer and (b) one full week in winter.

been suggestion that burst pulse sounds comprise the majority of bottlenose dolphin vocalizations (e.g., Herman & Tavolga, 1980; Herzing, 2000). However, burst pulse sounds in the May River estuary only accounted for 10%–48% of the total vocalizations near the headwaters and 4%–11% near the mouth. Whistles are frequency and amplitude modulated vocalizations that are used for identification and localization (Caldwell & Caldwell, 1968; Herzing, 2014). In the May River estuary, whistles accounted for approximately 1%–8% of the total vocalizations both near the headwaters and the mouth.

4.2 | Spatial patterns

In the May River estuary, echolocation was most commonly detected at the mouth, which suggests this habitat may be important for foraging. Many studies have found that in coastal areas, habitat selection for foraging is influenced

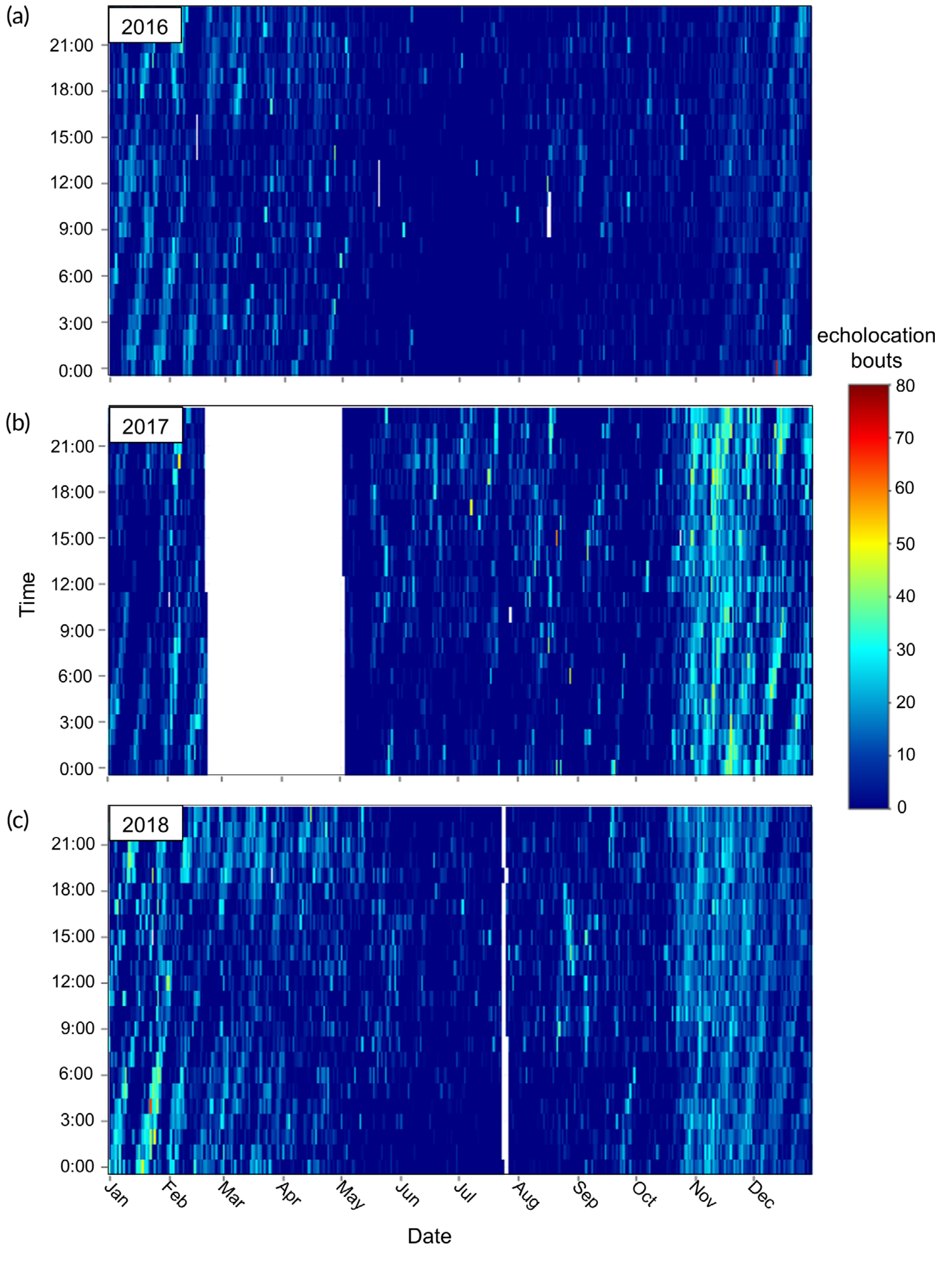

FIGURE 8 Temporal patterns of echolocation of bottlenose dolphins at station 37M in the May River estuary showing daily patterns collected at the mouth of the estuary for 3 years. Time interval indicated on the *y*-axis is between midnight and midnight the following day. The color scale indicates the number of echolocation bouts (warmer colors indicate more echolocation bouts detected). Gaps in data (white areas) are due to breaks in deployments or equipment failure. Stations 9M and 14M did not exhibit these patterns.

