

# Enhancing Interpretation of Cetacean Acoustic Monitoring: Investigating Factors that Influence Vocalization Patterns of Atlantic Bottlenose Dolphins in an Urbanized Estuary, Charleston Harbor, South Carolina, USA

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## Abstract

The Charleston Harbor in South Carolina (SC) is a major port that experiences high levels of vessel traffic. Historical analyses of coastal bottlenose dolphin (*Tursiops truncatus*, now *Tursiops erebennus*) sightings identified multiple core use areas in the harbor that overlap with these anthropogenic activities. Informed by these long-term spatial data, passive acoustic monitoring, visual surveys, and prey sampling were conducted from December 2017 to June 2019 to assess the relationships and multivariate interactions that may influence dolphin vocalization patterns. Vocalizations varied spatially and temporally, peaking in fall and winter months coinciding with decreases in water temperature and daylight hours, following patterns previously reported in other SC estuaries. Dolphin prey and total fish abundance decreased with water temperature, which may indicate that dolphins echolocate and whistle more frequently in the winter months when prey are scarce and sound-producing species are less soniferous. Dolphin sightings and vocalizations were highly correlated. Dolphin occurrence was highest in the areas surrounding the confluence of the Cooper and Wando Rivers, along the shipping channel, where vessel and sound-producing fish detections were greatest. When vessel noise occurred, dolphins increased their vocalizations, which suggests that this population may be modifying

its acoustic repertoire in response to increased noise levels. Multivariate interactions indicate strong spatial and seasonal patterns in vocalization rates that may be associated with dolphin and prey abundance as well as noise-induced redundancy.

**Key Words:** passive acoustics, visual sighting surveys, prey abundance, anthropogenic noise, vocal modification, bottlenose dolphins, *Tursiops truncatus*, *Tursiops erebennus*

## Introduction

Atlantic common bottlenose dolphins (*Tursiops erebennus*) are long-lived apex predators that are widely distributed in the coastal waters of South Carolina (SC) in the United States. They display high site fidelity in estuarine watersheds (Zolman, 2002; Speakman et al., 2010; Silva & Young, 2016) and may serve as bioindicators of ecosystem health (Wells et al., 2004; Bossart, 2011; Bassos-Hull et al., 2013). Monitoring sentinel populations over extended periods can help identify subtle shifts in behavior, abundance, and distribution that could indicate broader top-down or bottom-up effects (Castellote et al., 2020; Mintzer & Fazioli, 2021; Warren et al., 2021). In urbanized estuaries, dolphins face a multitude of threats such as the bioaccumulation of contaminants, vessel interactions, dredging operations, fisheries interactions, and noise pollution (Balmer

et al., 2012, 2018; Todd et al., 2015; Powell et al., 2018; Smott et al., 2018; Fair et al., 2019; Mintzer et al., 2022).

In Charleston Harbor, SC, bottlenose dolphins are exposed to chronic levels of noise associated with commercial and recreational vessels. Finished in December 2022, the Army Corps of Engineers Harbor Deepening Dredging Project established Charleston Harbor as the deepest on the East Coast, allowing for larger and more commercial vessels (U.S. Army Corps of Engineers, 2015). Associated underwater noise pollution can increase ambient sound pressure levels (SPLs), which can cause hearing loss, behavioral shifts, and auditory masking in bottlenose dolphins and lower trophic-level species that are reliant on acoustic cues (Clark et al., 2009; Jensen et al., 2009; Slabbekoorn et al., 2010; Smott et al., 2018). Auditory masking (i.e., the perceptual interference of a signal by noise) can result in missed foraging opportunities or loss of acoustic information during social interactions. Yet, cetaceans can alter their vocalizations and behaviorally adapt to noisy environments (Junqua et al., 1999; Lesage et al., 1999; Holt et al., 2009; van Ginkel et al., 2017). When exposed to noise, cetaceans can increase the amplitude, redundancy, and duration of their vocalizations, commonly known as the Lombard effect (van Ginkel et al., 2017). In urbanized estuaries like Charleston Harbor, it is important to understand how noise can influence the vocal repertoire of bottlenose dolphins to assess potential acute and chronic effects on behavior, distribution, and habitat use.

The Charleston Estuarine System Stock (CESS) is comprised of year-round resident bottlenose dolphins that inhabit Charleston Harbor and the surrounding bay, sound, and estuarine (BSE) tributaries. Visual surveys of the CESS began in 1994 and identified patterns in site fidelity, including annual residents, seasonal residents, and coastal transients (Zolman, 2002). Additional survey effort conducted across extended temporal and spatial scales identified 839 distinctive individual bottlenose dolphins in the Charleston Harbor estuary (Speakman et al., 2006). Dolphin abundance in the estuary peaked during the summer due to high numbers of seasonal residents and transients sighted near the mouth of the harbor (Speakman et al., 2010). Spatial analyses of sighting data from 2004 to 2009 found similar seasonality in abundance and identified several core use areas of the CESS (Bouchillon et al., 2019). The primary core use areas included a large area near the mouth of the harbor and several smaller hotspots, the majority of which were adjacent to or within the main shipping channel (Bouchillon et al., 2019).

Passive acoustic monitoring (PAM) of marine environments is an increasingly common, indirect

method used to describe the occurrence and distribution of marine mammal species (Rogers et al., 2013; Castellote et al., 2015; Monczak et al., 2019; Hersh et al., 2021; Marian et al., 2021). This approach focuses on understanding behavior while animals are submerged and not observable during visual surveys. PAM provides greater temporal resolution and data collection during adverse weather conditions and at night as compared to traditional survey methods (Mellinger et al., 2007). However, there are limitations to PAM, and vocalization rates are behavioral context-dependent, which can be challenging to extrapolate to abundance estimation (Marques et al., 2010; Rogers et al., 2013; Simard et al., 2015). Additional bias can be associated with dolphins that are present and not vocalizing (Barlow & Taylor, 2005; Dalpaz et al., 2021). Synchronous application of PAM with visual surveys provides greater certainty in detection rates, behavior, and site fidelity of cetacean species (Barlow & Taylor, 2005; Richman et al., 2014; Burnham et al., 2016; Dalpaz et al., 2021). This approach provides a comprehensive methodology to monitor cetaceans more efficiently and effectively, particularly in complex habitats like the Charleston Harbor, where noise may affect abundance, distribution, and behavior.

In a previous study, a brief report of the vocalization types of bottlenose dolphins as well as their spatial and temporal patterns was provided in a publication on the biological and anthropogenic soundscape of Charleston Harbor (Transue et al., 2023). However, it was outside the scope of that study to thoroughly investigate dolphin acoustic behavior and variables that may affect vocalization patterns. The current study utilized a combination of datasets (e.g., PAM, dolphin visual, fishery data) to investigate how abiotic, biotic, and anthropogenic factors influence bottlenose dolphin acoustic behavior across spatial and temporal scales in Charleston Harbor. This baseline acoustic study is necessary to understand the potential long-term impacts of the Charleston port expansion on bottlenose dolphins. A stepwise, multifaceted approach was taken to investigate vocalization patterns and factors that may influence these patterns in this urbanized estuary. Specific questions included the following: (1) What were the most common dolphin vocalizations detected? (2) Did specific dolphin vocalizations (echolocation bouts, burst pulse sounds, and whistles) vary spatially? (3) How did dolphin vocalizations vary over multiple temporal scales, including seasonal, lunar, diel, and tidal cycles? (4) Were dolphin vocalizations and visual sightings positively correlated? (5) Did seasonal prey abundance affect dolphin vocalization rates? and (6) How did anthropogenic noise affect dolphin vocalizations?

## Methods

### Study Area

Charleston Harbor (32° 40' N, 79° 55' W) is a natural tidal estuary formed by the confluence of the Ashley, Cooper, and Wando Rivers that eventually empties into the Atlantic Ocean (Figure 1). The harbor spans a total area of approximately 36.3 km<sup>2</sup> and is characterized by semi-diurnal tides, eastern oyster (*Crassostrea virginica*) reef beds, and *Spartina alterniflora* and *Juncus roemerianus* brackish salt marshes. Average depth in the harbor is 3.7 m at mean low water (MLW) but is three times deeper in the main shipping channel with an average tidal range of 1.6 m with mean spring tides of 1.9 m. Water temperature ranges from 3.5° to 30.7°C; salinity ranges from 0 to 35.6 ppt; and mean dissolved oxygen levels of 7.3 mg/l are found across the estuary with seasonal fluxes correlated to changes in water temperature (National Oceanic and Atmospheric Administration [NOAA], 2017).

On the western side of the harbor, the Ashley River extends 50 km southeast from its headwaters in Cypress Swamp, flowing west of the downtown peninsula and ultimately emptying into the harbor basin. The Ashley solely accommodates recreational boat traffic with mean depth ranging from 1.8 to 11.0 m. On the eastern side, the Cooper River is the largest of the tributaries, extending a total of 147 km from its headwaters at the Pinopolis Dam (west branch) and Hell Hole Bay (east branch) and flowing southwest to the harbor. Approximately 4.0 km above the mouth of the Cooper, the river splits into two channels that lead around Drum Island. Town Creek flows between Drum Island and the city waterfront, while the Cooper River continues east of the island and joins with the Wando River. The Wando flows 38 km from its headwaters in I'on Swamp and empties into the Cooper northeast of Drum Island. Located in the lower reaches of the Wando River, the Wando Welch Terminal (WWT) is the primary port in the harbor. The Columbus Street Terminal (CT) and Union Pier Terminal (UPT) are located along the southeastern downtown peninsula, while the Hugh K. Leatherman, Sr. Terminal (HLT) sits in the lower portion of the Cooper River (Figure 1). The entrance of the shipping channel at the mouth of the harbor is 14.3 m in depth and 13.7 m along the main channel (Figure 1B).

### Passive Acoustic and Environmental Data Collection

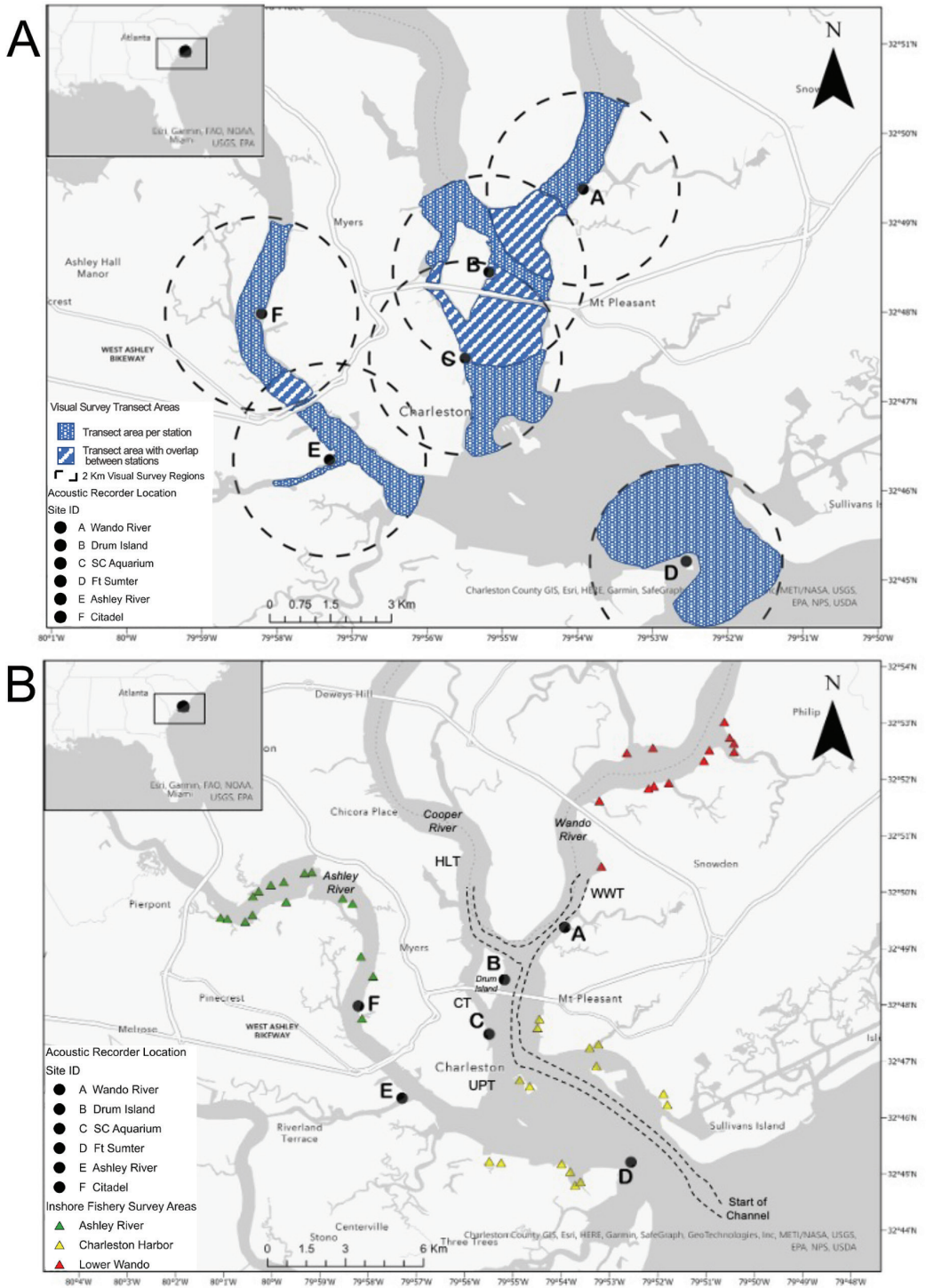
Autonomous passive acoustic recorders (DSG-ST; Loggerhead Instruments, Sarasota, FL, USA) were deployed at six stations in the Charleston Harbor from 11 December 2017 to 3 June 2019 (Figure 1). DSG-STs operated on a duty cycle of 2 min every

20 min at a sample rate of 96 kHz and were equipped with HTI-96-min hydrophones (High Tech Inc., Long Beach, MS, USA; hydrophone sensitivity of -201 dBV  $\mu$ Pa<sup>-1</sup>) with a flat frequency response between 2 and 30 kHz. The recorders had a system gain of 33 dB and system sensitivity of -168 dBV  $\mu$ Pa<sup>-1</sup>. Each recorder was mounted within a custom instrument frame (Mooring Systems Inc., Cataumet, MA, USA) and equipped with water temperature (HOBO Water Temperature Pro, Version 2 U22-001; Onset Computer, Bourne, MA, USA) and water level (HOBO 100-Foot Depth Water Level Data Logger U20-001-02-Ti; Onset Computer) loggers in PVC housing fastened to the frame. These environmental loggers recorded measurements every 20 min. Instrument frames were bottom mounted and attached to a 7 m chain. The chain was then attached to a line that was affixed to an auger along the shore (Stations B and E), a piling (Stations A and C), or dock (Stations D and F). Instruments were deployed for approximately 3 mo and were retrieved for downloading data and servicing, with weeklong gaps between re-deployments. All recordings were stored on 128-GB SD cards as DSG files and batch converted to wav files in post-processing. Before each deployment, recorders were tested by playing tones at 100, 200, 400, 800, 1,600, 3,200, 6,400, and 8,000 Hz. Root mean square (rms) sound pressure levels (SPLs) were calculated at each frequency to assess system functionality.

