Identifying and predicting occurrence and abundance of a vocal animal species based on individually specific calls

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Abstract. Passive acoustic monitoring (PAM) offers opportunities to collect data on the occurrence of vocal species for long periods of time, at multiple locations, and under a range of environmental conditions. Some species emit individually distinctive calls, including bottlenose dolphins (*Tursiops truncatus*) that produce signature whistles. Our study used PAM to determine the seasonal occurrence of bottlenose dolphins and utilized individually specific signature whistles to (1) track individuals spatially and temporally, (2) assess site fidelity off Maryland (MD), USA, (3) estimate the minimum abundance of dolphins in the study area, and (4) develop a dynamic habitat-based relative abundance model applicable as a real-time dolphin relative abundance prediction tool. Acoustic recorders were deployed at two sites offshore of Ocean City, MD, and at one site in the upper Chesapeake Bay, MD. Acoustic recordings from 2016 to 2018 were analyzed for signature whistles, and re-occurrences of individual whistles were identified using a combination of machine learning and manual verification. A habitat-based density model was created using the number of signature whistles combined with environmental conditions. A total of 1518 unique signature whistles were identified offshore of Maryland and in the upper Chesapeake Bay. There were 184 re-occurrences of 142 whistles, with a mean of 135 d between re-occurrences (range = 1–681 d). These repeated detections of the same individuals occurred most frequently at the site near Ocean City, MD, indicating the highest site fidelity. Re-occurrences were recorded among all three sites, indicating movement of dolphins between the Chesapeake Bay and off the Atlantic coast of Maryland. The weekly number of individual dolphins detected off the Atlantic coast was significantly related to two environmental variables: sea surface temperature and chlorophyll *a* concentration. This habitat model could be used to predict relative dolphin abundance offshore of Maryland and inform management within the region, including in relation to offshore wind energy development and other stakeholders.

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Introduction

Passive acoustic monitoring (PAM) is increasingly being used to monitor terrestrial and marine species as recorder battery and memory capabilities improve and automated detection algorithms are developed for a wide range of species (Luczkovich et al. 2008, Blumstein et al. 2011, Stowell et al. 2019). Compared to traditional species monitoring, such as visual surveys, PAM offers the potential for greater detection ranges, continuous monitoring at times and locations for which visual surveying may not be possible, higher spatial and temporal resolution of data collected, and improved detection for low-density species (Van Parijs et al. 2009, Rogers et al. 2013, Sugai et al. 2019). These passive acoustic data can be quantified at a variety of analytical levels, ranging from presence/absence, animal call rates, time budgets, or used to estimate density and abundance of individuals within the population (e.g., Kalan et al. 2015, McDonald et al. 2017). Typically, estimating animal densities based on acoustic recordings requires identifying the appropriate sound produced by the animal, determining the probability of detection and call rate, and then translating the number of calls into a density estimate (Marques et al. 2013). While some of this information may be obtained from ancillary data, it is unknown for many species, populations, locations, and times of year, increasing the consequent uncertainty in density estimates (Marques et al. 2013). Species densities are a key component in estimating the number of animals that may be adversely impacted by a particular activity within an environmental assessment and are routinely required to ensure compliance with regulations.

An alternative approach for estimating densities and abundance is to use individually recognizable marks or signals to identify and count the number of animals through repeated observations. Traditional methods using observations of natural or artificial markings on individuals generally require intensive monitoring, particularly if marks change over time. In contrast, acoustic monitoring for vocal individuality is non-invasive and utilizes calls or songs that are stable over long time periods (Terry et al. 2005). Acoustic monitoring of individuals is increasingly used in bird studies in the terrestrial environment (Mennill 2011, Petrusková et al. 2016), but has been rarely used for marine species due to increased difficulty in identifying and verifying individually distinctive calls (but see Aubin and Jouventin 2002, Fine and Thorson 2008, Antunes et al. 2011). The most studied vocalizing marine animals, cetaceans, have been shown to produce both individual and group-specific repertoires of calls (Weilgart and Whitehead 1987, Ford 1989). Bottlenose dolphins (*Tursiops truncatus*) produce individually distinct signature whistles developed during their first year, which remain relatively stable during their life (Caldwell and Caldwell 1968, Sayigh et al. 1990, Janik and Sayigh 2013, Jones et al. 2020). The unique sound frequency contour of a signature whistle conveys identity information (Janik et al. 2006). Approximately half of whistles produced by wild bottlenose dolphins are signature whistles (Cook et al. 2004), with the highest output when groups encounter each other (Quick and Janik 2012).

Information on patterns of species occurrence and density can be combined with environmental variables in a habitat-based model (a type of species distribution model; SDM) to identify relationships and develop predictions regarding species movement (Guisan and Zimmermann 2000, Elith and Leathwick 2009). Sighting records were the observations generally used in these models, often requiring a large sample size to provide adequate model fit (Roberts et al. 2016b). Advancements in PAM can now produce large species detection datasets that can be collated and analyzed; however, these data have generally been used for SDM validation, rather than direct model incorporation (e.g., Brookes et al. 2013, Wingfield et al. 2017). The application of PAM data within these SDMs could increase their utility because they tend to have higher detection probabilities across a range of environmental conditions that can improve model predictions (Soldevilla et al. 2011). SDMs increasingly serve as a management decision support tool for anthropogenic activities and environmental assessments (Guisan et al. 2013, Lewison et al. 2015, Maxwell et al. 2015).