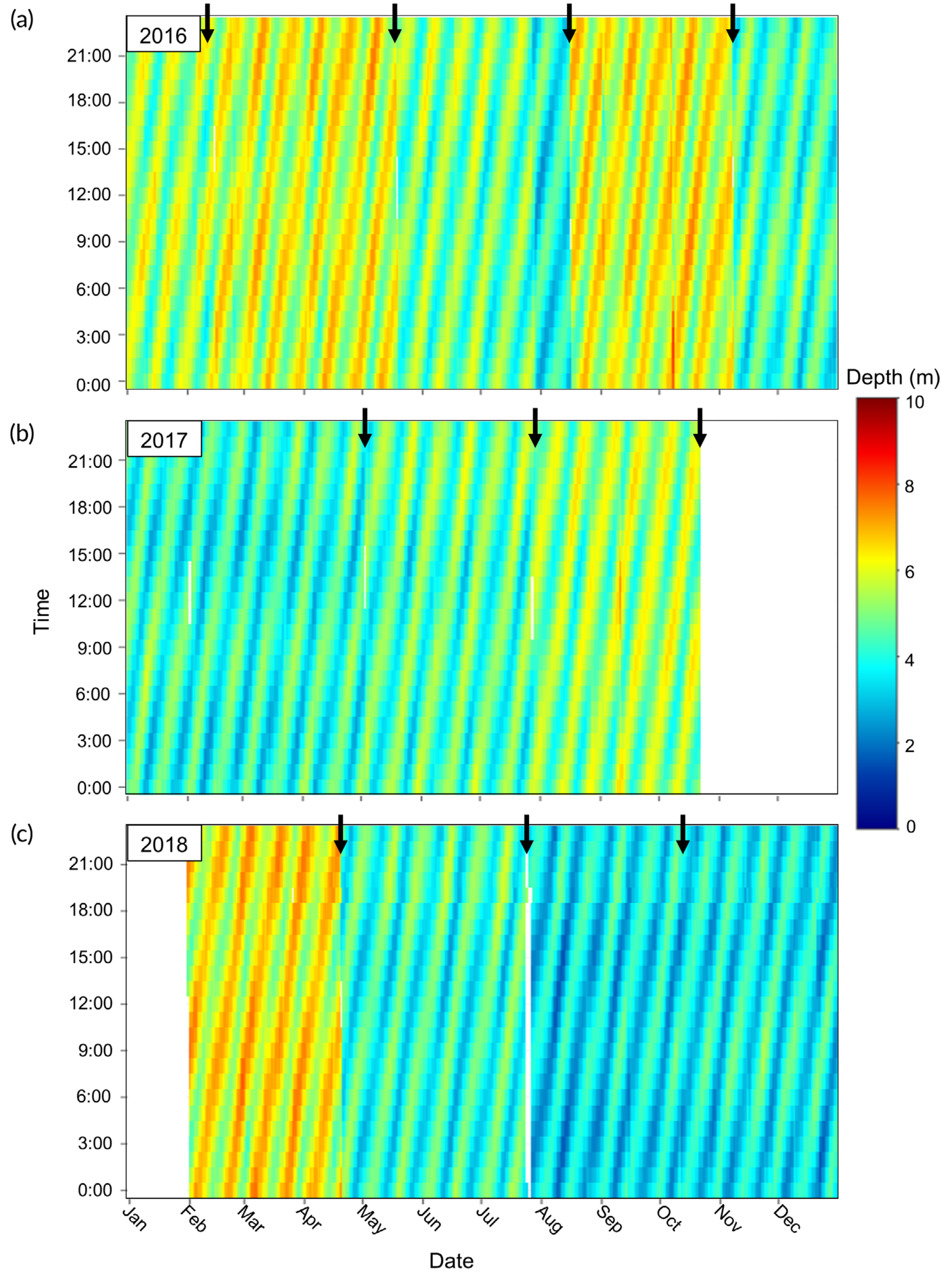

FIGURE 9 Depth data collected at station 37M in the May River estuary for 3 years. Depth loggers collected data every 10 min (HOBO 100-Foot Depth Water Level Data Logger U20-001-02-Ti; Onset Computer Corporation, Bourne, MA). Time interval is between midnight and midnight the following day. The color scale indicates depth (warmer colors indicate greater depths). In addition, warmer colors correspond to rising and high tides while cooler colors correspond to falling and low tides. Gaps in data (white areas) are due to breaks in deployments or equipment failure. Black arrows indicate servicing of recorders and loggers. Depth data from stations 9M and 14M exhibited similar patterns.