Recorder stations were chosen based on multiple criteria: (1) location of primary core use areas of the CESS dolphins (Bouchillon et al., 2019), (2) relative position within the harbor (i.e., mouth of the harbor, confluence regions, and upriver), and (3) proximity to the main shipping channel. Recorder stations included Station A (Wando River), Station B (Drum Island), Station C (SC Aquarium), Station D (Fort Sumter), Station E (Ashley River), and Station F (Citadel) (Figure 1).

### Review of Acoustic Files

Analysts manually reviewed passive acoustic data recorded in the first 2 min of the hour (e.g., 1200-1202 h, 1300-1302 h, 1400-1402 h, etc.) using *Adobe Audition*, Version CS5.5 (Adobe Inc., Mountain View, CA, USA). Spectrograms were visualized using a spectral resolution of 2,048 and a 10 s time window with 50% window overlap, no filter, and within the 0 to 48 kHz bandwidth. In each 2-min wav file, echolocation bouts, burst pulses, and whistles were counted separately and summed per file following methods previously described (e.g., Marian et al., 2021). Echolocation bouts were defined by the first and last visible click with an interbout interval two times greater than the preceding inter-click interval (Simard et al.,



**Figure 1.** (A) Map of study area of Charleston Harbor in South Carolina, displaying six passive acoustic stations that collected data from December 2017 to June 2019. Bimonthly visual bottlenose dolphin (*Tursiops erebennus*) surveys were conducted within a 2 km radius around each recorder station. (B) Passive acoustic stations and trammel net survey areas.

2010). Analysts did not count the individual clicks in echolocation click trains, which generally range from 50 to 80  $\mu\text{s}$  (Au, 1997). Discrete burst pulse sounds were determined by the beginning and end of distinctly outlined harmonic bands with high repetition (pulse intervals of 25 to 175 ms; Au, 1997; Marian et al., 2021) and not further categorized by subtypes (e.g., feeding buzzes, squawks, victory squeals). Whistles were defined as tonal signals and identified as distinct by the onset and termination of a single signal band (duration  $> 0.1$  s) with one or more frequency modulations or inflection points (Gridley et al., 2016; Marian et al., 2021). Due to constraints of PAM with multiple individuals vocalizing, overlapping whistles were observed occasionally and counted as single whistles to maintain uniformity in analysis.

Analysts quantified all other biological sounds (e.g., fish calls and/or choruses), physical sounds (e.g., waves, rain), and anthropogenic noise presence (e.g., from commercial and recreational vessels). Fish calls that were identified included silver perch (*Bairdiella chrysoura*), oyster toadfish (*Opsanus tau*), black drum (*Pogonias chromis*), spotted seatrout (*Cynoscion nebulosus*), and red drum (*Sciaenops ocellatus*). This process was completed by comparing spectrograms to previous studies (e.g., Luczkovich et al., 1999; Montie et al., 2015, 2016, 2017; Monczak et al., 2017). Analysts scored each 2-min wav file for each species based on four categories—0 = no calls, 1 = one call, 2 = multiple calls, and 3 = overlapping calls or chorusing—following methods previously described (Rountree & Luczkovich, 2002; Luczkovich et al., 2008; Monczak et al., 2017). Anthropogenic noise was marked as present (1) or absent (0) and not further categorized by source. Custom *MATLAB*, Version R2017b (MathWorks, Inc., Natick, MA, USA), scripts were used to calculate average rms broadband SPLs (1 to 40,000 Hz) for each 2-min wav file (i.e., every 20 min). Received broadband SPLs were calculated following Merchant et al. (2015) and Mueller et al. (2020):

$$S = h + g + 20 \log_{10}\left(\frac{1}{V_{\text{adc}}}\right) \quad (1)$$

$$b = 20 \log_{10}\{\sqrt{\text{mean}(y^2)}\} \quad (2)$$

$$a = b - S \quad (3)$$

where  $a$  is the calibrated sound level (dB re 1  $\mu\text{Pa}$ ),  $b$  is the uncorrected signal,  $S$  is the correction factor,  $h$  is the hydrophone sensitivity (i.e., -201 dBV  $\mu\text{Pa}^{-1}$ ),  $g$  is the DSG-ST gain (i.e., 33 dB),  $V_{\text{adc}}$  is the analog-to-digital conversion (i.e., 1 volt), and  $y$  is the signal (Monczak et al., 2017; Mueller et al., 2020).

Approximating recorder detection range of bottlenose dolphin vocalizations in an estuary such as Charleston Harbor is challenging due to variable bathymetry and depth, topography, seasonal perturbations, and diverse ambient noise (i.e., biological, anthropogenic, and physical sources) characterizing the region (Janik, 2000; Quintana-Rizzo et al., 2006; Urick, 2010; Jensen et al., 2012). Passive acoustic detection of directional calls, such as echolocation and burst pulses, is largely dependent on the orientation of the dolphin vocalizing with respect to the hydrophone (Au et al., 2012; Branstetter et al., 2012; Simard et al., 2015). Whistles are weakly directional and can assist in approximating recorder detection range under the assumption that dolphin orientation to the hydrophone is random (Jensen et al., 2012; Frankel et al., 2014; Simard et al., 2015). Investigation of bottlenose dolphin acoustic signals on the West Florida Shelf determined that the detection range of whistles was approximately 200 to 300 m using a cylindrical spreading model (Simard et al., 2015). In the present study, passive acoustic station locations were distanced 1 km or greater apart, with an average distance of 4.7 km between stations (Figure 1). In the Ashley River region, Stations E and F were approximately 3.1 km apart. In the harbor basin region, Stations E and C were approximately 7.4 and 5.8 km northwest of Station D, respectively. In the Cooper-Wando confluence region, Station A was approximately 2.3 km northeast of Station B. Near Drum Island and the mouth of the Cooper-Wando confluence, Stations B and C were approximately 1.6 km apart. Thus, duplication of dolphin acoustic detections across recorders was improbable.

#### Visual Bottlenose Dolphin Surveys

Visual photographic-identification (photo-ID) surveys in the Charleston Harbor spanned from December 2017 to May 2019. Line-transect boat surveys were conducted bimonthly within 2-km radii regions surrounding each recorder station (Figure 1A). Each station was surveyed for 50 min. Once bottlenose dolphin(s) were observed, the team recorded GPS location; start/end times of the sighting; group size estimates for total dolphins, calves, and neonates; dolphin behavior; weather conditions; water depth (m); and water quality measurements using a YSI ProDSS handheld multiparameter instrument (YSI Inc./Xylem Inc., Yellow Springs, OH, USA). Group size estimates included a minimum, maximum, and best estimated count for total dolphins, calves, and neonates. Water quality measures included water temperature ( $^{\circ}\text{C}$ ), salinity (ppt), dissolved oxygen (mg/L), and turbidity (NTU).

### *Inshore Fishery Trammel Net Surveys*

The South Carolina Department of Natural Resources (SCDNR) provided fishery-independent data on the abundance of salt marsh-edge fish species collected through their trammel net survey program (Wenner, 2000). This survey provides long-term abundance estimates on a wide range of fish species that inhabit SC estuarine waters. Surveys are performed using a stratified random sampling design and cover areas across strata that fall across five SC estuaries: (1) Port Royal Sound, (2) St. Helena Sound, (3) Charleston Harbor, (4) Cape Romain & Bulls Bay, and (5) Winyah Bay. Each stratum is surveyed monthly, and sites within each stratum are randomly selected and sampled during early, mid, or late ebb tides. Trammel nets are 184 m in length and 2.1 m deep with an outer layer of 177 mm mesh and an inner layer of 63 mm mesh. Nets are set adjacent to the shore by a fast-moving boat in less than 2 m depth. Prior to retrieval, the water surface is forcefully disturbed with long planks along the full length of the area to corral fish into the net (Arnott et al., 2010). Teams identify and quantify each species, and determine standard lengths for each fish.

In the present study, total prey species and fish abundance were assessed for the Ashley River, Lower Wando River, and Charleston Harbor strata (Figure 1B). Prey species included those fish belonging to the Families Mugilidae, Sciaenidae, Bothidae, Elopidae, Sparidae, Stromateidae, Anguillidae, Haemulidae, Synodontidae, and Engraulidae. This prey classification was based on diet composition analyses of stranded bottlenose dolphins off the SC coast (Pate & McFee, 2012). Total fish included prey species and all other species caught, but excluded turtle, crab, and elasmobranch species that would be unlikely prey.

### *Data Modeling and Statistical Analysis*

*Investigating Factors Influencing Dolphin Vocalizations*—All statistical analyses were performed using *R* software, Version 4.2.2. As a first step in assessing long-term trends in vocalization patterns, we tested the influence of spatial (i.e., location), temporal (i.e., lunar, day/night cycle, and tidal cycles), environmental (i.e., water temperature), biological (i.e., fish calling by species), and anthropogenic (i.e., noise presence) factors on each bottlenose dolphin vocalization type (i.e., counts of total vocalizations, echolocation bouts, whistles, and burst pulses) using random forest (RF) modeling. Four categories were used to distinguish the lunar cycle: (1) new moon (lunar days 27 to 4), (2) first quarter (lunar days 5 to 11), (3) full moon (lunar days 12 to 19), and (4) third quarter (lunar days 20 to 26) (Monczak et al., 2017, 2019, 2022; Marian et al., 2021). Tidal

stage was distinguished using four categories: (1) rising tide, (2) slack high, (3) falling tide, and (4) slack low. Day and night cycles were differentiated using sunrise and sunset times.

The *R* package ‘Boruta,’ an RF wrapper algorithm, builds numerous decision trees to assess and rank variable importance, and reports a boxplot of mean importance scores (‘Boruta’ Z-scores; Kursa & Rudnicki, 2010; Kursa, 2014; Wright et al., 2017; Degenhardt et al., 2019; Monczak et al., 2022). Random forest is a supervised learning algorithm that uses bootstrap aggregation (i.e., bagging) methods and feature randomness (i.e., randomization of the subset of features generated) to construct a multitude of decision trees against a training set and combines the output of all the trees to reach a result. This method decreases the chance of overfitting the model and increases accuracy of large datasets even in the presence of missing values. For standardization across models, the set seed was 42, and the *p* value was 0.01. The number of decision trees built and random sampling of variables at each split (the total number of variables divided by three) depended on the dolphin vocalization type and number of confirmed variables in the model. Models were chosen based on multiple criteria: (1) assessment of ‘Boruta’ variable importance boxplots, (2) mean variance explained, (3) root mean squared residual error (RMSE), and (4) out-of-bag (OOB) error plot with the number of decision trees of fitted model tested. Post-hoc, Dunnett-Tukey-Kramer tests determined significant differences for multi-level categorical variables using the ‘DTK’ package in *R* (Lau, 2013).

Due to high temporal variability observed in dolphin vocalizations, fish chorusing, and anthropogenic noise patterns, focused models confirmed variable importance and reduced the likelihood of collinearity. To investigate the influence of fish chorusing on dolphin vocalizations, one RF model focused on data from March to October (2018 only), a period when sciaenid fish species produce chorusing aggregations in the U.S. southeast (e.g., Monczak et al., 2017, 2019, 2022; Mueller et al., 2020). To investigate the influence of vessel noise on dolphin vocalizations, a second RF model focused on data from December 2017 to February 2018 and November 2018 to February 2019, periods when fish calls were absent or minimal. Wilcoxon rank-sums tested whether broadband SPLs were different ( $\alpha = 0.05$ ) when vessel noise was detected as compared to periods when noise was not present.