In this study, we used PAM recordings to detect bottlenose dolphins and identify individual signature whistles in the Mid-Atlantic Bight, offshore of Maryland (MD), USA, and within the

Chesapeake Bay in MD. Previously, relatively little was known about bottlenose dolphins in this region, although studies to the north (off New Jersey, USA) and south (off Virginia, USA) of this area indicated that they mainly occurred regionally from May to October (Barco et al. 1999, Toth et al. 2011). Our study aimed to determine the seasonal occurrence of dolphins from detection of their calls and use individual signature whistles to (1) track individuals spatially and temporally, (2) assess site fidelity at the scale of our detection range, (3) determine a minimum estimate of the number of dolphins occurring in the study area, and (4) develop a dynamic habitat-based relative abundance model that could be used as a near real-time prediction tool by managers and other stakeholders. Such a tool could support decision-making and environmental assessments within our study area, including within leased areas for offshore wind energy along the U.S. Atlantic Coast (Bailey et al. 2014, information on leasing and permitting at www.boem.gov). Individually identifiable signature calls are being discovered in other odontocete cetaceans (Lima and Le Pendu 2014, Panova et al. 2017) and other vocal species groups (e.g., Charlton et al. 2011, Petrusková et al. 2016), indicating this approach could also be applied more broadly to other populations and species.

METHODS

Study area

Our study area included three locations: the U.S. Mid-Atlantic Bight at 12 km (Site 1) and 31 km (Site 2) east of Ocean City, MD, and the upper Chesapeake Bay, MD, at the mouth of the Rhode River (Site 3; Fig. 1). Water depths ranged from approximately 20–28 m in oceanic waters, and acoustic recording instruments were deployed from 2016 to 2018 at two sites (Sites 1 and 2), approximately 3 m above the ocean floor using bottom-anchored moorings (see Garrod et al. 2018). In the Rhode River (Site 3), the water depth was 2.5 m, and the instrument was deployed approximately 1.5 m from the bottom during summer 2018.

Dolphin occurrence

To determine the seasonal pattern of dolphin occurrence, echolocation click detectors (C-POD;

Chelonia, Cornwall, UK) were deployed at Sites 1 and 2. C-PODs continuously monitored frequencies of 20–160 kHz for odontocete click trains, and detections were logged and classified using the high and moderate filters of the KERNO classifier processed by the CPOD.exe program (Chelonia). Hours in which there was at least one click train were identified as a detection positive hour (DPH), a robust measure of dolphin occurrence in this study area (Garrod et al. 2018).

In the Rhode River where we had an acoustic recorder but no C-POD, the PAMGUARD Whistle and Moan Detector (Gillespie et al. 2013) was utilized to help determine acoustic dolphin presence from the acoustic recordings (see *Whistle detection*). Given numerous false-positive detections caused by background noise, all recording hours were reviewed manually for the presence of any dolphin clicks and/or whistles. Hours in which there were manually verified dolphin detections were classified as the number of DPH within the Rhode River. All hours with dolphin detections included both clicks and whistles.

We calculated the daily sum of DPH and mean DPH per month for each site to determine the seasonal pattern of dolphin occurrence. We tested for significant temporal patterns using generalized auto-regressive moving average (GARMA) models (Benjamin et al. 2003) at Sites 1 and 2 where there were multi-year data. The response variable was the daily sum of DPH, and the explanatory variables were day of year and year. Day of year was transformed using a pair of sine and cosine functions (as in Wingfield et al. 2017), and year was included as a categorical variable.

Whistle detection

Archival acoustic recorders, SM3Ms (Wildlife Acoustics, Maynard, Massachusetts, USA), were deployed from 2016 to 2018 at Sites 1 and 2 (Fig. 1). The SM3M recorder sampled at 48 kHz with a hydrophone sensitivity of 165 dB re 1 V/μPa and a gain of 12 dB re 1 μPa in 2016 and 2017. The gain was reduced to 0 dB re 1 μPa in 2018 in anticipation of loud construction activities related to the planned installation of a meteorological tower that was ultimately delayed beyond our recording period. To maximize battery life during deployments, the duty cycle for recordings was set to two minutes on and four minutes off in 2016, and five minutes on and ten
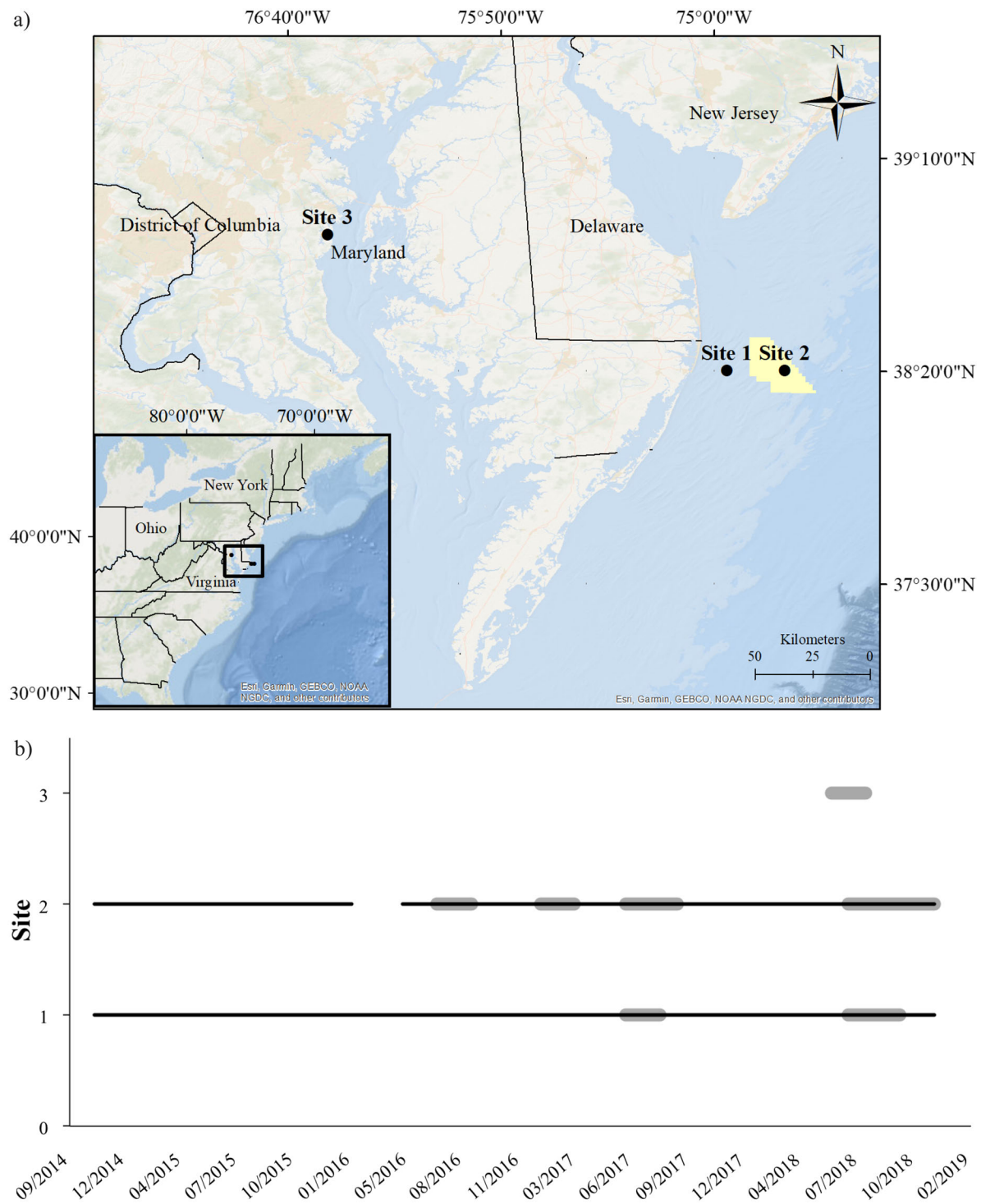
Fig. 1. (a) Map of the study area with Site 1 and Site 2 in the Mid-Atlantic Bight and Site 3 within the Rhode River in the Chesapeake Bay, Maryland, USA. The yellow area indicates the Maryland Wind Energy Area. (b) Recording effort at each site by acoustic detection method, with a C-POD shown as a thin black line and the acoustic recorder (SM3M or DSG) as a thick gray line.