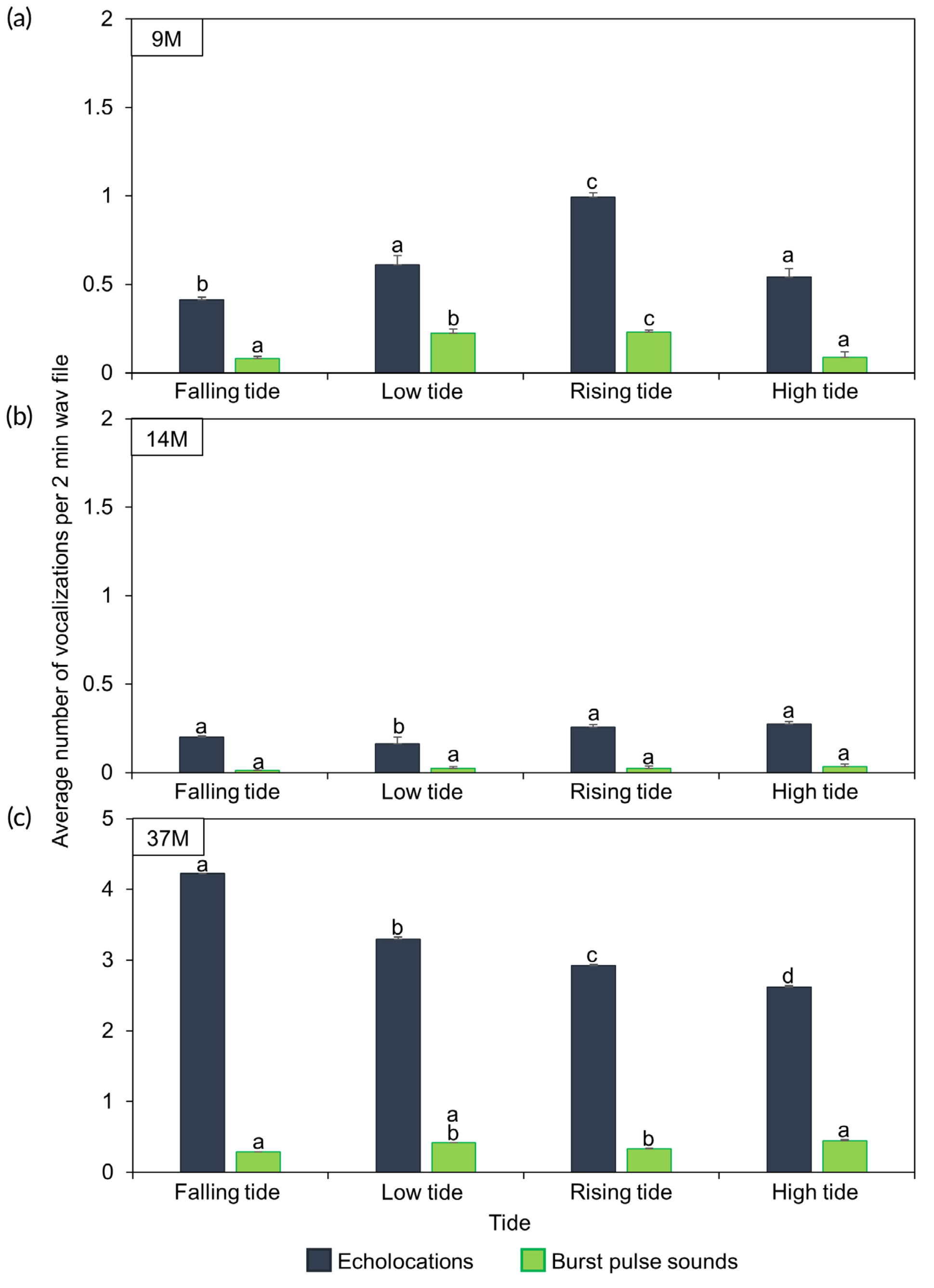

FIGURE 10 Detections of bottlenose dolphin vocalizations in the May River estuary during each phase of the tidal cycle at three stations for 2013–2018 collectively. Whistles were not included because tide was not a significant factor in the statistical model. In order to see patterns at stations 9M and 14M, y-axes are not the same as 37M. Error bars indicate the standard error. Lettering above bars are based on Dunnett's post hoc tests. Different letters indicate significant differences in group means ($p < .05$).

by changing depth and dynamic environmental variables, level of human development, and fish abundance (Allen et al., 2001; Harzen, 1998; Ingram & Rogan, 2002; Miller & Baltz, 2009). Previous research in the May River estuary detected fewer fish calls in the headwaters as compared to the mouth suggesting that the mouth may be a more favorable spawning location (Monczak et al., 2017; Montie et al., 2015). Bottlenose dolphins do prey on soniferous (sound-producing) fish such as those from the family Sciaenidae (Barros & Wells, 1998; Gannon et al., 2005; McCabe et al., 2010). These fish species, specifically spotted seatrout (*Cynoscion nebulosus*), red drum (*Sciaenops ocellatus*), black drum (*Pogonias cromis*), and silver perch (*Bairdiella chrysoura*), call more frequently at the mouth of the May River, possibly indicating higher abundance and larger spawning aggregations (Monczak et al., 2017; Montie et al., 2015). In Galveston, Texas, the mouth of the Galveston Shipping Channel was a core feeding area for bottlenose dolphins, most likely because it is an area of confluence with a visible tidal front, which may lead to the aggregation of prey (Moreno, 2005). Similarly, the mouth of Tampa Bay is known to have higher densities of dolphins as well as greater acoustic detections (Irvine et al., 1982; Simard et al., 2015). The Gulf of California is also an area in which dolphins have been observed in higher densities at the mouth of estuaries; dolphins use this area primarily for foraging (Ballance, 1992). Perhaps, the mouth of the May River estuary operates similarly and is an important area for feeding.

4.3 | Temporal patterns

Acoustic detections varied across multiple temporal scales with the clearest patterns seen at the mouth of the estuary. On an annual level, we detected more echolocation, burst pulse sounds, and whistles at the mouth during 2013, 2017, and 2018. These yearly patterns did not have any clear relationships with average yearly salinity or rainfall levels. During 2014, 2015, and 2016, it is possible that the overall abundance of dolphins in the estuary decreased or acoustic behavioral patterns changed.

Acoustic detections were also influenced by month with more echolocation, burst pulse sounds, and whistles detected at the mouth during November, January, and December. Preliminary visual survey data indicate that dolphin abundance at the mouth of the May River estuary is the highest in the spring and summer (data not shown). One alternative explanation for seasonal changes in acoustic behavior may be related to prey patterns. Dolphins have been found to select for soniferous fish; therefore, it may be possible that during times when fish are producing more sound (during their courtship and reproductive seasons) dolphins may rely on passive listening to forage (Barros & Wells, 1998; Gannon et al., 2005; McCabe et al., 2010). In the May River estuary, silver perch and black drum call from March to May, spotted seatrout begin calling in May and end in October, and red drum call mostly September to November (Monczak et al., 2017; Montie et al., 2015). The months in which dolphin vocalizations at the mouth were highest (November, December, and January) coincided with the fewest fish calls and choruses (Monczak et al., 2017; Montie et al., 2015). Thus, one hypothesis is that dolphins use passive listening during foraging in spring and summer when more fish are calling, resulting in a lower abundance of echolocation. In the winter, when less fish are calling and prey is scarce, dolphins may need to rely more on echolocation to locate and find food (Gannon et al., 2005; McCabe et al., 2010). This finding can have major implications for passive acoustic monitoring. How you interpret your results when using passive acoustics to monitor the occurrence of dolphins or foraging activity may be affected by times of the year when dolphins are utilizing more passive listening or changing echolocation rates based upon prey availability. Changes in foraging tactics by dolphins is why it may be necessary to count vocalizations other than echolocation, as we have done here. Future research such as fish sampling during different seasons throughout the May River estuary would provide insight into the abundance, distribution, and temporal changes in prey species in relation to echolocation detections.