*Relationships Between Dolphin Vocalizations and Sighting Abundance*—Acoustic and visual photo-ID survey data were matched systematically by recorder location and time. In *ArcGIS Pro*

(Esri, Redlands, CA, USA), geoprocessing tools ('Near Feature Analysis,' geodesic method, search radius of 2 km) matched all visual bottlenose dolphin sighting events to the nearest recorder station within a 2 km radius using GPS coordinate data of sighting events and recorder stations. Sightings that took place in Town Creek that occurred during the visual survey around Drum Island (Station B) were instead matched to the SC Aquarium (Station C). Acoustic files within 10 min or less of the start or end time of a dolphin sighting event were selected from the matched recorder station to connect vocalization and sighting detections.

While bottlenose dolphin visual surveys occurred in 2-km radii regions around each recorder station, recorders collected acoustic data for 2 min every 20 min. For matching vocalizations to sightings, additional acoustic files were analyzed on the 20- and 40-min time marks to match sightings closest in time to acoustic sampling. This adjustment in analysis strengthened temporal resolution. To account for occurrences when no dolphins were sighted at a particular site and time, the zero abundance estimates from surveys were matched to vocalizations detected on the hour that fell within or closest to the 50-min visual survey period.

Multiple linear regression modeling evaluated the relationship between vocalizations (i.e., counts of total vocalizations, echolocation bouts, whistles, and burst pulse sounds as dependent variables) and sighting abundance (i.e., total dolphin best estimate counts), station, and water temperature as independent variables. Model selection was based on a backward stepwise selection and used Akaike information criterion (AIC) for model comparisons. Multiple models were assessed for best fit and included multiple regression (AIC total vocalizations = 39.40; echo bouts = 34.29; whistles = -44.09) and generalized linear models (GLMs) with Gaussian (AIC total vocalizations = 347.89; echo bouts = 342.78; whistles = 264.40), Negative Binomial (AIC total vocalizations = 681.64; echo bouts = 614.90; whistles = 317.28), and Poisson (AIC total vocalizations = 2,053.40; echo bouts = 1,690.3; whistles = 563.47) distributions. Multiple linear regression modeling with a  $\log_{10}$  transformation of vocalization data had the lowest AIC. Boxplots were used to identify extreme outliers, and normality was confirmed by visual inspection of histograms, residual variance, and QQ-plots. Tukey Kramer Honest Significant Difference (HSD) tests identified differences among categorical variables.

*Relationships Between Dolphin Vocalizations and Prey Abundance*—Trammel net survey strata and recorder stations were matched by geographic location: Lower Wando stratum matched to Wando

River (Station A) and Drum Island (Station B) acoustics; Charleston Harbor stratum matched to SC Aquarium (Station C) and Fort Sumter (Station D) acoustics; and Ashley River stratum matched to Ashley River (Station E) and Citadel (Station F) acoustics (Figure 1B). Total fish and prey species were summed for total abundance and then divided by total number of net throws (i.e., catch per unit effort [CPUE]). Echolocation bouts and whistles occurring on the days of trammel surveys were summed daily and paired recorder stations averaged. They were then matched to the corresponding total prey and total fish abundance (CPUE corrected). Echolocation and whistles were selected to assess foraging behavior.

To investigate the relationship of prey or total fish abundance (CPUE corrected) with dolphin vocalizations, Kendall's tau-b correlations assessed the influence of water temperature on prey/total fish abundance and dolphin vocalizations separately. Kendall's tau-b was chosen because it is a nonparametric, rank-based test of strength and directionality of association between two variables, and all variables (except total fish abundance) assessed were not normally distributed.

## Results

### *Spatial Patterns in Dolphin Vocalizations*

From 11 December 2017 to 3 June 2019, a total of 165,886 bottlenose dolphin vocalizations were detected across 70,400 files collected from all six stations (Table 1). Across all stations, echolocation occurred in the most 2-min wav files (15,535) as compared to whistles (3,732) and burst pulse sounds (2,221). Burst pulse sounds displayed the highest variability in occurrence and frequency with resultant RF models exhibiting poor performance. Thus, burst pulse sounds were not evaluated in multivariate analyses.

Bottlenose dolphin vocalizations varied spatially among stations (Figures 2 & 3). All RF models tested (i.e., total vocalizations, echolocation bouts, or whistles) ranked station first or second in predicting vocalizations and explaining variance in acoustic behavior ( $p < 0.01$ ; Figure 3). Near the mouth of the Cooper-Wando confluence, vocalizations were greatest at the Wando River (Station A), Drum Island (Station B), and SC Aquarium (Station C) locations (Tables 1 & 2; Figures 2 & 3). Vocalizations were higher at the mouth of the Ashley River (Station E) compared to Fort Sumter (Station D), near the mouth of the harbor (Table 2; Figure 2). Further upriver in the Ashley, the Citadel (Station F) detected the least number of vocalizations (Tables 1 & 2; Figure 2).

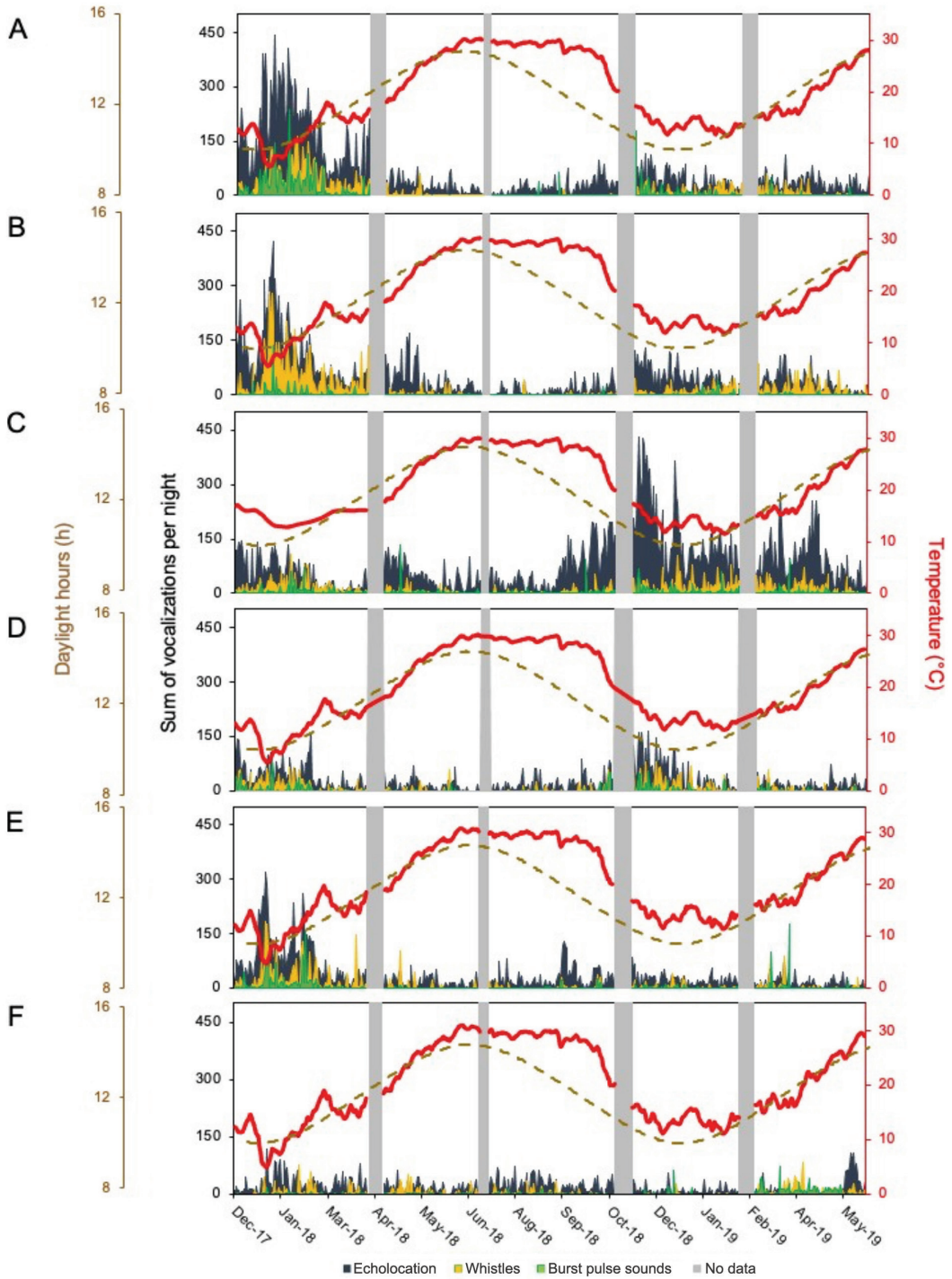
**Table 1.** Bottlenose dolphin (*Tursiops erebennus*) vocalizations in Charleston Harbor, SC, from 11 December 2017 to 3 June 2019

Year	Station	Total files analyzed	Echo bouts (%)*	Burst pulse sounds (%)*	Whistles (%)*	Total vocalizations counted	Echo bouts (%)**	Burst pulse sounds (%)**	Whistles (%)**
2017	A	488	254 (52.05)	32 (6.56)	49 (10.04)	3,088	2,493 (80.73)	242 (7.84)	353 (11.43)
	B	488	230 (47.13)	2 (0.41)	28 (5.74)	2,467	2,149 (87.11)	40 (1.62)	278 (11.27)
	C	488	182 (37.30)	12 (2.46)	28 (5.74)	1,827	1,635 (89.49)	28 (1.53)	164 (8.98)
	D	492	119 (24.19)	23 (4.67)	57 (11.59)	1,684	1,141 (67.76)	165 (9.80)	378 (22.45)
	E	488	139 (28.48)	19 (3.89)	139 (28.48)	1,385	1,140 (83.31)	80 (3.39)	165 (11.91)
	F	488	62 (12.70)	1 (0.20)	65 (13.32)	242	230 (95.04)	1 (0.41)	11 (4.55)
2018	A	7,921	2,464 (31.11)	452 (5.71)	664 (8.38)	31,041	22,406 (72.18)	3,230 (10.41)	5,405 (17.41)
	B	7,858	1,782 (22.68)	100 (1.27)	547 (6.96)	20,446	14,757 (70.77)	569 (2.73)	5,120 (24.56)
	C	7,862	2,420 (30.78)	336 (4.27)	504 (6.41)	28,374	23,598 (83.17)	1,396 (4.92)	3,380 (11.91)
	D	7,915	975 (12.32)	115 (1.45)	292 (3.69)	12,275	8,791 (71.62)	1,032 (8.40)	2,452 (19.98)
	E	7,916	1,695 (21.41)	291 (3.68)	289 (3.65)	17,344	12,605 (72.68)	1,372 (7.91)	3,367 (19.41)
	F	7,917	1,062 (13.41)	110 (1.39)	131 (1.65)	7,941	6,313 (79.50)	373 (4.70)	1,255 (15.80)
2019	A	3,348	712 (21.27)	70 (2.09)	137 (4.09)	5,460	4,077 (74.67)	278 (5.09)	1,105 (20.24)
	B	3,347	687 (20.53)	43 (1.28)	233 (6.96)	6,234	4,085 (65.53)	233 (3.74)	1,916 (30.73)
	C	3,346	1,490 (44.53)	185 (5.53)	293 (8.76)	15,639	12,587 (80.48)	640 (4.09)	2,412 (15.42)
	D	3,349	311 (9.29)	33 (0.99)	75 (2.24)	2,951	2,127 (72.08)	188 (6.37)	636 (21.55)
	E	3,340	359 (10.75)	31 (0.93)	57 (1.71)	2,726	1,920 (70.43)	356 (13.06)	450 (16.51)
	F	3,349	592 (17.68)	366 (10.93)	144 (4.30)	3,145	1,632 (51.89)	799 (25.41)	714 (22.70)