minutes off in 2017 and 2018 (20 min per hour in both duty cycles). A DSG acoustic recorder (Loggerhead Instruments, Sarasota, Florida, USA) was deployed at Site 3 at the mouth of the Rhode River between May and September 2018 and sampled at 44.1 kHz, with a sensitivity of 169.7 dB re 1 V/μPa and a gain of 20 dB, duty-cycled for five minutes on and ten minutes off (Fig. 1).

To determine when dolphin whistles were present during recording periods, the PAMGUARD Whistle and Moan Detector (Gillespie et al. 2013) was utilized with its default settings, detecting whistles between 2 kHz and 10 kHz and requiring a minimum of an 8 dB difference between background sound and the whistle for detection. These detections were manually reviewed and analyzed in the Raven Pro 2.0 Interactive Sound Analysis Software (Cornell Lab of Ornithology, Center for Conservation Bioacoustics, Ithaca, New York, USA) to determine the presence of high signal-to-noise ratio whistles (Heiler et al. 2016), which were then reviewed for signature whistles.

Signature whistle analysis

Whistles with high signal-to-noise ratios were analyzed to determine whether they met the criteria for categorization as a signature whistle. We identified a signature whistle by its repeated pattern of two or more whistles (known as a bout; Cook et al. 2004) within 1–10 s of the same whistle and a minimum length of 0.2 s (Janik et al. 2013, Gridley et al. 2014; Appendix S1: Fig. S1). Harmonics were excluded from our analysis.

For each signature whistle selected, the frequency contour (shape within the spectrogram) of the whistle was extracted with Beluga (https://synergy.st-andrews.ac.uk/soundanalysis), a sound analysis program in MATLAB (MathWorks, Natick, Massachusetts, USA). Once all whistle contours were extracted in Beluga, the adaptive resonance theory neural network (ARTwarp; Deecke and Janik 2006) in MATLAB was used to identify whistle matches across all years and sites. A human analyst manually verified each match identified by ARTwarp in Raven Pro 2.0 (CCB, 2020) and checked for any missed whistle matches.

Within ARTwarp, the vigilance threshold indicates the percentage of similar characteristics required for whistles to be considered a match. To determine the appropriate vigilance for these analyses, 94%, 96%, and 98% vigilance thresholds were tested. The number of whistles incorrectly matched was lowest at the vigilance threshold of 98%, but the number of missed whistle matches was fewest at a vigilance of 94% (Appendix S1: Table S1). At a vigilance of 96%, ARTwarp's analysis mismatched less than half of the whistles that were incorrectly matched at 94% (22% vs. 49%, respectively) and had only a slightly higher number of missed whistle matches (3% vs. 2%, respectively). The process of inspecting large numbers of whistles for missed matches was very time intensive. A higher vigilance threshold (98%) was therefore utilized only when running ARTwarp to identify individual whistle types for smaller datasets (less than 100 whistles), such as those from a single month at a single site, to minimize incorrectly matched whistles. After manual verification of the 98% threshold analysis results on smaller datasets, unique signature whistles were then compiled across time and sites using the 96% vigilance for the larger dataset. This lower threshold ensured fewer missed whistle matches. ARTwarp analysis was performed for a maximum of five iterations on each dataset.

During manual verification of whistle matches, to ensure consistency among observers, a second analyst confirmed whistle matches. Matches within the same hour were not considered reoccurrences as these could have occurred within the same encounter. We classified the best whistle in each match as the whistle with the highest signal-to-noise ratio and most clearly defined contour. These best signature whistles of each match were used in subsequent ARTwarp analyses. Data were synthesized in a final database with the occurrence and re-occurrence of individual signature whistles on a daily scale.