Another hypothesis that may explain the distinct monthly patterns in acoustic detections near the mouth of the May River estuary is potential seasonal shifts in dolphin movements during the fall and winter from BSE (resident individuals) and overlapping coastal stocks. Movement patterns of these stocks may alter the abundance of dolphins in the May River estuary, particularly at the mouth, which is more accessible to the Atlantic Ocean. As we mentioned previously, we detected more vocalizations at the mouth during late fall and winter (November, December, and January). During this time of year, individuals from the Southern Migratory and/or South Carolina/Georgia Coastal

Stocks may enter the estuary. In addition, there is potential overlap from adjacent BSE stocks in this region. Preliminary visual data in the May River estuary suggests there may be a shift in overall distribution of residents towards the mouth during the fall and winter months; however, the overall abundance of dolphins is lowest in the fall and winter months (data not shown). Further studies integrating visual surveys are warranted and underway.

Movement of prey may explain the tidal patterns of echolocation we observed at the mouth of the estuary. Studies have shown that fish will follow the flooding tide into the marsh in search of shelter or food and then retreat to deeper water on the ebbing tide (Boesch & Turner, 1984; Butner & Brattstrom, 1960; Nixon & Oviatt, 1973; Peterson & Turner, 1994; Shenker & Dean, 1979). Perhaps during the ebb tide, dolphins increase their foraging behavior or shift their distribution from shallower tidal creeks to the main channels of the May River estuary, resulting in increased echolocation detections.

4.4 | Limitations

With passive acoustics come certain limitations, the first of which is decreased reliability of species identification and group size (Marques et al., 2013). In addition, in order for dolphins to be detected, animals need to be producing sound, and acoustic behavior can be influenced by many factors including anthropogenic activity, vessel presence, group size, and perhaps prey availability (Jones & Sayigh, 2002; Simard et al., 2015; Quick & Janik, 2008). Furthermore, we do not know the precise detection range of our acoustic recorders. Sound propagation varies depending on the environment and is affected by bottom type, salinity, temperature, bathymetry, and vegetation (Nowacek et al., 2001). Detection range can be determined using cylindrical spreading models or through empirical measurement via playback experiments (e.g., Jensen et al., 2012; Simard et al., 2015). However, both methods can be complicated and logistically challenging. One study conducted in the West Florida Shelf that used DSG Ocean recorders (with similar hydrophone sensitivity of −186 dBV/μPa) found that the detection range of bottlenose dolphin whistles using a cylindrical spreading model was approximately 200–300 m (Simard et al., 2015). Lastly, there is the physical act of deploying and retrieving equipment (Nuuttila et al., 2017). In our study, there were unavoidable gaps in data collection due to weather and equipment failure. All of these limitations need to be taken into consideration when interpreting these results.

4.5 | Summary

Our study demonstrated the utility of passive acoustics for studying the ecology and distribution of estuarine marine mammals. We used long-term passive acoustic data to monitor dolphins with much higher temporal resolution (sampling 24 hr, 7 days/week, 2 min every hour) than is possible with other methods. We found that higher numbers of echolocation bouts, burst pulse sounds, and whistles occurred at the mouth as compared to the headwaters. At the mouth, vocalizations were greatest in fall and winter for multiple years, and echolocation was greatest during falling and low tides. These results suggest that the mouth is a particularly important area for dolphins, likely for foraging. These data provide important information regarding acoustic behavior below the surface and may help to identify core foraging areas. Long-term monitoring of the acoustic patterns of bottlenose dolphins may be an additional gauge used to measure habitat and estuarine health. This approach allows us to eavesdrop on key behaviors that may change in response to environmental and human-induced changes, thus providing a measure of resilience or shifting baselines in a globally changing environment.

ACKNOWLEDGMENTS

We thank the following individuals for their assistance in collecting and analyzing acoustic data: Bradshaw McKinney, Andrea Parra, Hao Nguyen, Steven Vega, Rebecca Rawson, Travis Kinard, Ashley Freeman, Matt Hoover, Mike

Powell, Chris Kehrer, Andrea Berry, Alishia Zyer, Jenna MacKinnon, Mackenna Neuroth, Hannah Nylander, Michaela Miller, Claire Mueller, Somers Smott, Ashlee Seder, Joshua Himes, Shaneel Bivek, Debra Albanese, Jake Morgenstern, Caleb Shedd, Eva May, Austin Roller, Miane Jackson, Allison Davis, Lincoln Fuller, Corey Chase, Michelle Mixson, Stephanie Keller, and Shane Carey. We also thank Gorka Sancho from the University of Charleston for serving on the thesis committee under which this study was conducted. This work was supported by the Spring Island Trust, Town of Bluffton/Beaufort County, multiple University of South Carolina (USC) ASPIRE internal awards, Community Foundation of the Lowcountry, SC EPSCoR/IDeA Program award (#17-RE02), South Carolina Aquarium, Research Initiative for Summer Engagement (RISE) grant from USC, The LowCountry Institute, USCB Sea Islands Institute, Palmetto Bluff Conservancy, and the Port Royal Sound Foundation. This work was also supported, in part, by the Southeast Coastal Ocean Observing Regional Association (SECOORA) with NOAA financial assistance award number NA16NOS0120028. NOAA Integrated Ocean Observing System (IOOS). The statements, findings, conclusions, and recommendations are those of the author(s) and do not necessarily reflect the views of SECOORA or NOAA. In addition, A.M. received a Kathryn D. Sullivan Earth and Marine Science Graduate Fellowship to perform this work, which was supported by the South Carolina Sea Grant Consortium and S.C. Space Grant Consortium.