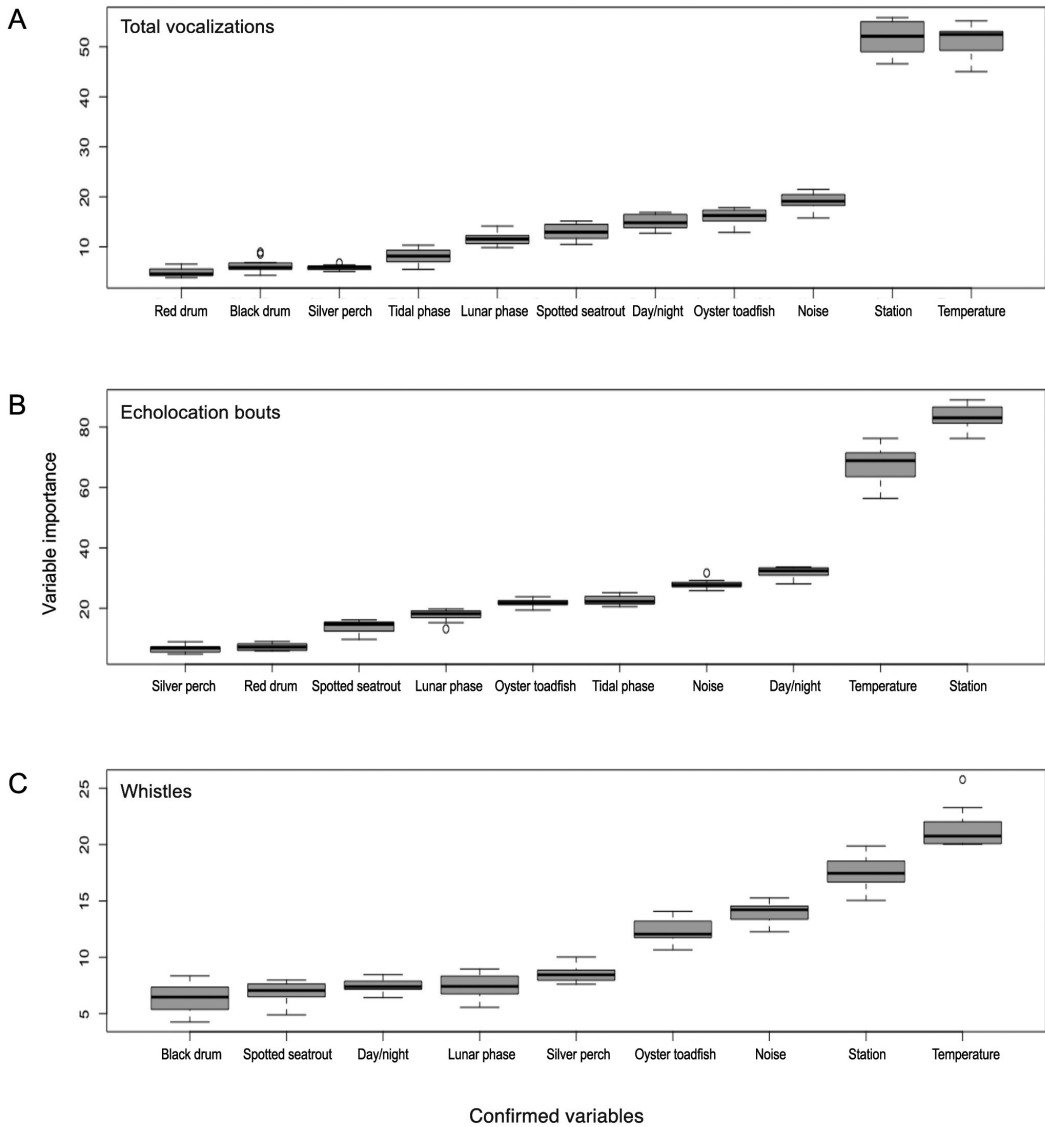
\*Total # of files with vocalization detections/total # of files analyzed, then multiplied by 100% for a percent detection (%)

\*\*Total # of specific vocalizations/total # counted multiplied by 100% for a percent vocalization (%)





**Figure 2.** Seasonal and spatial patterns of bottlenose dolphin vocalizations in the Charleston Harbor from December 2017 to June 2019. Sum of echolocation bouts, whistles, and burst pulses per night at (A) Wando River, (B) Drum Island, (C) SC Aquarium, (D) Fort Sumter, (E) Ashley River, and (F) Citadel. Also shown are hours of daylight (brown dotted line) and water temperature (red line). Gray bars indicate gaps in data due to maintenance of equipment.



**Figure 3.** Variable importance of confirmed factors that influenced bottlenose dolphin vocalizations as determined through random forest modeling. Vocalizations assessed included (A) total vocalizations, (B) echolocation bouts, and (C) whistles from 11 December 2017 to 1 June 2019 at all six stations.

#### *Temporal Patterns in Dolphin Vocalizations*

Seasonal (i.e., water temperature), lunar, day/night, and tidal cycles influenced vocalizations, but season had the strongest effect (Figures 2 & 3). Across all stations excluding the Citadel, vocalizations peaked in abundance in the fall and winter with decreasing water temperatures before declining significantly in late spring and into summer as temperatures increased (Figure 2). Total vocalizations and echolocation bouts were greatest on the

falling tide and lowest on the rising tide (Table 2). The influence of the tidal cycle on bottlenose dolphin vocalizations was most apparent in the diagonal pattern observed in the echolocation heat map, where echolocation bouts increased dramatically on the low tides (Supplemental Figure 1; supplemental figures for this article are available in the “Supplemental Material” section of the *Aquatic Mammals* website). This tidal effect on echolocation was observed only during fall and winter

**Table 2.** Significant differences of Dunnett's Tukey-Kramer Multiple Comparison post hoc tests for factors that influenced bottlenose dolphin vocalizations using all long-term data in random forest (RF) model; *n*tree = number of decision trees in RF model.

RF model	Total vocalizations factor ranks	Echo bout factor ranks	Whistle factor ranks
	<i>n</i> tree = 440	<i>n</i> tree = 400	<i>n</i> tree = 380
% variance explained	14.49	17.66	2.52
Mean sq. residuals	46.97	20.73	9.46
Station*	C > A > B > E > D > F	C > A > B > E > D > F	A = C > B > E > D > F
Lunar phase	Third > full > first, new	Third > full > first, new	Third > full > first, new
Tidal phase	Falling > rising	Falling > rising	Factor rejected
Day/night	Night > day	Night > day	Night > day
Noise**	1 > 0	1 > 0	1 > 0
Oyster toadfish***	0 > 2 = 1, 3 > 2	0 > 2 > 1 = 3	0 > 2 = 3 = 1
Spotted seatrout***	0 > 2 > 3 = 1	0 > 3 = 2 = 1	0 > 3 = 2 = 1
Silver perch***	0 > 2 = 3 = 1	0 > 2 = 1 = 3	0 > 2 = 3 = 1
Red drum***	0 > 2 = 3, 0 = 1	0 > 2 > 3 = 1	Factor rejected
Black drum***	0 > 2 = 3, 0 = 1	Factor rejected	0 > 2 = 3 = 1

\*Stations: (A) Wando River, (B) Drum Island, (C) SC Aquarium, (D) Fort Sumter, (E) Ashley River, and (F) Citadel

\*\*0 = no noise present; 1 = noise present

\*\*\*Fish calling scores: 0 = no calls, 1 = one call, 2 = multiple calls, and 3 = chorusing

months, most prominently at the SC Aquarium from 31 October 2018 to 3 March 2019, and the Wando River and Drum Island from 11 December 2017 to 1 March 2018 (Supplemental Figure 1).

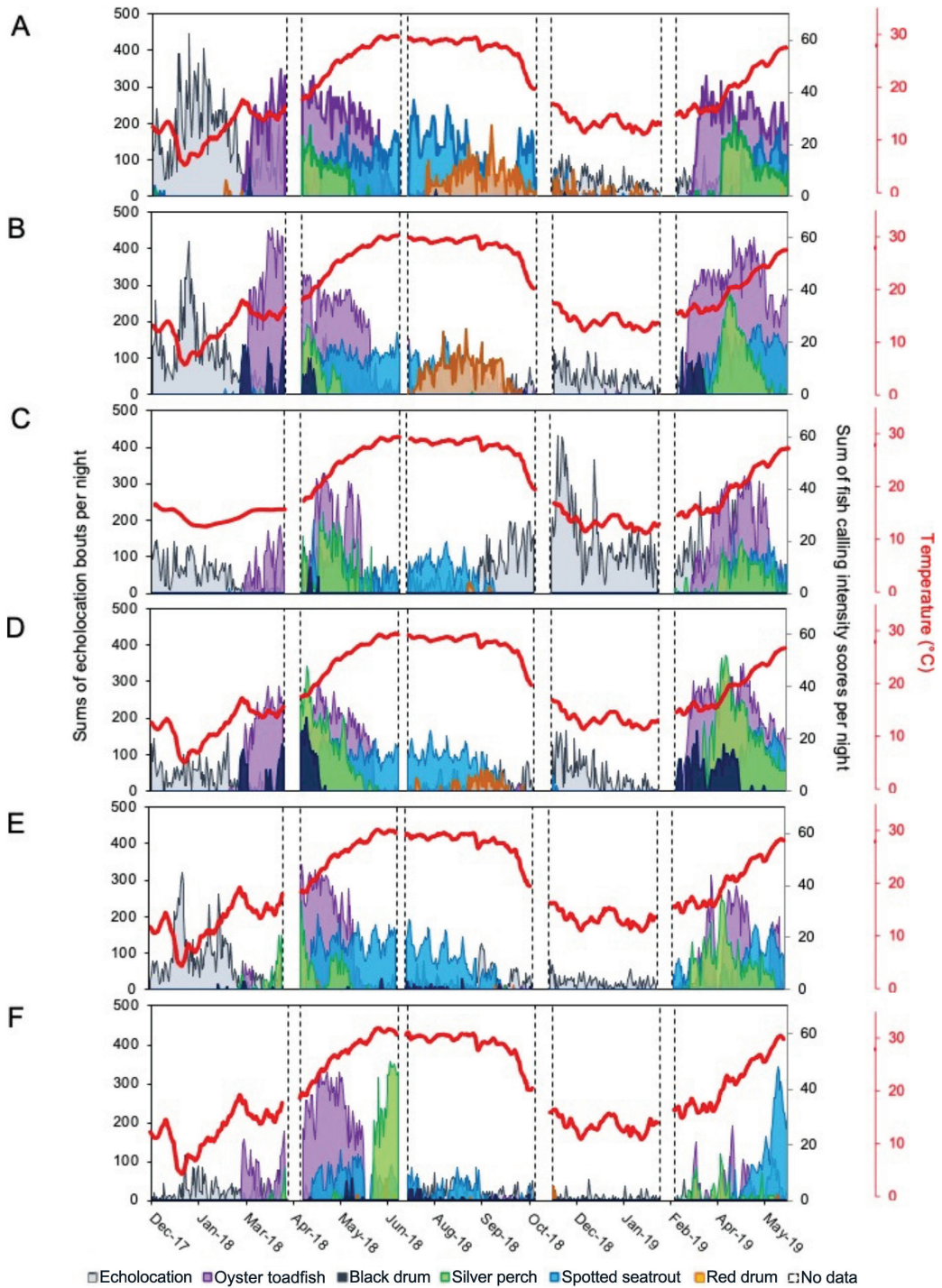
#### *Quantifying the Role of Biological Sounds and Vessel Noise on Dolphin Vocalizations*

RF models illustrated the influence of fish calling and vessel noise on bottlenose dolphin vocalizations (Figure 3). Vocalizations were higher when no fish were calling (i.e., a calling intensity score of 0) as compared to periods with multiple fish calls (i.e., calling intensity score of 2) and chorusing events (i.e., calling intensity score of 3) (Table 2; Figures 3 & 4). Across all RF models, noise presence influenced dolphin vocalizations more than fish calling (Figure 3). All vocalization types were higher when anthropogenic noise was present (Table 2).

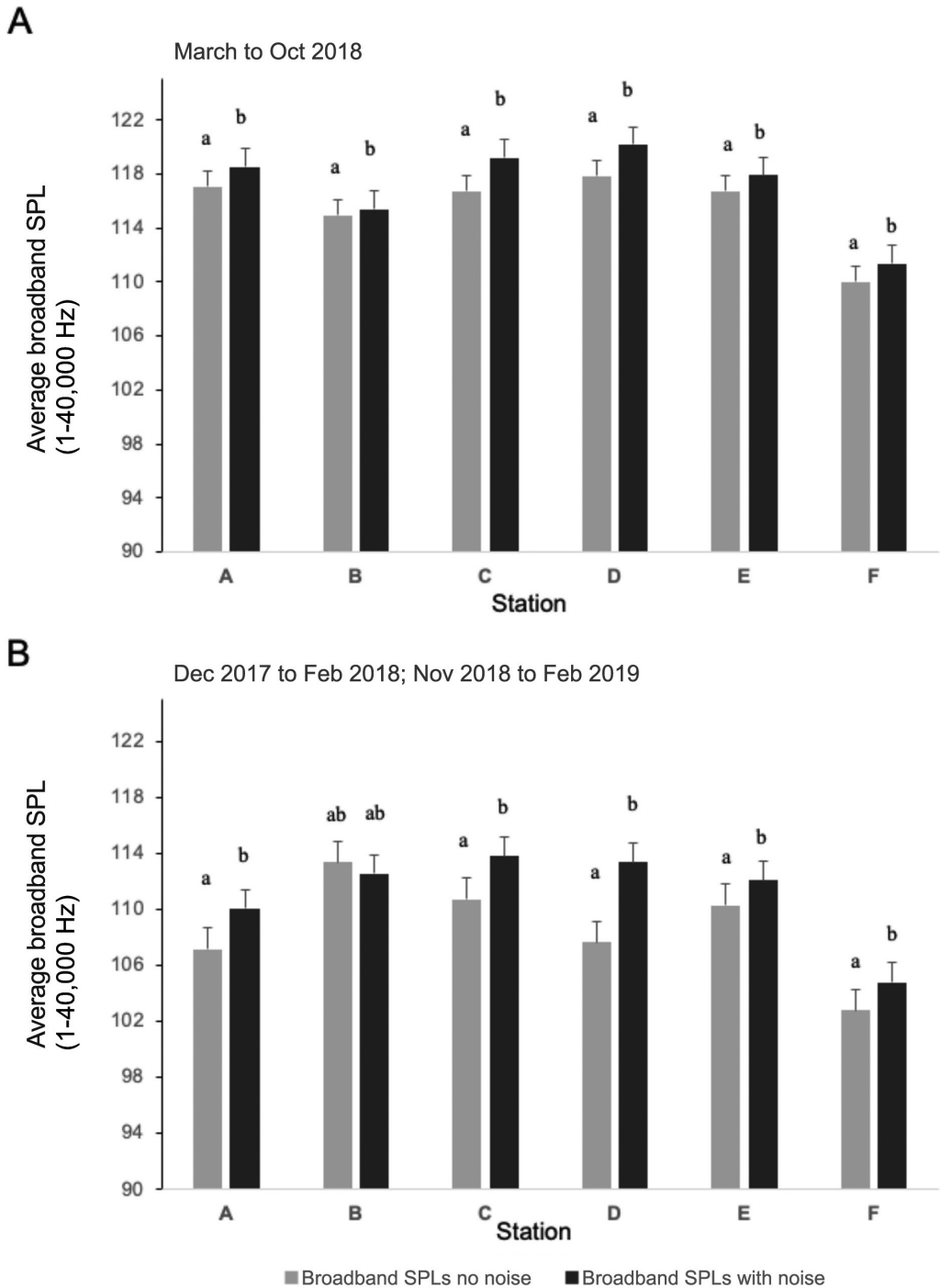
Fish chorusing periods were species-specific, with species-specific peaks occurring from March through October during the evening hours (Figures 4 & 5). Generally, broadband SPLs were higher when vessel noise was present as compared to periods when vessel noise was not detected ( $p < 0.01$ ; Figure 5). From November to February, fish calling was minimal, and

contributions to SPLs were predominantly from vessel noise (Figures 4 & 5). From November to February as compared to the period of March to October, SPLs were much higher in the presence of noise (Figure 5). This difference was most prominent at Fort Sumter (Station D), the SC Aquarium (Station C), and Wando River (Station A) locations, respectively (Figure 5).