To determine the whistle detection range of our SM3M recorders, signature whistles were selected during a period when we had multiple acoustic recorders simultaneously deployed in the U.S. Mid-Atlantic Bight. When a signature whistle was detected at a hydrophone, simultaneous audio recordings at distances of 3, 8, and 20 km from the original detection were inspected to determine whether the whistle was also recorded at these farther sites.

Habitat-based model

Signature whistle identification by manual review of spectrograms was highly time intensive, particularly at Sites 1 and 2, where there were large numbers (thousands) of whistles recorded. Consequently, data from Sites 1 and 2 were subsampled; analysis was completed on the two hours in each day with the highest detections from the PAMGUARD Whistle and Moan detector. To examine the effect of data subsampling on the estimated total number of signature whistles per day, at each site (Sites 1 and 2) and season, five 24-h periods were fully analyzed for signature whistles. The signature whistle detection rate, the percentage of signature whistles detected by this two-hour subsampling compared to the total number of signature whistles per day, was used to estimate the total daily number of signature whistles for each site and season.

To model the number of unique dolphin signature whistles detected, indicating the minimum number of individual dolphins, at Sites 1 and 2 from our multi-year dataset, a generalized additive model (GAM) with a log link function was used. The 8-d sum of the estimated total minimum daily number of signature whistles was used as the response variable because this reduced the amount of remotely sensed environmental data that was missing at the 1-d scale because of cloud cover. At the beginning or end of a hydrophone deployment, when there may have been an incomplete eight days of recording, the 8-d sum was estimated by calculating an average daily count of whistles from the days with recordings and applying this value to any unsampled days. The explanatory variables in the GAM were site, sea surface temperature (SST), log-transformed chlorophyll *a* concentration (chl *a*), and mean ambient sound level.

Ambient sound levels were calculated from the SM3M acoustic recordings. Acoustic data from the hydrophones were analyzed using the Raven-X toolbox (Cornell Lab of Ornithology Bioacoustics Research Program, Ithaca, New York, USA) in MATLAB (Dugan et al. 2016). The metric of equivalent continuous sound pressure level (Leq) was used to calculate the root-mean-square (rms) pressure within one-hour time bins to represent the ambient sound levels. These binned values were averaged to obtain mean daily ambient sound levels and further averaged over eight days to match the 8-d composites of SST and chl *a* concentration. We tested for collinearity between the explanatory variables by calculating the variance inflation factor. All of the variance inflation factor values were <3 indicating there was no significant collinearity (Zuur et al. 2009). Smoothers were restricted to four degrees of freedom to avoid over-fitting (Wood 2017). The SST (°C) and chl *a* concentration (mg/m^3) data were obtained from NOAA's ERDDAP database (Simons 2018) as 8-d composite measures. Both datasets had a 4-km^2 spatial resolution from the Aqua spacecraft with the Moderate Resolution Imaging Spectroradiometer (MODIS).

Models were fit using the RStudio software (Version 1.1.5033; R Core Team 2018) package mcgv (Wood 2017). The best model was selected based on the R^2 value. Model sensitivity to explanatory variables was explored to create a simplified model more operationally feasible, with similar success at predicting the minimum number of dolphins. A data selection of 80% was included to train the model, and the model's ability to predict dolphin occurrence was tested with the remaining 20% of data following final model selection.

RESULTS

Dolphin occurrence

Dolphin presence showed a significant seasonal pattern at Site 1 with dolphins mainly occurring between April and November, which was consistent across all three years (Table 1, Fig. 2). There was a similar seasonal pattern at Site 2 (Table 1, Fig. 2). Dolphin occurrence was generally higher during the summer and lower during the winter at both sites (Table 1, Fig. 2). Dolphins were detected at Site 3 in the Rhode River between June and August with the peak in early to mid-July, although dolphins occurred less frequently at Site 3 than Site 1 or 2.

Signature whistle detections

A total of 1518 unique signature whistles were identified off the coasts of Maryland, USA, at our sites within the Atlantic Ocean and Chesapeake Bay. The largest number of unique individual signature whistles was identified at Site 1, with 693 signature whistles detected in 2017 and 479

Table 1. Significant results of the generalized auto-regressive moving average (GARMA) determining the seasonal (sin and cos of 2π*(Julian day)/number of days in the year) and inter-annual variation in bottlenose dolphin presence at Sites 1 and 2.

Parameter	Estimate	SE	P
Site 1			
Intercept	2.83	0.23	
Sin	−0.89	−3.15	<0.01
Cos	−3.15	0.30	<0.01
Site 2			
Intercept	2.75	0.25	
Cos	−0.64	0.18	<0.01
Year: 2017	0.84	0.36	0.02

Note: Year (2016–2018) was treated as a categorical variable, and 2015, the first full year of data, was the reference year.

detected in 2018 (Table 2). In 2016, the mooring caused loud, repetitive noise at Site 1, which prevented detection of high signal-to-noise ratio signature whistles and this period was not used in the analysis. This issue was remedied for the later deployments.

At Site 2, 91 unique signature whistles were detected during 2016, 109 were detected in 2017, and 127 were detected in 2018 (Table 2). In summer 2018, 19 unique dolphin signature whistles were detected at Site 3 in the Rhode River (Table 2). The shallow depth of Site 3 resulted in high ambient sound levels (including wave and boat noise), ultimately reducing the identification of signature whistles with high signal-to-noise ratios. From our subsampling analysis (2 h per day), the largest number of signature whistles was detected from June to August at Site 1 in 2017 ($n = 412$) and from July to August at Site 1 in 2018 ($n = 293$; Table 3). At Site 2, 29 whistles were detected in only seven hours of acoustic recordings during December 2018 (Table 3).