AUTHOR CONTRIBUTIONS

Alyssa Marian: Formal analysis; investigation; methodology; visualization; writing-original draft; writing-review & editing. **Agnieszka Monczak:** Data curation; investigation; methodology; writing-review & editing. **Brian Balmer:** Writing-review & editing. **Leslie Burdett Hart:** Formal analysis; writing-review & editing. **Jamileh Soueidan:** Data curation; methodology; writing-review & editing. **Eric Montie:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; software; supervision; validation; visualization; writing-original draft; writing-review & editing.

ORCID

Eric W. Montie https://orcid.org/0000-0003-4568-4963

REFERENCES

Allen, M. C., Read, A. J., Gaudet, J., & Sayigh, L. S. (2001). Fine-scale habitat selection of foraging bottlenose dolphins *Tursiops truncatus* near Clearwater, Florida. *Marine Ecology Progress Series*, *222*, 253–264. https://doi.org/10.3354/meps222253

Au, W. W. L. (1997). Echolocation in dolphins with a dolphin-bat comparison. *Bioacoustics*, *8*, 137–162. https://doi.org/10.1080/09524622.1997.9753357

Ballance, L. T. (1992). Habitat use patterns and ranges of the bottlenose dolphin in the Gulf of California, Mexico. *Marine Mammal Science*, *8*, 262–274. https://doi.org/10.1111/j.1748-7692.1992.tb00408.x

Balmer, B. C., Schwacke, L. H, Wells, R. S., Adams, J. D., George, R. C., Lane, S. M., McLellan, W. A., Rosel, P. E., Sparks, K., Speakman, T., Zolman, E. S., & Pabst, D. A. (2013). Comparison of abundance and habitat usage for common bottlenose dolphins between sites exposed to differential anthropogenic stressors within the estuaries of southern Georgia, U.S.A. *Marine Mammal Science*, *29*, E114–E145. https://doi.org/10.1111/j.1748-7692.2012.00598.x

Balmer, B. C., Wells, R. S., Schwacke, J. H., Danielson, B., George, R. C., Lane, S. M., McLellan, W. A., Pabst, D. A., Sparks, K., Speakman, T. R., Townsend, F. I., & Zolman, E. S. (2014). Integrating multiple techniques to identify stock boundaries of common bottlenose dolphins (*Tursiops truncatus*). *Aquatic Conservation: Marine and Freshwater Ecosystems*, *24*, 511–521. https://doi.org/10.1002/aqc.2357

Balmer, B., Zolman, E., Rowles, T., Smith, C., Townsend, F., Fauquier, D., George, C., Goldstein, T., Hansen, L., Quigley, B., McFee, W., Morey, J., Rosel, P., Saliki, J., Speakman, T., & Schwacke, L. (2018). Ranging patterns, spatial overlap, and association with dolphin morbillivirus exposure in common bottlenose dolphins (*Tursiops truncatus*) along the Georgia, USA coast. *Ecology and Evolution*, *8*, 12890–12904. https://doi.org/10.1002/ece3.4727

Barlow, J., & Taylor, B. L. (2005). Estimates of sperm whale abundance in the northeastern temperate Pacific from combined acoustic and visual survey. *Marine Mammal Science*, *21*, 429–445. https://doi.org/10.1111/j.1748-7692.2005.tb01242.x

Barros, N. B., & Wells, R. S. (1998). Prey and feeding patterns of resident bottlenose dolphins (*Tursiops truncatus*) in Sarasota bay, Florida. *Journal of Mammalogy*, *79*, 1045–1059. https://doi.org/10.2307/1383114

Bejder, L., Samuels, A., Whitehead, H., Gales, N., Mann, J., Connor, R., Heithaus, M., Watson-Capps, J., Flaherty, C., & Krützen, M. (2006). Decline in relative abundance of bottlenose dolphins exposed to long-term disturbance. *Conservation Biology*, *20*, 1791–1798. https://doi.org/10.1111/j.1523-1739.2006.00540.x

Boesch, D. F., & Turner, R. E. (1984). Dependence of fishery species on salt marshes: The role of food and refuge. *Estuaries*, *7*, 460–468. https://doi.org/10.2307/1351627

Bossart, G. D. (2011). Marine mammals as sentinel species for oceans and human health. *Veterinary Pathology*, *48*, 676–690. https://doi.org/10.1177/0300985810388525

Buckstaff, K. C. (2004). Effects of watercraft noise on the acoustic behavior of bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, *Florida. Marine Mammal Science*, *20*, 709–725. https://doi.org/10.1111/j.1748-7692.2004.tb01189.x

Butner, A., & Brattstrom, B. H. (1960). Local movement in Menidia and Fundulus. *Copeia*, *1960*, 139–141. https://doi.org/10.2307/1440210

Caldwell, M. C. & Caldwell, D. K. (1968). Vocalization of naive dolphins in small groups. *Science*, *159*, 1121–1123. https://doi.org/10.1126/science.159.3819.1121

Castellote, M., Brotons, J. M., Chicote, C., Gazo, M., & Cerdà, M. (2015). Long-term acoustic monitoring of bottlenose dolphins, *Tursiops truncatus*, in marine protected areas in the Spanish Mediterranean Sea. *Ocean and Coastal Management*, *113*, 54–66. https://doi.org/10.1016/j.ocecoaman.2015.05.017

Cook, M. L., Sayigh, L. S., Blum, J. E., & Wells, R. S. (2004). Signature-whistle production in undisturbed free-ranging bottlenose dolphins (*Tursiops truncatus*). *Proceedings of the Royal Society B: Biological Sciences*, *271*, 1043–1049. https://doi.org/10.1098/rspb.2003.2610

Dalrymple, R. W., Zaitlin, B. A., & Boyd, R. (1991). Estuarine facies models: Conceptual basis and stratigraphic implications. *Journal of Sedimentary Petrology*, *62*, 1130–1146. https://doi.org/10.1306/D4267A69-2B26-11D7-8648000102C1865D

Eggleston, D. B., Lipcius, R. R., Marshall, L. S., Jr., & Ratchford, S. G. (1998). Spatiotemporal variation in post larval recruitment of the Caribbean spiny lobster in the central Bahamas: lunar and seasonal periodicity, spatial coherence, and wind forcing. *Marine Ecology Progress Series*, *174*, 33–49.