Due to the infrequency of whistles spanning March to October, attempts at RF modeling showed overfitting and were excluded. In the focused fish models, black drum and red drum calling did not influence the total vocalizations and echolocation bouts of bottlenose dolphins, while spotted seatrout, silver perch, and oyster calling did affect these vocalizations, although variable importance was minimal (Table 3; Supplemental Figure 2). In the focused fish model, total vocalizations and echolocation bouts were higher when spotted seatrout were not calling; while conversely, these vocalizations were higher when oyster toadfish and silver perch were calling (i.e., calling intensity scores of 2 and 3; Table 3). In the focused noise models, noise presence influenced total vocalizations, echolocation bouts, and whistles (Supplemental Figure 2). In all cases, vocalizations were higher in the presence of noise (Table 4).



**Figure 4.** Seasonal and spatial patterns of soniferous fish calling and chorusing in the Charleston Harbor from December 2017 to June 2019: (A) Wando River, (B) Drum Island, (C) SC Aquarium, (D) Fort Sumter, (E) Ashley River, and (F) Citadel. Sum of echolocation bouts per night are overlaid in gray. Also shown are water temperature (red line) and data gaps (gray dotted bars).



**Figure 5.** Average root mean square (rms) broadband (1 to 40,000 Hz) sound pressure levels (SPLs) for files with noise presence compared to those files without noise across stations surveyed: (A) differences in SPL during the period when fish were calling and chorusing (i.e., March to October 2018); and (B) differences in SPL during the period when fish were not calling and chorusing (i.e., December 2017 to February 2018; November 2018 to February 2019). Different letters above bars indicate a significant difference between broadband SPLs no noise and broadband SPLs with noise.

*Relationships Between Dolphin Vocalizations and Sighting Abundance*

Across 34 visual surveys, 1,219 bottlenose dolphins (975 adults, 240 calves, and four neonates) were observed. On a broad level, dolphin abundance displayed strong spatial and temporal patterns comparable to those observed in vocalizations (Figure 6). Mean total vocalizations and

abundance were comparable across station and season (Figure 6). This trend was strongest in the Cooper-Wando confluence region (Stations C and B, respectively) and during the fall and winter months when mean water temperature was lower (Figure 6).

Fine-scale analysis of temporally matched sighting events and acoustic files further conveyed

**Table 3.** Significant differences of Dunnett’s Tukey-Kramer Multiple Comparison post hoc tests for factors that influenced bottlenose dolphin vocalizations using focused fish calling data in RF model; *ntree* = number of decision trees in RF model.

RF model	Total vocalizations factor ranks	Echo bout factor ranks
	<i>ntree</i> = 400	<i>ntree</i> = 400
% variance explained	3.69	5.20
Mean sq. residuals	24.06	14.35
Station*	C > A > B > D, E > D, B = E = F	C > A > B = E > D = F, E = F
Lunar phase	All equal	All equal
Tidal phase	Factor rejected	Factor rejected
Day/night	Night > day	Night > day
Noise**	1 = 0	1 = 0
Oyster toadfish***	3 > 2 > 1 = 0	3 > 2 > 1 = 0
Spotted seatrout***	0 > 3 = 2, 0 = 1	0 > 3 = 2, 0 = 1
Silver perch***	3 = 2 > 0, 0 = 1	3 = 2 > 0, 0 = 1
Red drum***	Factor rejected	Factor rejected
Black drum***	Factor rejected	Factor rejected

\*Stations: (A) Wando River, (B) Drum Island, (C) SC Aquarium, (D) Fort Sumter, (E) Ashley River, and (F) Citadel

\*\*0 = no noise present; 1 = noise present

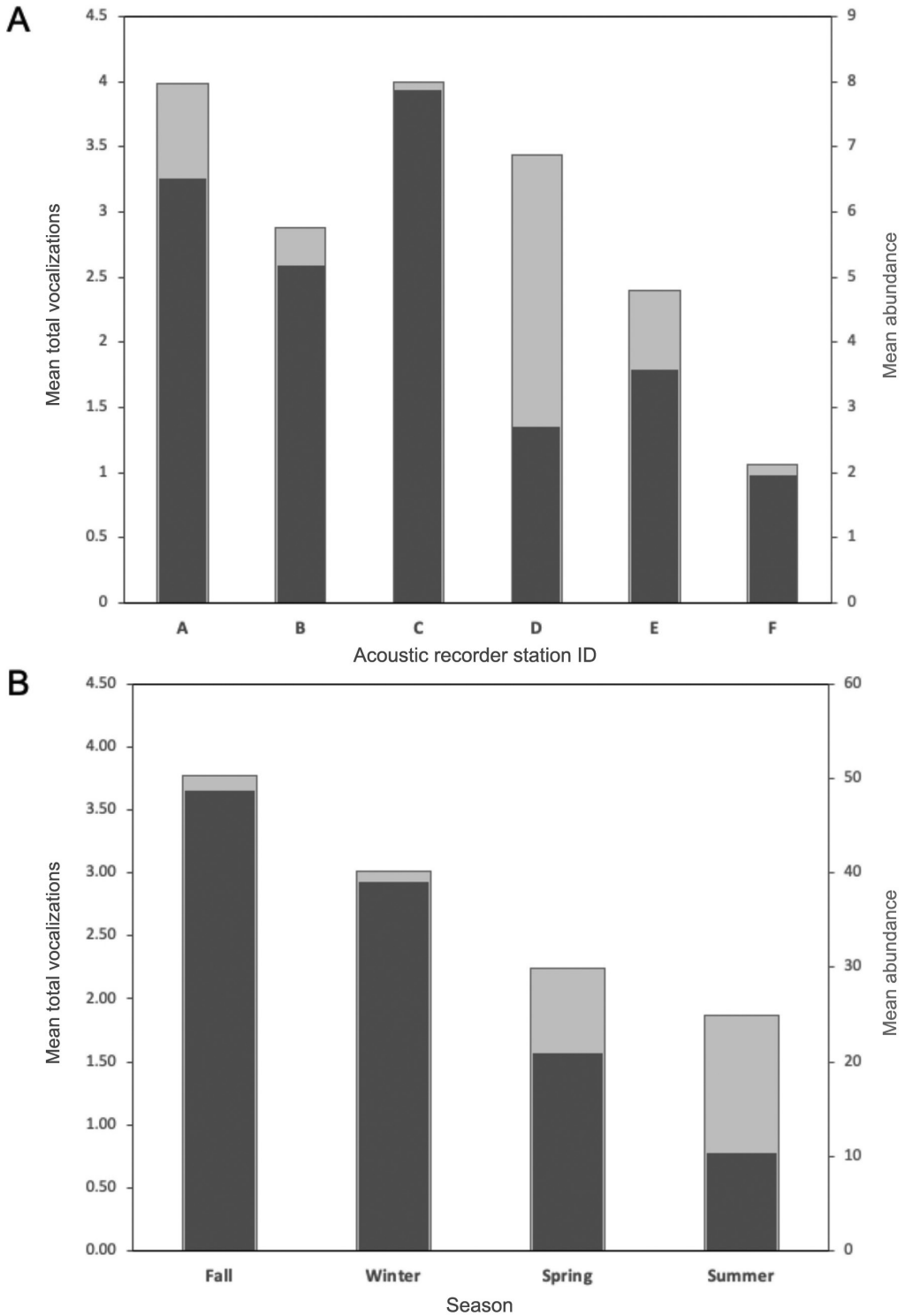
\*\*\*Fish calling scores: 0 = no calls, 1 = one call, 2 = multiple calls, and 3 = chorusing

**Table 4.** Significant differences of Dunnett’s Tukey-Kramer Multiple Comparison post hoc tests for factors that influenced bottlenose dolphin vocalizations using focused noise data in RF model; *ntree* = number of decision trees in RF model.

RF model	Total vocalizations factor ranks	Echo bout factor ranks	Whistle factor ranks
	<i>ntree</i> = 240	<i>ntree</i> = 240	<i>ntree</i> = 200
% variance explained	15.76	20.84	3.52
Mean sq. residuals	87.01	33.49	18.37
Station*	A > C > B > E = D > F	A = C > B > E > D > F	B = A > C = E = D > F
Lunar phase	Last = full > first > new	Full = last > first > new	Last = full > first = new
Tidal phase	Falling > high, rising = low	Falling > high = low >	Factor rejected rising
Day/night	Night > day	Night > day	Day = night
Noise**	1 > 0	1 > 0	1 > 0

\*Stations: (A) Wando River, (B) Drum Island, (C) SC Aquarium, (D) Fort Sumter, (E) Ashley River, and (F) Citadel

\*\*0 = no noise present; 1 = noise present



**Figure 6.** Mean vocalizations (black) and abundance (grey) of bottlenose dolphins (A) across stations and (B) over different seasons: A = Wando River, B = Drum Island, C = SC Aquarium, D = Fort Sumter, E = Ashley River, and F = Citadel.

**Table 5.** Output of multiple regression modeling assessing the effect of sighting abundance, station, and water temperature on bottlenose dolphin vocalizations

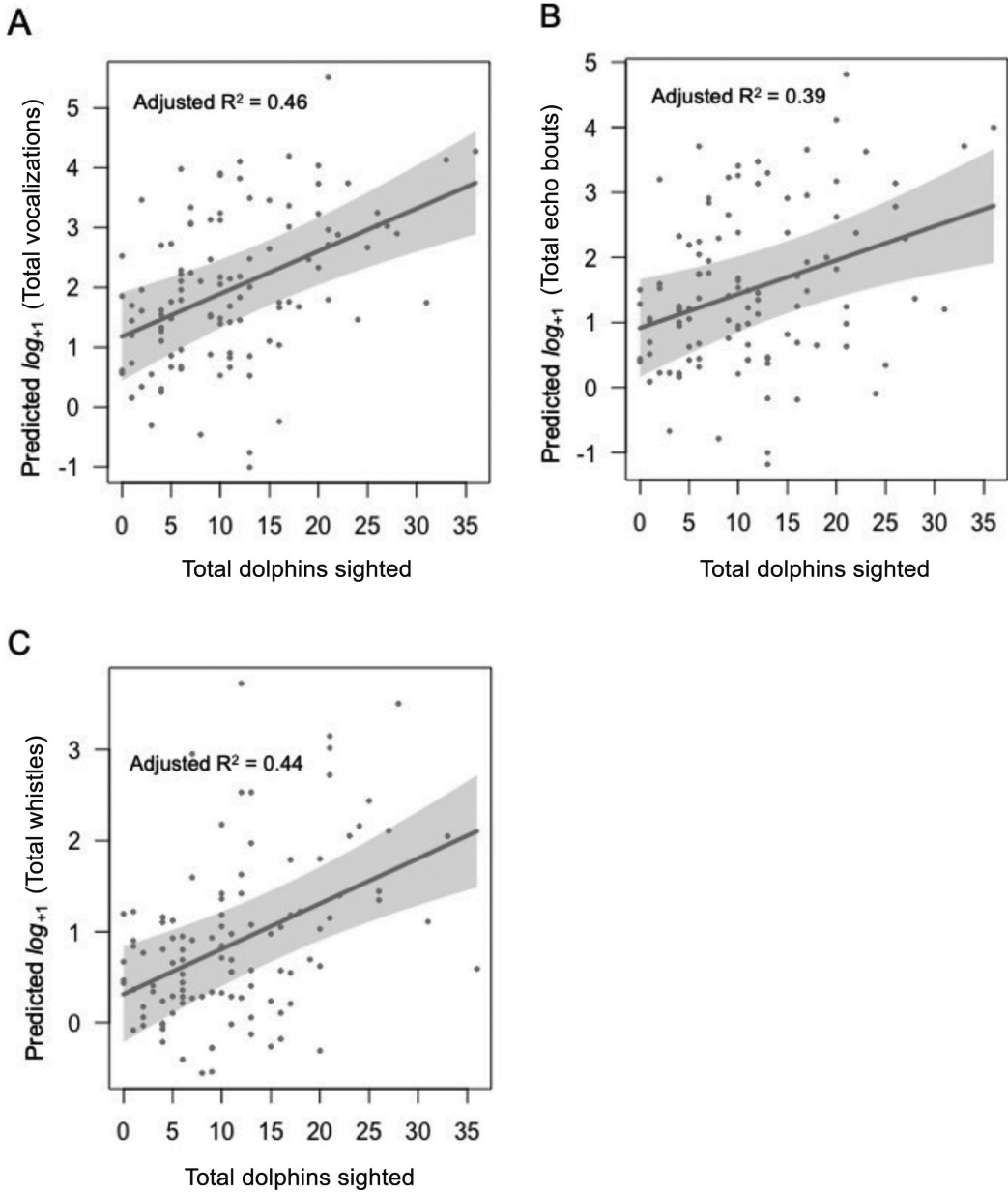
Regression models	Independent variables	Coeff. estimate	Std error	T value	$p (>  t )$
Total vocals*	(Intercept)	2.44	0.50	4.89	< 0.01
	Total dolphins sighted	0.07	0.02	4.38	< 0.01
	Station B	0.36	0.39	0.93	0.36
	Station C	0.83	0.39	2.16	< 0.01
	Station D	-0.93	0.39	-2.40	< 0.01
	Station E	-0.72	0.40	-1.80	< 0.05
	Station F	-0.53	0.43	-1.24	0.22
	Water temperature	-0.07	0.02	-4.58	< 0.01
Echo bouts*	(Intercept)	1.83	0.51	3.61	< 0.01
	Total dolphins sighted	0.05	0.02	3.14	< 0.01
	Station B	0.27	0.40	0.68	0.50
	Station C	1.05	0.39	2.69	< 0.01
	Station D	-0.61	0.39	-1.55	0.12
	Station E	-0.35	0.41	-0.86	0.39
	Station F	-0.36	0.43	-0.84	0.40
	Water temperature	-0.05	0.02	-3.27	< 0.01
Whistles*	(Intercept)	1.27	0.36	3.57	< 0.01
	Total dolphins sighted	0.05	0.01	4.27	< 0.01
	Station B	0.27	0.28	0.98	0.33
	Station C	-0.00	0.28	-0.01	0.99
	Station D	-0.49	0.28	-1.76	< 0.05
	Station E	-0.47	0.29	-1.65	0.10
	Station F	-0.20	0.31	-0.67	0.51
	Water temperature	-0.05	0.01	-4.89	< 0.01