Among all sites and seasons, 142 whistles re-occurred 184 times (11% of all detected signature whistles were re-occurrences; Figs. 3, 4). Whistles typically re-occurred once (77%), but nine whistles were detected four times (5%; Fig. 4), three whistles were detected five times (2%; Fig. 4), and one whistle was detected seven times (1%; Fig. 4). There were 14 whistles with only one day between re-occurrences, and the longest period between re-occurrences was 681 d at Site 2 (20

January 2017–2 December 2018; Fig. 4). There was a mean of 135 d between re-occurrences of whistles (SD = 192 d).

Whistles re-occurred most often at the same site (81%) and in the same season (73%, SD = 25%) they were originally detected. Re-occurring signature whistles were most frequently detected within the same summer or between summers (54%). Whistles detected at different sites (19% of all re-occurrences) were most often detected between Sites 1 and 2 (from Site 1 to Site 2; 13%, from Site 2 to Site 1; 5%). There were two occurrences of a whistle detected in 2017 at the Mid-Atlantic Bight sites that re-occurred at Site 3 in the Rhode River in 2018 (one from Site 1; 0.5%, and one from Site 2; 0.5%).

Analysis of the detection range of our acoustic recorders revealed the same whistles could be detected 85.3% of the time at a recorder 3 km away, 34.6% of the time 8 km away, and 0.0% of the time (no detections) 20 km away (Appendix S1: Fig. S2). Therefore, we estimated a 50% detection rate at 6.5 km from our recorder. The distance between Sites 1 and 2 is approximately 20 km, and the in-water distance to Site 3 exceeds 20 km (approximately 381 km and 392 km from Sites 1 and 2, respectively; Fig. 1), resulting in no overlap between the whistle detection ranges of our three sites.

Habitat-based model

The percentage of total daily signature whistles detected during the two-hour subsampled periods varied among sites and seasons. The highest detection rates of signature whistles within subsampled periods occurred at Site 1 during the fall (77%; Table 3) and at Site 2 during the winter (76%; Table 3). At Site 1 during the summer, 49% (SE = 6%) of whistles in a day were captured in the two-hour subsample (Table 3). Summer and fall at Site 2 had a similar detection rate as summer at Site 1 (43%, SE = 2%; 49%, SE = 0.2%, respectively; Table 3). The signature whistle detection rate during the spring (March–May) at Site 2 was calculated by averaging the summer and winter (December–February) values for this site (59%). These percentages were used to estimate the number of daily signature whistles, indicating the number of individual bottlenose dolphins, for Sites 1 and 2 for each season (Table 3).
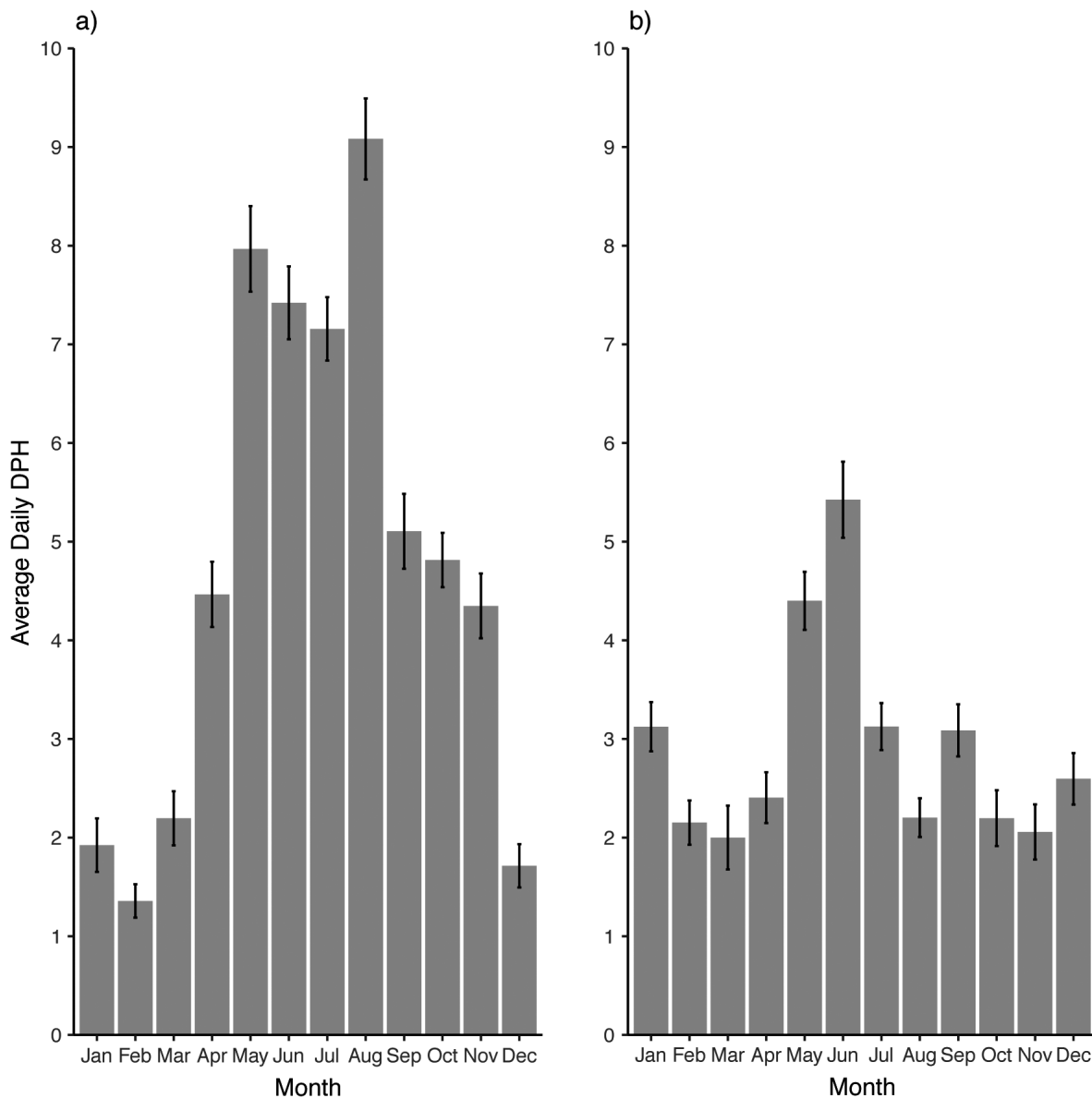
Fig. 2. Number of dolphin detection positive hours (DPH) per day, averaged monthly at Site 1 (a) and Site 2 (b), 12 km and 31 km offshore of Ocean City, Maryland, respectively.