Esch, H. C., Sayigh, L. S., Blum, J. E., & Wells, R. S. (2009). Whistles as potential indicators of stress in bottlenose dolphins (*Tursiops truncatus*). *Journal of Mammalogy*, *90*, 638–650. https://doi.org/10.1644/08-MAMM-A-069R.1

Gannon, D. P., Barros, N. B., Nowacek, D. P., Read, A. J., Waples, D. M., & Wells, R. S. (2005). Prey detection by bottlenose dolphins, *Tursiops truncatus*: An experimental test of the passive listening hypothesis. *Animal Behaviour*, *69*, 709–720. https://doi.org/10.1016/j.anbehav.2004.06.020

Gridley, T., Elwen, S. H., Rashley, G., Krakauer, A. B., & Heiler, J. (2017). Bottlenose dolphins change their whistling characteristics in relation to vessel presence, surface behavior and group composition. *Acoustical Society of America*, *27*, 010030. https://doi.org/10.1121/2.0000312

Gubbins, C. (2002). Use of home ranges by resident bottlenose dolphins (*Tursiops truncatus*) in a South Carolina estuary. *Journal of Mammalogy*, *83*, 178–187. https://doi.org/10.1644/1545-1542(2002)083%3C0178:UOHRBR%3E2.0.CO;2

Harzen, S. (1998). Habitat use by the bottlenose dolphin (*Tursiops truncatus*) in the Sado estuary, Portugal. *Aquatic Mammals*, *24*(3), 117–128.

Hayes, S. A., Josephson, E., Maze-Foley, K., Rosel, P. E. (2019). *US Atlantic and Gulf of Mexico Marine Mammal Stock Assessments – 2018*. (NOAA Technical Memorandum NMFS-NE 258). U.S. Department of Commerce. http://www.nefsc.noaa.gov/nefsc/publications/

Heithaus, M. R., Frid, A., Wirsing, A. J., & Worm, B. (2008). Predicting ecological consequences of marine top predator declines. *Trends in Ecology and Evolution*, *23*, 202–210. https://doi.org/10.1016/j.tree.2008.01.003

Hendry, J. L. (2004). *The ontogeny of echolocation in the Atlantic bottlenose dolphin* (Tursiops truncatus). (Doctoral dissertation). University of Southern Mississippi.

Herman, D. L., & Tavolga, W. N. (1980). Communication systems of cetaceans. In L. M. Herman (Ed.), *Cetacean behaviour: Mechanisms and function* (pp. 149–197). Wiley Interscience.

Herzing, D. L. (1996). Vocalizations and associated underwater behavior of free-ranging Atlantic spotted dolphins, *Stenella frontalis* and bottlenose dolphins *Tursiops truncatus*. *Aquatic Mammals*, *22*, 61–79.

Herzing, D. L. (2000). Acoustics and social behavior of wild dolphins: Implications for a sound society. In W. L. Au, R. R. Fay, & A. N. Popper (Eds.), *Hearing by whales and dolphins* (pp. 225–272). Springer.

Herzing, D. L (2014). Clicks, whistles, and pulses: Passive and active signal use in dolphin communication. *Acta Astronautica*, *105*, 534–537. https://doi.org/10.1016/j.actaastro.2014.07.003

Ingram, S. N., & Rogan, E. (2002). Identifying critical areas and habitat preferences of bottlenose dolphins *Tursiops truncatus*. *Marine Ecology Progress Series*, *244*, 247–255. https://doi.org/10.3354/meps244247

Irvine, A. B, Caffin, J. E., & Kochman, H. I. (1982). Aerial surveys for manatees and dolphins in western peninsular Florida. *Fishery Bulletin*, *80*, 621–630.

Jacobs, M., Nowacek, D. P., Gerhart, D. J., Cannon, G., Nowicki, S., & Forward, R. B. (1993). Seasonal changes in vocalizations during behavior of the Atlantic bottlenose dolphin. *Estuaries*, *16*, 241–246. https://doi.org/10.2307/1352496

Janik, V. M. (2000). Source levels and the estimated active space of bottlenose dolphin (*Tursiops truncatus*) whistles in the Moray Firth, Scotland. *Journal of Comparative Physiology A: Sensory, Neural, and Behavioral Physiology*, *186*, 673–680. https://doi.org/10.1007/s003950000120

Janik, V. M., & Slater, P. J. B. (1999). Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. *Animal Behavior*, *56*, 829–838. https://doi.org/10.1006/anbe.1998.0881

Janik, V. M., King, S. L., Sayigh, L. S., & Wells, R. S. (2013). Identifying signature whistles from recordings of groups of unrestrained bottlenose dolphins (*Tursiops truncatus*). *Marine Mammal Science*, *29*, 109–122. https://doi.org/10.1111/j.1748-7692.2011.00549.x

Jensen, F. H., Beedholm, K., Wahlberg, M., Bejder, L., & Madsen, P. T. (2012). Estimated communication range and energetic cost of bottlenose dolphin whistles in a tropical habitat. *Journal of the Acoustical Society of America*, *131*, 582–592. https://doi.org/10.1121/1.3662067

Jensen, F. H., Bejder, L., Wahlberg, M., Soto, A., Johnson, M., & Madsen, P. T. (2009). Vessel noise effects on delphinid communication. *Marine Ecology Progress Series*, *395*, 161–175. https://doi.org/10.3354/meps08204

Jones, G. J., & Sayigh, L. S. (2002). Geographic variation in rates of vocal production of free-ranging bottlenose dolphins. *Marine Mammal Science*, *18*, 374–393. https://doi.org/10.1111/j.1748-7692.2002.tb01044.x