\* = variable  $\log_{10}$  transformed

these patterns. Total bottlenose dolphins sighted was positively correlated with total vocalizations ( $F(7,100) = 13.84$ ;  $p < 0.01$ ), echolocation bouts ( $F(7,100) = 8.41$ ;  $p < 0.01$ ), and whistles ( $F(7,100) = 9.98$ ;  $p < 0.01$ ) (Table 5; Figure 7). Total dolphins sighted, station, and water temperature explained approximately 46, 33, and 37% of the variance (i.e., Adjusted  $R^2$ ) in total vocalizations, echolocation bouts, and whistles, respectively. Total vocalization and echolocation bouts were significantly higher at the SC Aquarium (Station C) as compared to Fort Sumter (Station D), Ashley River (Station E), and Citadel (Station F) ( $p < 0.01$ ; Table 5; Figure 8). At Fort Sumter, dolphin sightings were higher as

compared to total vocalizations (Figures 6 & 8). Water temperature was inversely correlated with total vocalizations ( $p < 0.01$ ), echolocation bouts ( $p < 0.01$ ), and whistles ( $p < 0.01$ ), similar to those patterns observed in the long-term time series (Table 5; Figures 2 & 9). Pairwise comparisons among vocalization types and water temperature supported these correlations; however, no association between total dolphins sighted and water temperature was observed (Figure 9). To further assess seasonal patterns in vocalizations, total echolocation bouts were standardized for dolphins sighted. Echolocation bouts were still higher during the fall and winter (Figure 10).



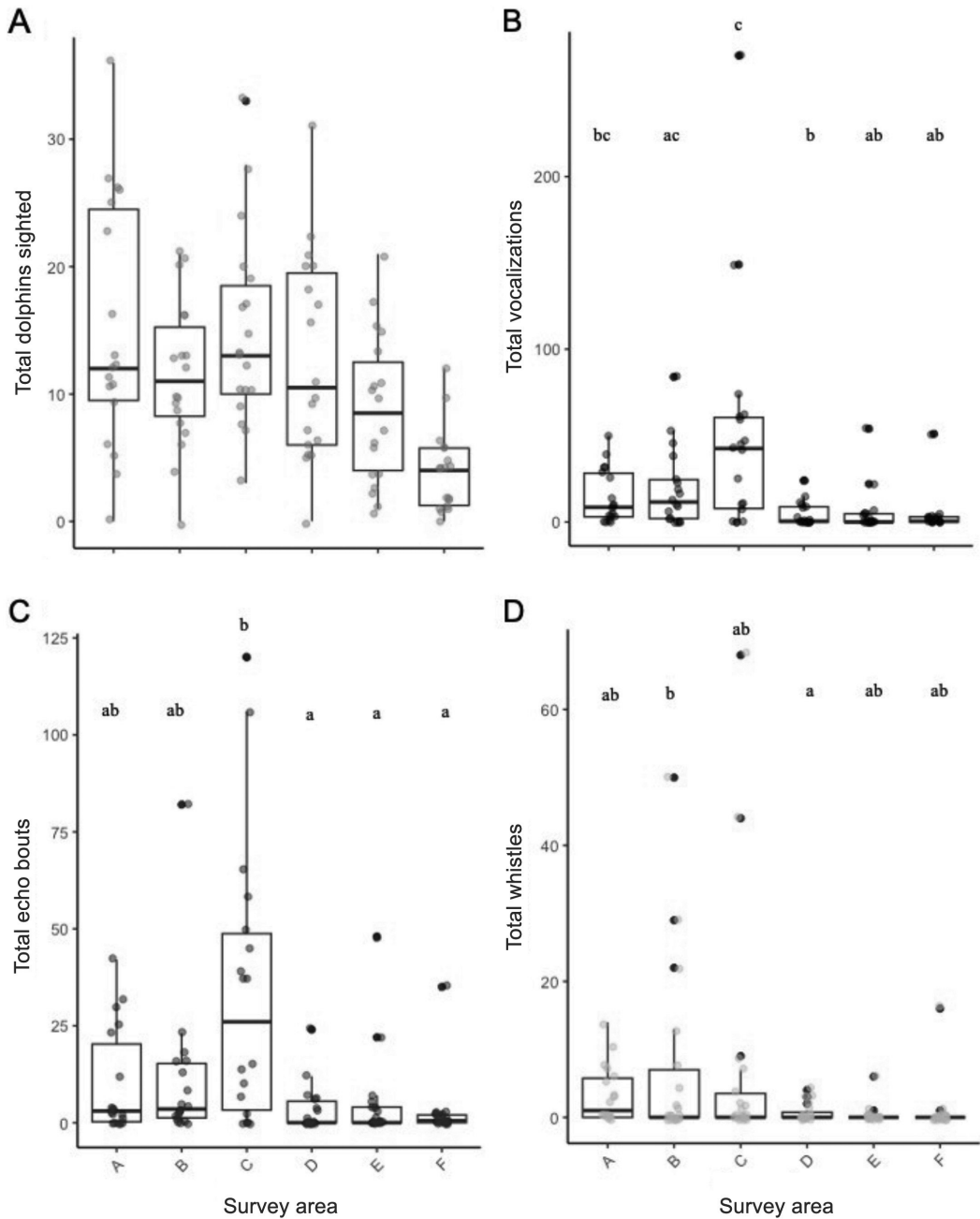


**Figure 7.** Relationships between the number of bottlenose dolphin vocalizations and the number of dolphins sighted: (A) total vocalizations, (B) total echolocation bouts, and (C) whistle regression modeling.

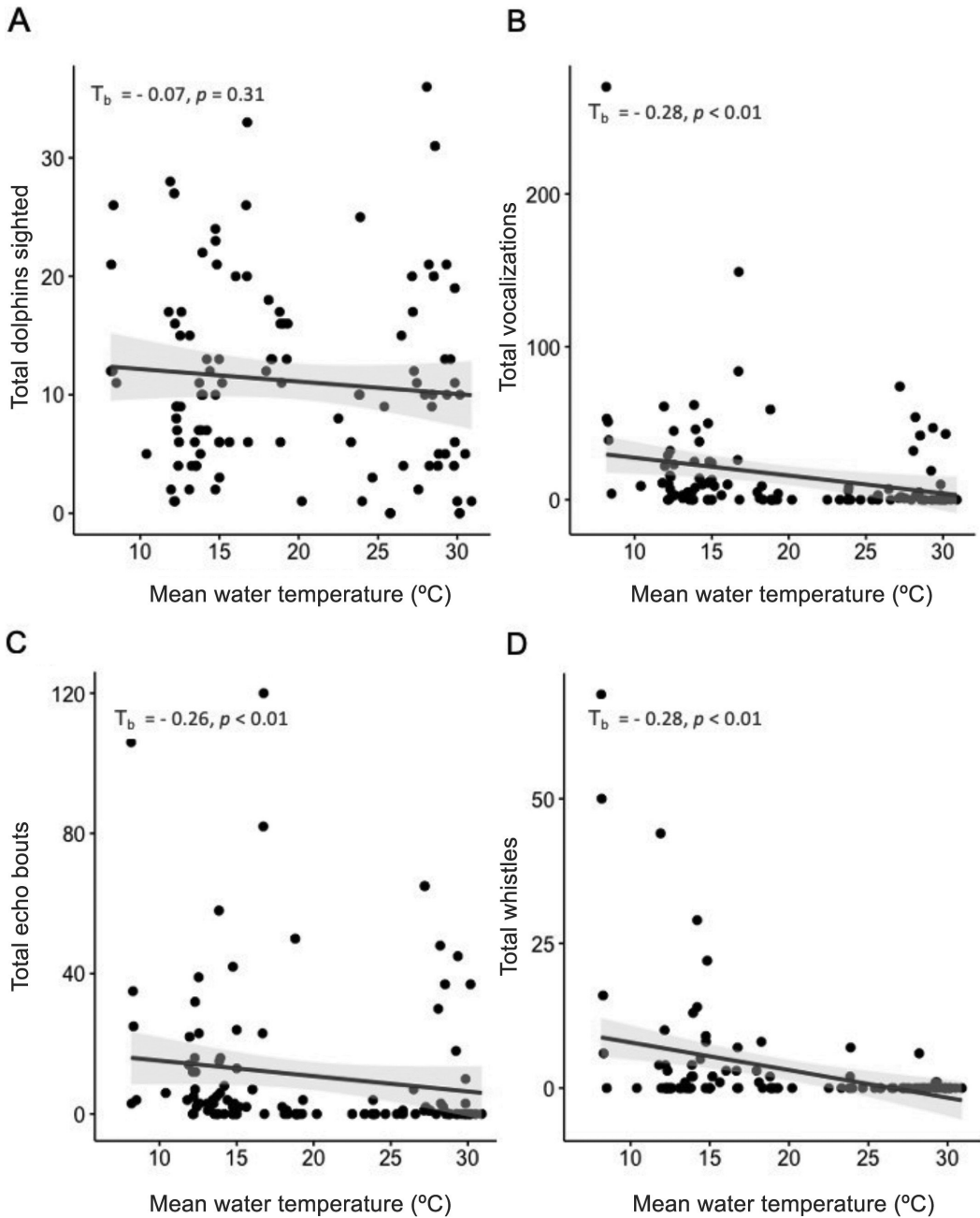
*Relationships Between Dolphin Vocalizations and Prey Abundance*

Across 48 trammel net surveys conducted throughout the harbor, over 43 total fish and 26 bottlenose dolphin prey fish species were observed (Tables 6 & 7). Percent abundance (species catch divided by total catch, multiplied by 100%) showed striped mullet