The model that best explained the variability in the minimum number of dolphins utilized a Poisson distribution and included site and a smoothing spline for mean SST (Table 4, Fig. 5a). While both SST and chl a concentration were significant when included in the model, a simplified model with only site and mean SST performed similarly to the model with both explanatory variables (Table 4). As a result, the simplified model was chosen as the final model. This final model, which was created with 80% of the dataset, was used to predict the number of signature whistles for the test dataset (Fig. 5b, Table 4). The minimum number of dolphins predicted by the model was highly positively correlated with the actual number of unique signature whistles detected in the test dataset (Pearson's correlation: $r = 0.86$, $P < 0.001$).

Table 2. The number of unique signature whistles (with only the first occurrence of a whistle included), length of the recording period, and hours of acoustic data analyzed for each site and year.

Deployment	Site	2016	2017	2018	Total/ average
Deployment length (h)	1	N/A	3024	2256	5280
	2	1584	4872	3528	8400
	3	N/A	N/A	3000	3000
Data analyzed (h)	1	N/A	252	194	457
	2	88	224	262	564
	3	N/A	N/A	2488	2488
No. unique signature whistles	1	N/A	693	479	1172
	2	91	109	127	327
	3	N/A	N/A	19	19
No. signature whistles per hour recorded	1	N/A	0.229	0.212	0.221
	2	0.057	0.022	0.036	0.038
	3	N/A	N/A	0.006	0.006

Note: N/A denotes where data were not available.

DISCUSSION

Our analysis of multi-year, multi-site acoustic recordings off Maryland, USA, represents the largest catalog of bottlenose dolphin signature whistles that we are aware of, to date. We identified 1518 unique signature whistles, a minimum number of dolphins within our study area, which is within the range of the Western North Atlantic

Northern Migratory Coastal Stock of bottlenose dolphins that has an abundance estimate of 6639 based on aerial surveys from Virginia to New Jersey (Garrison et al. 2017a). There were 184 re-occurrences of 142 whistles (between 1 and 681 d apart) among all three sites within the Chesapeake Bay and offshore of Maryland. This indicates the movement of dolphins between these areas, as well as site fidelity to these sites between seasons and years. It was previously unknown whether the same individuals that occur offshore would enter the Chesapeake Bay, which is within the seasonal range of another population, the Western North Atlantic Southern Migratory Coastal Stock (Hayes et al. 2018). Although bottlenose dolphins have been intensively studied in many estuarine and coastal areas (e.g., Bearzi et al. 2008, Cheney et al. 2014, Mann and Karniski 2017), the identification and tracking of individuals farther offshore indicates that habitat use in these areas may have previously been underestimated. This more complete understanding of bottlenose dolphin habitat use can aid in determining their risk of exposure to anthropogenic activities, including vessels, fishing, and offshore energy development.

At Site 1, we identified 693 unique signature whistles during 2017 and 479 in 2018 (Table 2). These numbers represent a minimum dolphin

Table 3. Summary of the hours of acoustic recordings reviewed, number of signature whistles identified within two-hour subsamples, signature whistle detection rates within two-hour subsamples, and corrected daily dolphin abundance estimations based on the signature whistle detection rate with average daily whistle abundances added for days without data.