Marley, S. A., Salgado Kent, C. P., Erbe, C. & Pamum, I. M. (2017). Effects of vessel traffic and underwater noise on movement, behavior and vocalisations of bottlenose dolphins in an urbanised estuary. *Scientific Reports*, *7*, 13427. https://doi.org/10.1038/s41598-017-13252-z

Marques, T. A., Thomas, L., Martin, S. W., Mellinger, D. K., Ward, J. A., Moretti, J., Harris, D., & Tyack, P. L. (2013). Estimating animal population density using passive acoustics. *Biological Reviews*, *88*, 287–309. https://doi.org/10.1111/brv.12001

McCabe, E. J. B., Gannon, D. P., Barros, N. B., & Wells, R. S. (2010). Prey selection by resident common bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. *Marine Biology*, *157*, 931–942. https://doi.org/10.1007/s00227-009-1371-2

Meade, R. H. (1969). Landward transport of bottom sediment in estuaries of the Atlantic coastal plain. *Journal of Sedimentary Petrology*, *39*, 222–234.

Mellinger, D. K., Stafford, K. M., Moore, S. E., Dziak, R. P., & Matsumoto, H. (2007). An overview of fixed passive acoustic observation methods for cetaceans. *Oceanography*, *20*, 36–45. https://doi.org/10.5670/oceanog.2007.03

Miller, C. E., & Baltz, D. M. (2009). Environmental characterizations of seasonal trends and foraging habitat of bottlenose dolphins (*Tursiops truncatus*) in northern Gulf of Mexico bays. *Fishery Bulletin*, *108*, 79–86. https://doi.org/10.1371/journal.pone.0005661

Monczak, A., Berry, A., Kehrer, C., & Montie, E. W. (2017). Long-term acoustic monitoring of fish calling provides baseline estimates of reproductive timelines in the May River estuary, southeastern USA. *Marine Ecology Progress Series*, *581*, 1–19. https://doi.org/10.3354/meps12322

Monczak, A., McKinney, B., Mueller, C., & Montie, E. W. (2020). What's all that racket! Soundscapes, phenology, and biodiversity in estuaries. *PloS ONE*, *15*(9), e0236874. https://doi.org/10.1371/journal.pone.0236874

Monczak, A., Mueller, C., Miller, M. E., Ji, Y., Borgianini, S. A., & Montie, E. W. (2019). Sound patterns of snapping shrimp, fish, and dolphins in an estuarine soundscape of the southeastern USA. *Marine Ecology Progress Series*, *609*, 49–68. https://doi.org/10.3354/meps12813

Montie, E. W., Vega, S., & Powell, M. (2015). Seasonal and spatial patterns of fish sound production in the May River, South Carolina. *Transactions of the American Fisheries Society*, *144*, 705–716. https://doi.org/10.1080/00028487.2015.1037014

Moreno, M. P. T. (2005). *Environmental predictors of bottlenose dolphin distribution and core feeding densities in Galveston Bay, Texas* (Doctoral dissertation). Texas A&M University.

Nixon, S. W., & Oviatt, C. A. (1973). Ecology of a New England salt marsh. *Ecological Monographs*, *43*, 463–498. https://doi.org/10.2307/1942303

Nowacek, S. M., Wells, R. S., & Solow, A. R. (2001). Short-term effects of boat traffic on bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, *Florida. Marine Mammal Science*, *17*, 673–688. https://doi.org/10.1111/j.1748-7692.2001.tb01292.x

Nuuttila, H. K., Courtene-Jones, W., Baulch, S., Simon, M., & Evans, P. G. H. (2017). Don't forget the porpoise: Acoustic monitoring reveals fine scale temporal variation between bottlenose dolphin and harbour porpoise in Cardigan Bay SAC. *Marine Biology*, *164*, 50. https://doi.org/10.1007/s00227-017-3081–35

Peterson, G. W., & Turner, R. E. (1994). The value of salt marsh edge vs interior as a habitat for fish and decapod crustaceans in a Louisiana tidal marsh. *Estuaries*, *17*, 235–262. https://doi.org/10.2307/1352573

Pirotta, E., Merchant, N. D., Thompson, P. M., Barton, T. R., & Lusseau, D. (2015). Quantifying the effect of boat disturbance on bottlenose dolphin foraging activity. *Biological Conservation*, *181*, 82–89. https://doi.org/10.1016/j.biocon.2014.11.003

Powell, J. R., & Wells, R. S. (2011). Recreational fishing depredation and associated behaviors involving common bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. *Marine Mammal Science*, *27*, 111–129. https://doi.org/10.1111/j.1748-7692.2010.00401.x

Quick, N. J., & Janik, V. M. (2008). Whistle rates of wild bottlenose dolphins (*Tursiops truncatus*): Influences of group size and behavior. *Journal of Comparative Psychology*, *122*, 305–311. https://doi.org/10.1037/0735-7036.122.3.305

Ritchie, E. G., & Johnson, C. N. (2009). Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, *12*, 982–998. https://doi.org/10.1111/j.1461-0248.2009.01347.x

Rosel, P. E., Mullin, K. D., Garrison, L., Schwacke, L., Adams, J., Balmer, B., Conn, P., Conroy, M. J., Eguchi, T., Gorgone, A., Hohn, A., Mazzoil, M., Schwartz, C., Sinclair, C., Speakman, T., Urian, K., Vollmer, N., Wade, P., Wells, R., & Zolman, E. (2011). *Photo-identification capture-mark-recapture techniques for estimating abundance of bay, sound, and estuary, populations of bottlenose dolphins along the U.S. east coast and Gulf of Mexico: A workshop report*. (NOAA Technical Memorandum NMFS SEFSC-621). U.S. Department of Commerce.