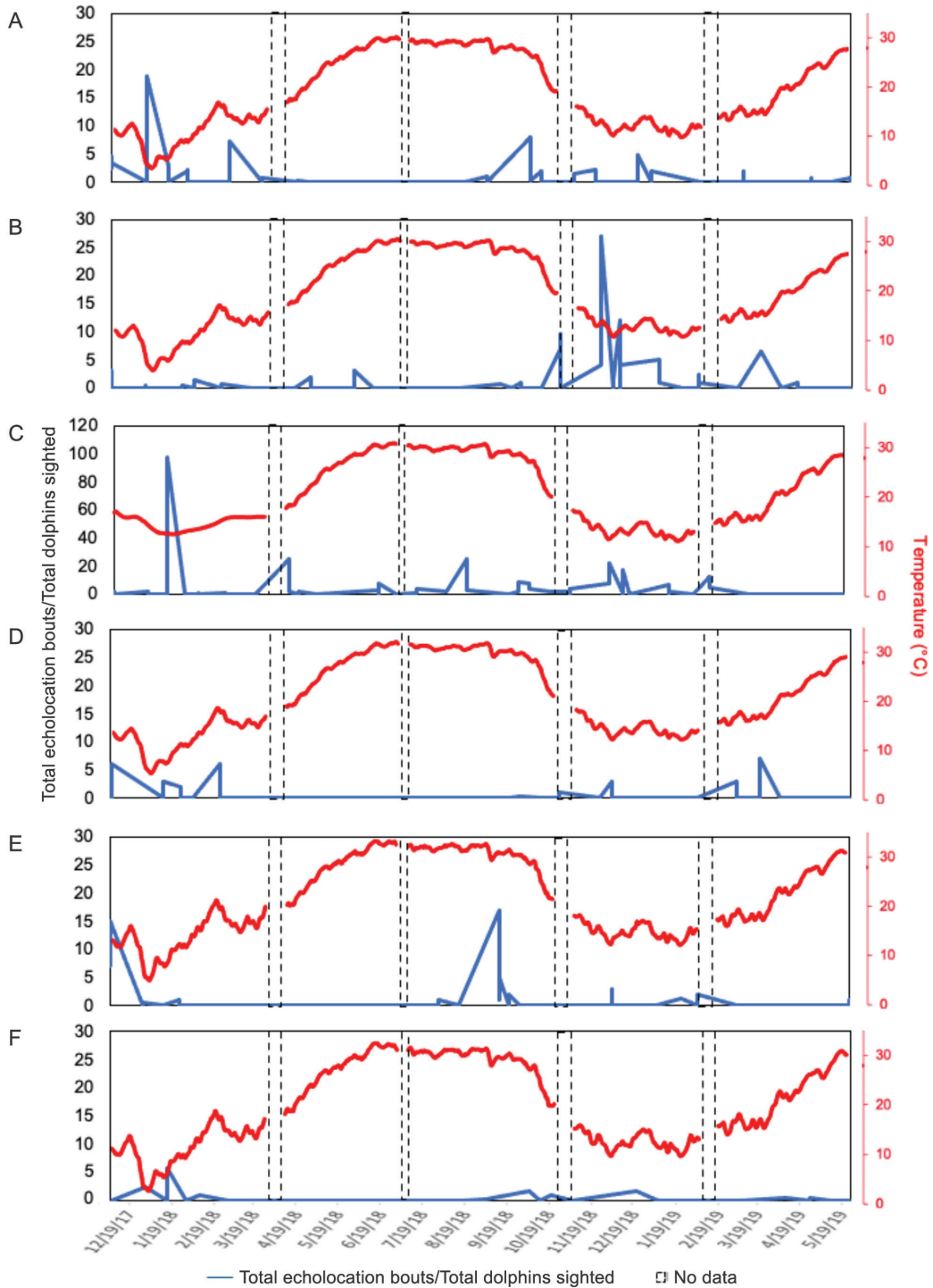
(*Mugil cephalus*), spotted seatrout, and red drum as the most abundant species caught (Tables 6 & 7). Less common prey species (ranging from 6 to 1% abundance) included spot (*Leiostomus xanthurus*), southern flounder (*Paralichthys lethostigma*), Atlantic croaker (*Micropogonias undulatus*), ladyfish (*Elops saurus*), Atlantic menhaden (*Brevoortia*



**Figure 8.** Detections of bottlenose dolphins sighted and vocalizations across stations: (A) total dolphins sighted, (B) total vocalizations, (C) total echolocation bouts, and (D) total whistles. Different letters above boxplots represent significant differences among group means ( $p < 0.05$ ): A = Wando River, B = Drum Island, C = SC Aquarium, D = Fort Sumter, E = Ashley River, and F = Citadel.



**Figure 9.** Kendall's tau-b correlation plots comparing mean water temperature (°C) and (A) total dolphins sighted, (B) total vocalizations, (C) total echolocation bouts, and (D) total whistles in the dolphin transect dataset.



**Figure 10.** Total echolocation bouts (blue line) standardized for the number of bottlenose dolphins sighted at each station: (A) Wando River, (B) Drum Island, (C) SC Aquarium, (D) Fort Sumter, (E) Ashley River, and (F) Citadel. Also shown is the water temperature (red line).

**Table 6.** Bottlenose dolphin prey abundance obtained from South Carolina Department of Natural Resources (SCDNR) trammel net surveys conducted in Charleston Harbor from 18 December 2017 to 22 May 2019 that were included in vocalization analyses

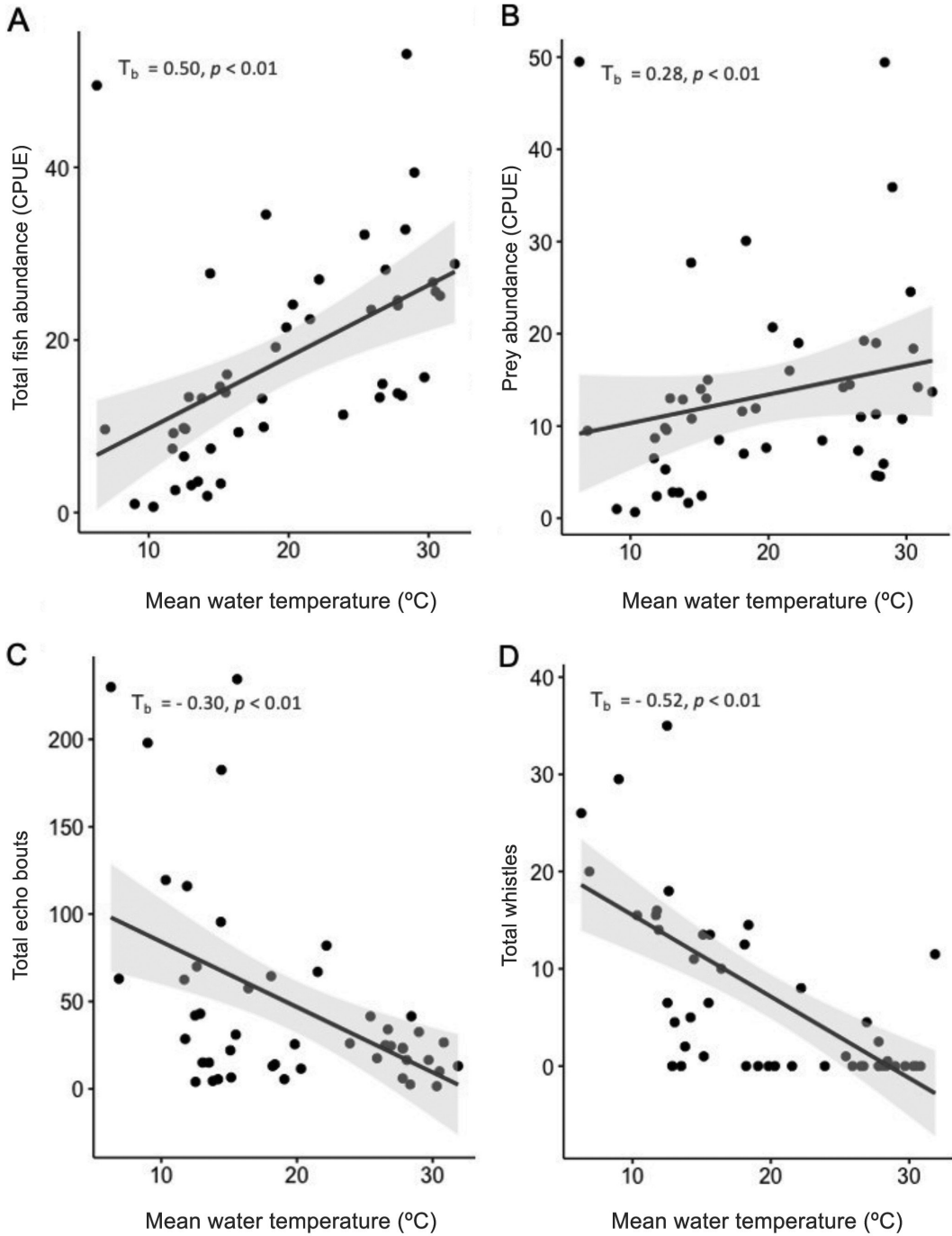
Common name	Scientific name	Family	% abundance*
Striped mullet	<i>Mugil cephalus</i>	Mugilidae	38.31
Spotted seatrout	<i>Cynoscion nebulosus</i>	Sciaenidae	23.27
Red drum	<i>Sciaenops ocellatus</i>	Sciaenidae	20.06
Spot	<i>Leiostomus xanthurus</i>	Sciaenidae	6.05
Southern flounder	<i>Paralichthys lethostigma</i>	Bothidae	4.16
Atlantic croaker	<i>Micropogonias undulatus</i>	Sciaenidae	2.37
Ladyfish	<i>Elops saurus</i>	Elopidae	1.60
Atlantic menhaden	<i>Brevoortia tyrannus</i>	Clupeidae	1.13
Black drum	<i>Pogonias cromis</i>	Sciaenidae	1.13
Pinfish	<i>Lagodon rhomboides</i>	Sparidae	1.09
Silver perch	<i>Bairdiella chrysoura</i>	Sciaenidae	0.34
Southern kingfish	<i>Menticirrhus americanus</i>	Sciaenidae	0.26
Atlantic butterflyfish	<i>Peprilus triacanthus</i>	Stromateidae	0.09
American eel	<i>Anguilla rostrata</i>	Anguillidae	0.05
Pigfish	<i>Orthopristis chrysoptera</i>	Haemulidae	0.05
Inshore lizardfish	<i>Synodus foetens</i>	Synodontidae	0.02
Striped anchovy	<i>Anchoa hepsetus</i>	Engraulidae	0.02
Summer flounder	<i>Paralichthys dentatus</i>	Bothidae	0.02
Atlantic cutlassfish	<i>Trichiurus lepturus</i>	Trichiuridae	0.00
Atlantic moonfish	<i>Selene setapinnis</i>	Carangidae	0.00
Bay anchovy	<i>Anchoa mitchilli</i>	Engraulidae	0.00
Oyster toadfish	<i>Opsanus tau</i>	Sciaenidae	0.00
Rock sea bass	<i>Centropristis philadelphica</i>	Serranidae	0.00
Shrimp eel	<i>Ophichthus gomesi</i>	Ophichthidae	0.00
Silver seatrout	<i>Cynoscion nothus</i>	Sciaenidae	0.00
Star drum	<i>Stellifer lanceolatus</i>	Sciaenidae	0.00

\*Species with 0% abundance were excluded from statistical analyses.

**Table 7.** Prey and additional fish abundance obtained from SCDNR trammel net surveys conducted in Charleston Harbor from 18 December 2017 to 22 May 2019 that were included in bottlenose dolphin vocalization analyses

Common name	Scientific name	Family	% abundance*
Striped mullet	<i>Mugil cephalus</i>	Mugilidae	35.11
Spotted seatrout	<i>Cynoscion nebulosus</i>	Sciaenidae	21.32
Red drum	<i>Sciaenops ocellatus</i>	Sciaenidae	18.38
Spot	<i>Leiostomus xanthurus</i>	Sciaenidae	5.54
Southern flounder	<i>Paralichthys lethostigma</i>	Bothidae	3.81
Gizzard shad	<i>Dorosoma cepedianum</i>	Clupeidae	2.37
Longnose gar	<i>Lepisosteus osseus</i>	Lepisosteidae	2.22
Atlantic croaker	<i>Micropogonias undulatus</i>	Sciaenidae	2.17
Bluefish	<i>Pomatomus saltatrix</i>	Pomatomidae	1.82
Ladyfish	<i>Elops saurus</i>	Elopidae	1.46
Atlantic menhaden	<i>Brevoortia tyrannus</i>	Clupeidae	1.04
Black drum	<i>Pogonias cromis</i>	Sciaenidae	1.04
Pinfish	<i>Lagodon rhomboides</i>	Sparidae	1.00
Sheepshead	<i>Archosargus probatocephalus</i>	Sparidae	0.61
Striped burrfish	<i>Chilomycterus schoepfi</i>	Diodontidae	0.31
Silver perch	<i>Bairdiella chrysoura</i>	Sciaenidae	0.31
Southern kingfish	<i>Menticirrhus americanus</i>	Sciaenidae	0.24
Northern puffer	<i>Sphoeroides maculatus</i>	Tetraodontidae	0.20
American harvestfish	<i>Peprilus paru</i>	Stromateidae	0.14
Crevalle jack	<i>Caranx caninus</i>	Carangidae	0.10
Atlantic butterfish	<i>Peprilus triacanthus</i>	Stromateidae	0.09
Atlantic tripletail	<i>Lobotes surinamensis</i>	Lobotidae	0.07
White mullet	<i>Mugil curema</i>	Mugilidae	0.07
Spanish mackerel	<i>Scomberomorus maculatus</i>	Scombridae	0.07
American eel	<i>Anguilla rostrata</i>	Anguillidae	0.04
American shad	<i>Alosa sapidissima</i>	Clupeidae	0.04
Pigfish	<i>Orthopristis chrysoptera</i>	Haemulidae	0.04
White catfish	<i>Ameiurus catus</i>	Ictaluridae	0.04
Hogchoker	<i>Trinectes maculatus</i>	Achiridae	0.03
Pirate perch	<i>Aphredoderus sayanus</i>	Aphredoderidae	0.03
Atlantic bumper	<i>Chloroscombrus chrysurus</i>	Carangidae	0.03
Lookdown	<i>Selene vomer</i>	Carangidae	0.03
Hickory shad	<i>Alosa mediocris</i>	Clupeidae	0.03
Atlantic spadefish	<i>Chaetodipterus faber</i>	Ephippidae	0.03
Bay whiff	<i>Citharichthys spilopterus</i>	Paralichthyidae	0.03
Summer flounder	<i>Paralichthys dentatus</i>	Bothidae	0.01
Horse-eye jack	<i>Caranx latus</i>	Carangidae	0.01
Common snook	<i>Centropomus undecimalis</i>	Centropomidae	0.01
Blueback herring	<i>Alosa aestivalis</i>	Clupeidae	0.01
Threadfin shad	<i>Dorosoma petenense</i>	Clupeidae	0.01
Striped anchovy	<i>Anchoa hepsetus</i>	Engraulidae	0.01
Tarpon	<i>Megalops atlanticus</i>	Megalopidae	0.01
Inshore lizardfish	<i>Synodus foetens</i>	Synodontidae	0.01
Bighead searobin	<i>Prionotus tribulus</i>	Triglidae	0.01

\*Species with 0% abundance were excluded from statistical analyses and not shown here.