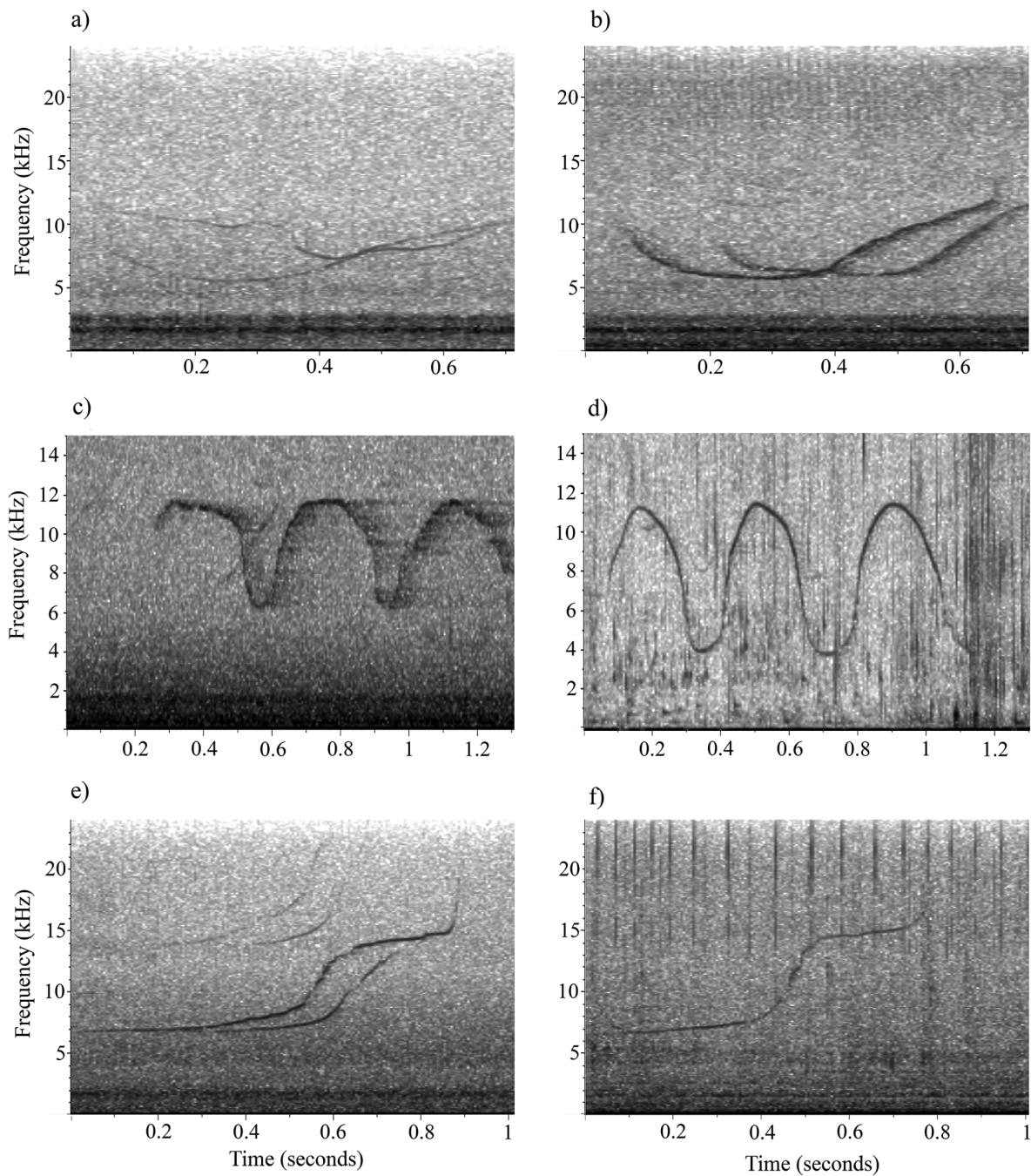| Year by site	Months	No. hours analyzed	No. signature whistles detected	Signature whistle detection rate (%)	Corrected dolphin abundance estimate
1					
2017	Jun–Aug	121	412	49.12	1286
2018	Jul–Aug	75	293	49.12	638
	Sep–Oct	72	240	76.60	347
2					
2016	Jul–Aug	46	77	43.14	243
	Sep	41	4	48.98	16
2017	Jan–Feb	63	56	75.56	94
	Mar–Apr	25	14	59.35	61
	Jun–Aug	100	43	43.14	111
	Sep–Oct	29	1	48.98	2
2018	Jun–Aug	98	45	43.14	125
	Sep–Nov	105	67	48.98	307
	Dec	7	29	75.56	76

Fig. 3. Spectrograms of three signature whistle detections (a, c, e) and their re-occurrences (b, d, f, respectively). A signature whistle detected at Site 1 on 5 July 2017 (a) re-occurred at Site 2 on 12 October 2018 (b), a signature whistle at offshore Site 2 on 30 July 2017 (c) re-occurred in 2018 in the Rhode River (d), and a signature whistle that occurred at Site 2 on 20 September 2017 (e) re-occurred nearly one year later at Site 1 on 16 September 2018 (f).
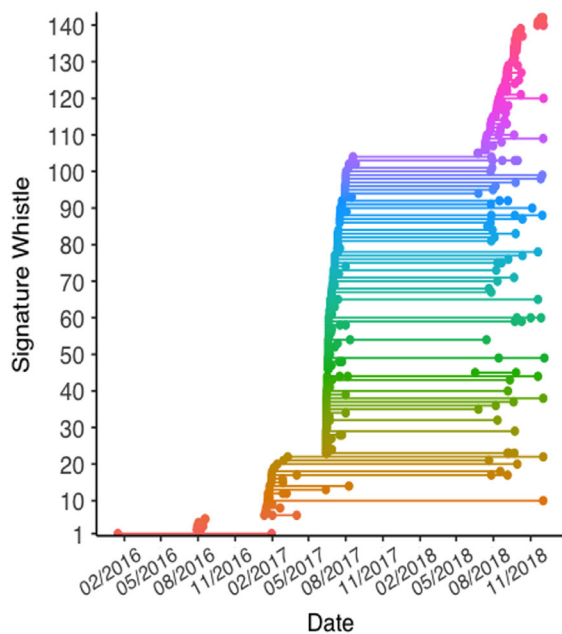
Fig. 4. Re-occurrence of 142 bottlenose dolphin signature whistles at all sites between summer 2016 and winter 2018. Each color is an individual, and each point is one occurrence of an individual, with 184 re-occurrences of these 142 signature whistles.

abundance estimate within our detection range at that site (approximately 6.5 km radius). Based on two years of monthly aerial surveys, previous abundance estimates of bottlenose dolphins within the area off Ocean City, MD (encompassing Sites 1 and 2), ranged from 24 (CV = 1.05) to 8351 (CV = 0.45) individuals per survey (Barco et al. 2015). Given our devices' detection radius of 6.5 km and bottlenose dolphin density between 1.3 and 1.8 animals per km^2 (Barco et al. 2015), we would expect to detect 173–239 animals within each of our sites' 132.7 km^2 survey areas. The number of signature whistles identified at Site 1 during the summer exceeded this estimate (mean = 353, SD = 84), but was lower at Site 2 (mean = 55, SD = 19; Table 3). The summer abundance estimated by the aerial surveys is similar, however, to the mean number of signature whistles identified during the summer from the two sites combined (mean = 174, SD = 169 signature whistles). Other studies utilizing shipboard and aerial surveys estimated densities ranging from 0 to 617 individuals per km^2 (Roberts et al. 2016a, b). Derived habitat-based density models from these shipboard and aerial survey data for the month of July predict density values equivalent to 46 and 6.8 individuals per 100 km^2 in the area of Sites 1 and 2, respectively (Roberts et al. 2016a, b). This is equivalent to 61 and 9 individuals within the detection range of Sites 1 and 2, respectively, and much lower than the number of unique signature whistles we detected.