Ross, P. S., Barlow, J., Jefferson, T. A., Hickie, B. E., Lee, T., MacFarquhar, C., Parsons, E. C., Riehl, K. N., Rose, N. A., Slooten, E., Tsai, C., Wang, J. Y., Wright, A. J., & Yang, S. C. (2011). Ten guiding principles for the delineation of priority habitat for endangered small cetaceans. *Marine Policy*, *35*, 483–488. https://doi.org/10.1016/j.marpol.2010.11.004

Schwacke, L., Smith, C. R., Townsend, F. I., Wells, R. S., Hart, L. B., Balmer, B. C., Collier, T. K., Guise, S. D., Fry, M. M., Guillette, L. J., Lamb, S. V., Jr., Lane, S. M., McFee, W. E., Place, N. J., Tumlin, M. C., Ylitalo, G. M., Zolman, E. S., & Rowles, T. K. (2014). Health of common bottlenose dolphins (*Tursiops truncatus*) in Barataria Bay, Louisiana, following the *Deepwater Horizon* oil spill. *Environmental Science & Technology*, *48*, 93–103. https://doi.org/10.1021/es403610f

Shenker, J. M., & Dean, J. M. (1979). The utilization of an intertidal salt marsh creek by larval and juvenile fishes: Abundance, diversity and temporal variation. *Estuaries*, *2*, 154–163. https://doi.org/10.2307/1351729

Silva, D., Tranutolo, B., DeSalvio, E., Speakman, T., & Young, R. (2019). Abundance and movements of the Northern South Carolina Estuarine System Stock of bottlenose dolphins (*Tursiops truncatus*) (USA). *Journal of Marine Animals and Their Ecology*, *11*, 8–18.

Simard, P., Hibbard, A. L., McCallister, K. A., Frankel, A. S., Zeddies, D. G., Sisson, G. M., Gowans, S., Forys, E. A., & Mann, D. A. (2010). Depth dependent variation of the echolocation pulse rate of bottlenose dolphins (*Tursiops truncatus*). *Journal of the Acoustical Society of America*, *127*, 568–578. https://doi.org/10.1121/1.3257202

Simard, P., Wall, C. C., Allen, J. B., Wells, R. S., Gowans, S., Forys, E. A., Würsig, B., & Mann, D. A. (2015). Dolphin distribution on the west Florida shelf using visual surveys and passive acoustic monitoring. *Aquatic Mammals*, *41*, 167–187. https://doi.org/10.1121/1.3508911

Sloan, P. E. (2006). *Residency patterns, seasonality and habitat use among bottlenose dolphins,* Tursiops truncatus, *in the Cape Romain National Wildlife Refuge, SC* (Master's thesis). University of North Carolina Wilmington.

Speakman, T. R., Lane, S. M., Schwacke, L. H., Fair, P. A., & Zolman, E. S. (2010). Mark-recapture estimate of seasonal abundance and survivorship for bottlenose dolphins (*Tursiops truncatus*) near Charleston, South Carolina, USA. *Journal of Cetacean Research and Management*, *11*, 153–162.

Tellechea, J. S., Bouvier, D., Cambon-Tait, D., & Norbis, W. (2014). Passive acoustic monitoring of bottlenose dolphins (*Tursiops truncatus*) on the Uruguayan coast: Vocal characteristics and seasonal cycles. *Aquatic Mammals*, *40*, 173–184. https://doi.org/10.1578/AM.40.2.2014.173

Tyack, P. L. (1986). Whistle repertoires of two bottlenose dolphins, *Tursiops truncatus*: Mimicry of signature whistles? *Behavioral Ecology and Sociobiology*, *18*, 251–257. https://doi.org/10.1007/BF00300001

Van Ginkel, C., Becker, D. M., Gowans, S., & Simard, P. (2017). Whistling in a noisy ocean: Bottlenose dolphins adjust whistle frequencies in response to real-time ambient noise levels. *Bioacoustics*, *27*(4), 391–405. https://doi.org/10.1080/09524622.2017.1359670.

Watkins, W. A. (1968). The harmonic interval: Fact or artifact in spectral analysis of pulse trains. In W. N. Tavolga (Ed.), *Marine bioacoustics* (pp. 15–43). Pergamon Press. https://doi.org/10.1575/1912/2726

Weilgart, L. S. (2007). The impacts of anthropogenic ocean noise on cetaceans and implications for management. *Canadian Journal of Zoology*, *85*, 1091–1116. https://doi.org/10.1139/Z07-101

Wells, R. S., Allen, J. B., Hofmann, S., Bassos-Hull, K., Fauquier, D. A., Barros, N. B., DeLynn, R. E., Sutton, G., Socha, V., & Scott, M. D. (2008). Consequences of injuries on survival and reproduction of common bottlenose dolphins (*Tursiops truncatus*) along the west coast of Florida. *Marine Mammal Science*, *24*, 774–794. https://doi.org/10.1111/j.1748-7692.2008.00212.x

Wells, R. S., Rhinehart, H. L., Hansen, L. J., Sweeney, J. C., Townsend, F. I., Stone, R., Casper, D. R., Scott, M. D., Hohn, A. A., & Rowles, T. K. (2004). Bottlenose dolphins as marine ecosystem sentinels: Developing a health monitoring system. *EcoHealth*, *1*, 246–254. https://doi.org/10.1007/s10393-004-0094-6

Zolman, E. S. (2002). Residence patterns of bottlenose dolphins (*Tursiops truncatus*) in the Stono River estuary, Charleston County, South Carolina, U.S.A. *Marine Mammal Science*, *18*, 879–892. https://doi.org/10.1111/j.1748-7692.2002.tb01079.x

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

How to cite this article: Marian AD, Monczak A, Balmer BC, Hart LB, Soueidan J, Montie EW. Long-term passive acoustics to assess spatial and temporal vocalization patterns of Atlantic common bottlenose dolphins (*Tursiops truncatus*) in the May River estuary, South Carolina. *Mar Mam Sci*. 2021;1–25. https://doi.org/10.1111/mms.12800