**Figure 11.** Kendall's tau-b correlation plots comparing mean water temperature (°C) and (A) total fish abundance, (B) prey abundance, (C) total echolocation bouts, and (D) total whistles in the inshore fishery dataset.

*tyrannus*), black drum, and pinfish (*Lagodon rhomboides*) (Table 6). Infrequently caught prey species (ranging from 0.34 to 0.02% abundance) included silver perch, southern kingfish (*Menticirrhus americanus*), Atlantic butterfish (*Peprilus triacanthus*), American eel (*Anguilla rostrata*), pigfish (*Orthopristis chrysoptera*), inshore lizardfish (*Synodus foetens*), striped anchovy (*Anchoa hepsetus*), and summer flounder (*Paralichthys dentatus*) (Table 6). Prey and overall fish abundance (mean  $\pm$  SD) were highest in Charleston Harbor (prey =  $15.71 \pm 12.06$ ; total fish =  $19.08 \pm 14.26$ ) and Lower Wando River (prey =  $15.98 \pm 11.04$ ; total fish =  $18.36 \pm 11.06$ ) stratum, and lowest in the Ashley River (prey =  $8.22 \pm 7.16$ ; total fish =  $15.81 \pm 11.20$ ). Overall fish ( $T_b = 0.50$ ;  $p < 0.01$ ) and prey ( $T_b = 0.28$ ;  $p < 0.01$ ) abundance were positively correlated with mean water temperature, while the number of echolocation bouts ( $T_b = -0.30$ ;  $p < 0.01$ ) and whistles ( $T_b = -0.52$ ;  $p < 0.01$ ) were negatively correlated with mean water temperature (Figure 11).

## Discussion

### *Bottlenose Dolphin Acoustic Repertoire*

Bottlenose dolphins produced a variety of vocalizations in the harbor, including whistles, echolocation click trains of variable rates, and a wide range of burst pulse sounds. These vocalizations were comparable to repertoires of other bottlenose dolphin populations occurring within the southeast U.S. and around the world (Nuutila et al., 2013; Simard et al., 2015; Longden et al., 2020; Luís et al., 2021; Marian et al., 2021). Across the western and southern Atlantic Ocean, bottlenose dolphins display an assemblage of common signals, including whistles, variable rate click trains, and specialized pulsed signals (e.g., creaks, squawks, bangs, squeaks), exhibiting a complex repertoire (Luís et al., 2021). Divergence is prominent in social signals (e.g., whistles); however, commonalities were observed among populations occupying regions similar in habitat and ambient noise levels (Luís et al., 2021). Geographic variation in whistle structure has also been documented in populations of the central-eastern North Atlantic and Mediterranean Sea (Papale et al., 2013; La Manna et al., 2017).

### *Spatial Patterns of Dolphin Vocalizations*

Spatial and temporal variation in vocalization detection rates has been documented in multiple odontocetes in relation to distribution, habitat use, and behavior (Lin et al., 2015; Simard et al., 2015; Marian et al., 2021; Díaz López, 2022). In the current study, acoustic detections were highest at the three sites of the Cooper-Wando confluence

region—the Wando River, Drum Island, and SC Aquarium stations—suggesting this area is preferential habitat for bottlenose dolphins, similar to the core use areas described by Bouchillon et al. (2019) and Transue et al. (2023). In the Bouchillon et al. (2019) study, visual surveys also indicated high numbers of dolphins sighted at the Wando River station, which could explain the higher number of vocalizations detected in this area. In addition, the high occurrence of echolocation suggests that this location may be an important foraging area for dolphins. Chorusing of soniferous fish species, which are known prey items of bottlenose dolphins (Pate & McFee, 2012), were also higher at the Wando River and Drum Island stations (Transue et al., 2023). In other similar salt marsh ecosystems, higher dolphin densities also occur at the confluence of multiple rivers (e.g., SC's Cape Romain National Wildlife Refuge; Sloan, 2006).

Ecological features such as diverse habitat structure, colliding currents, eddy formation, and high mixing areas that occur in the confluence of the Cooper and Wando Rivers may provide favorable conditions that support greater fish abundance and diversity (Moreno, 2005; Braaten & Guy, 1999; Boddy et al., 2019). Bottlenose dolphins have exhibited fine-scale selection of foraging habitats that promote enhanced prey detection and capture efficiency in Georgia and South Carolina, where steep mud banks in tidal marshes were documented as one preferred habitat for feeding (Hoese, 1971; Petricig, 1993; Allen et al., 2001; Eierman & Connor, 2014). The rise in echolocation observed in this study at Stations A, B, and C with the falling tide is a pattern observed in SC's May River and is likely a specialized foraging strategy used to target prey leaving the *Spartina* as the tide recedes (Peterson & Turner, 1994; Marian et al., 2021). In addition, there was a notably higher occurrence of whistles and burst pulse sounds at these stations, which have been shown to function as integral aspects of social and foraging behaviors in other bottlenose dolphin populations (Herzing, 1996, 2015; Janik & Slater, 1998; Janik, 2000; Luís et al., 2016).

### *Relationships of Dolphin Vocalizations, Sightings, and Fish Abundance*

In Charleston Harbor, long-term patterns in acoustic repertoire showed multi-year peaks in vocalizations during fall and winter as first reported by Transue et al. (2023). Visual surveys indicated a higher abundance of bottlenose dolphins in the fall and winter as compared to the spring and summer, which matched the vocalization patterns. In fact, the number of dolphins sighted during a visual survey were positively correlated with the number



of vocalizations detected. These patterns were most apparent in the confluence region (i.e., the Wando River, Drum Island, and SC Aquarium stations) and may be related to seasonal shifts in foraging habitat use (Bouchillon et al., 2019; Silva et al., 2019).

Peaks in vocalizations coinciding with declining water temperatures in the fall and winter may result from declining estuarine productivity, which, in turn, may trigger shifts in bottlenose dolphin habitat use and foraging strategies. Fish abundance correlated positively with water temperature; higher abundance of fish occurred in the spring and summer, while dolphin echolocation bouts and whistles decreased during this period. During the summer, fish are plentiful, and it is possible that dolphins find prey easily and are not relying so heavily on echolocation. However, during the colder winter months, dolphins may rely more on echolocation and other vocalizations to increase foraging success and meet energetic demands. Thus, changes in vocalization rates may correlate with seasonal changes in prey abundance. In fact, primary productivity in a marsh-estuarine ecosystem such as Charleston Harbor increases in the spring and summer as daylight hours and water temperature increase. This can lead to bottom-up increases in fish abundance (Dame & Kenny, 1986; Boyer et al., 1993; Cloern et al., 2014). Ecological modeling of annual primary production in the North Inlet, SC (i.e., a similar salt marsh ecosystem to Charleston Harbor's), indicates primary production is lowest during the winter; however, energetic demands of bottlenose dolphins increased significantly during these winter months (Young & Phillips, 2002).

In the fall and winter, when primary productivity and subsequent prey abundance decrease, bottlenose dolphins may alter their foraging strategies and diversify their acoustic repertoire to better coordinate foraging. Multiple studies have shown that during group coordinated foraging events, dolphins increase whistle production rates (King & Janik, 2015; Hamilton et al., 2022). Vocalizations are highly complex and may play different roles in different behaviors. Dolphins produce specific whistles with food-associated calls, suggesting a strong social aspect in foraging (King & Janik, 2015). Dolphins may participate in more group foraging to maximize catch and efficiency during these periods when prey is scarce, such as during the colder winter months in Charleston Harbor. Bottlenose dolphins observed in feeding groups, especially during specialized "driver-barrier" group feeding (i.e., wherein one dolphin is the driver and other dolphins act as the barrier), emitted significantly higher whistle rates as compared to individual foraging dolphins (Acevedo-Gutiérrez & Stienessen, 2004; Hamilton et al., 2022).

An additional hypothesis is that bottlenose dolphins may rely on passive listening to find their prey in warmer months when prey species are chorusing (Barros & Wells, 1998; Gannon & Waples, 2006; Berens McCabe et al., 2010). Charleston Harbor is an important nursery and year-round habitat for various offshore and inshore fish species (Wenner et al., 1984; Arnott, 2013). In the present study, the majority of species caught in trammel nets belonged to the Family Sciaenidae. Stomach content analyses from stranded dolphins in the waters around Charleston Harbor found that fish species in the Family Sciaenidae comprised a prominent portion of dolphin diet composition (Pate & McFee, 2012). This finding has been supported in similar studies across the southeast United States in North Carolina (Gannon & Waples, 2006) and in Florida (Berens McCabe et al., 2010). Soniferous fish calling intensity in Charleston Harbor increased during the spring and summer evenings and displayed species-specific chorusing periods resembling those described in the May River and Chechessee Creek, SC, estuaries (Monczak et al., 2019; Mueller et al., 2020; Transue et al., 2023). In the May River, chorusing seasons (occurrence and duration) were highly correlated to young-of-the-year abundance, supporting the assumption that chorusing initiates fish spawning (Monczak et al., 2022). Previous studies have suggested coastal dolphins target soniferous fish and passively listen to locate prey items (Barros & Wells, 1998). Thus, it is possible that in the spring and summer when fish are chorusing, dolphins are listening to find their prey rather than echolocating.

*Assessing the Influence of Anthropogenic Noise*  
Bottlenose dolphin vocalizations in Charleston Harbor increased significantly when anthropogenic noise was present as first reported by Transue et al. (2023). Vocalizations and visual sighting abundance were highest in the loudest and most heavily trafficked regions of the harbor, near the major shipping terminals, as compared to the Ashley River. Behavioral shifts associated with anthropogenic noise have been documented in multiple cetacean species. In bottlenose dolphins specifically, vessel and/or dredge presence has been attributed to increased whistle production (i.e., Lombard effect; Gridley et al., 2016; Heiler et al., 2016), decreased foraging buzzes (click trains with inter-click intervals < 10 ms; Pirotta et al., 2015), and displaced home range (Pirotta et al., 2013; Todd et al., 2015; Marley et al., 2016, 2017).

Bottlenose dolphins may need to vocalize more frequently to navigate, communicate, and forage in this noisy environment. This explanation may partially explain why dolphin vocalizations occurred more frequently in the presence of vessel noise.

Dolphins have been shown to alter their acoustic behavior in response to anthropogenic noise presence and other changes in surrounding sound levels (Buckstaff, 2004; Jensen et al., 2009; van Ginkel et al., 2017). In response to high ambient noise in Tampa Bay, Florida, bottlenose dolphins increased minimum, maximum, and peak whistle frequencies (van Ginkel et al., 2017). In Walvis Bay, Namibia, bottlenose dolphins increased non-signature and signature whistle production rates in the presence of tour boats and displayed an upward shift in whistle frequency (minimum, maximum, start, and end) parameters (Gridley et al., 2016; Heiler et al., 2016). Further investigation of specialized vocalization types and whistle parameters in the harbor could elucidate further adaptations of bottlenose dolphins to noise.

### Conclusions

In the present study, acoustic behavior of bottlenose dolphins followed patterns influenced by geographic location within the harbor, season and water temperature, dolphin abundance, prey availability, and noise presence. Long-term patterns in acoustic repertoire showed multi-year peaks in vocalizations during fall and winter as first reported by Transue et al. (2023), resembling those patterns observed in dolphins inhabiting waters near the mouth of the May River estuary (Marian et al., 2021). Abundance estimates of dolphins obtained from visual survey methods correlated with vocalization counts. Vocalizations and sightings occurred more frequently at the confluence of the Cooper and Wando Rivers (Stations A, B, and C) along the shipping channel as compared to the Ashley River. Interestingly, fish and prey abundance were higher in the Wando River and Charleston Harbor strata as compared to the Ashley River stratum. These differences may explain why dolphin sightings and vocalizations were higher along the shipping channel and lower in the Ashley River. Additionally, in the fall and winter, when prey was less abundant, dolphins increased their echolocation bouts and whistles, possibly illustrating an increased effort to search for prey. In summary, multivariate interactions indicated strong spatial and seasonal patterns in vocalization rates that may be associated with dolphin and prey abundance as well as noise-induced redundancy.

In Charleston Harbor, findings suggest that bottlenose dolphins are more abundant in areas with increased anthropogenic noise, where prey is more abundant. Evidence indicates that dolphins modified their acoustic behavior by increasing their vocalization rates to compensate for masking. Although this study has identified adaptations of dolphins to current levels of anthropogenic noise in Charleston Harbor, continued long-term

monitoring is essential to assess if future expansion will have adverse effects on the Charleston Estuarine System Stock dolphins.

**Note:** The supplemental figures for this article are available in the “Supplemental Material” section of the *Aquatic Mammals* website: [https://www.aquaticmammalsjournal.org/index.php?option=com\\_content&view=article&id=10&Itemid=147](https://www.aquaticmammalsjournal.org/index.php?option=com_content&view=article&id=10&Itemid=147).

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