These results indicate that previous surveys and models may have underestimated the number of bottlenose dolphins within this region of the Mid-Atlantic Bight, likely a result of the

Table 4. Results and root-mean-square error (RMSE) of the generalized additive models (GAMs) used to determine the relationship between the number of dolphin signature whistles, recording site (Site 2 was the reference level), and environmental conditions (sea surface temperature [SST] and log chl a).

Parameter	Parametric coefficients				Smooth terms			
	Estimate	SE	z	P	Est df	Ref df	χ^2	P
Full restricted model								
Intercept	2.69	0.05	59.32	<0.01				
Site 1	2.13	0.08	28.36	<0.01				
SST					2.93	3	131.2	<0.01
log chl a					2.38	3	110.3	<0.01
Simplified model								
Intercept	2.75	0.04	67.08	<0.01				
Site 1				<0.01				
SST					3.00	3	342.4	<0.01

Notes: The smoothers in the GAM were restricted to four degrees of freedom (df). For the full restricted model, $R^2 = 0.37$, deviance explained = 47.90%, and RMSE = 5.50; for the simplified model, $R^2 = 0.43$, deviance explained = 52.00%, and RMSE = 5.13.
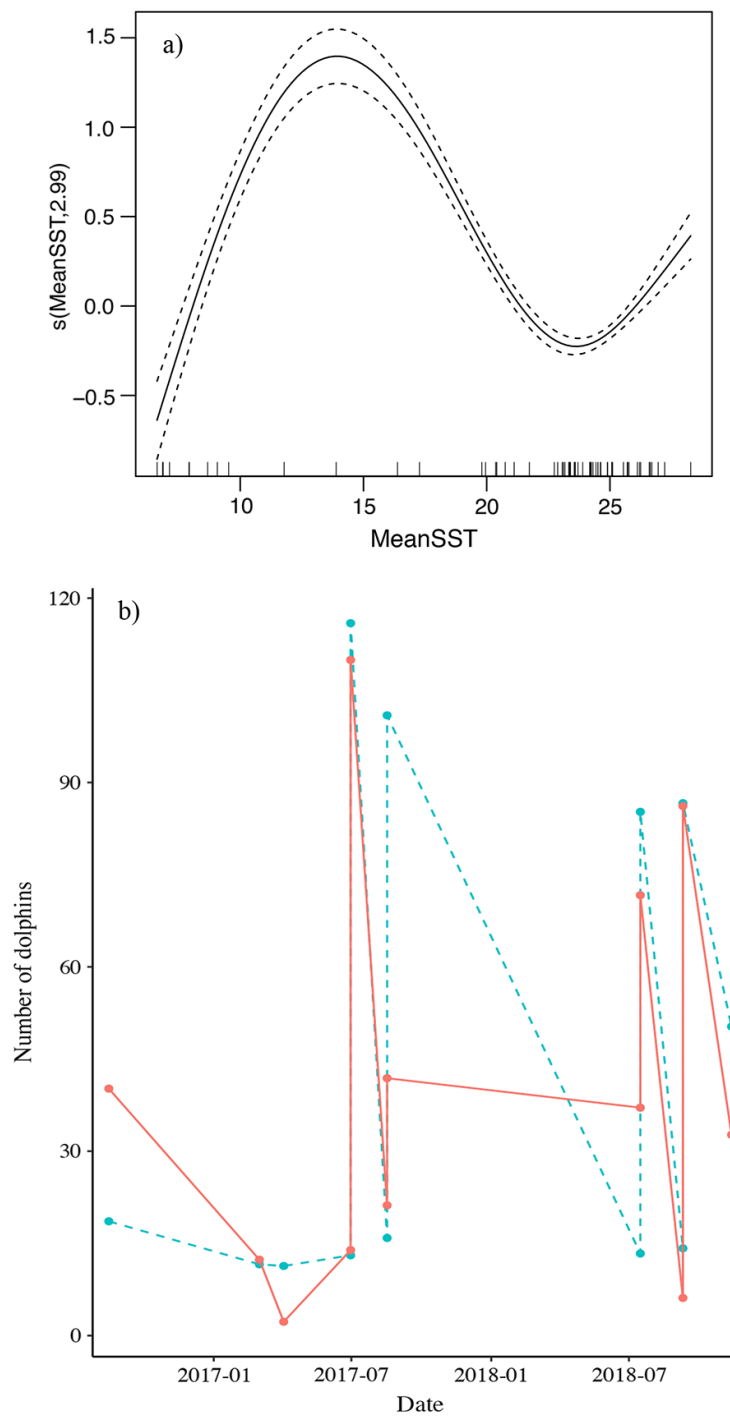
Fig. 5. (a) Visualization of the smoothing spline (restricted to four degrees of freedom) for sea surface tempera-ture (SST) in the final generalized additive model (GAM). (b) The number of dolphins predicted by the final model (using 80% to train the GAM and 20% to test its performance; blue dashed) and the estimated number of dolphins actually detected based on the number of signature whistles detected in two-hour subsamples (solid red).

relatively low survey effort (Roberts et al. 2016*a*, *b*). Passive acoustic monitoring can provide a valuable technique for surveying in all conditions and when species occurrence is rare (Rayment et al. 2011). Previous survey methods required visual observation of dolphins at the surface, affecting their probability of detection. Although the detection rate of bottlenose dolphin signature whistles is unknown, it is expected that the detection probability was less than 100%. Therefore, analysis of signature whistles would similarly underestimate the number of individual dolphins present. Free-ranging bottlenose dolphins most frequently emit their signature whistle when they meet a new group of individuals (Quick and Janik 2012) and do not emit them continuously (Janik and Sayigh 2013). When emitted, our ability to detect signature whistles is impacted by the orientation of the dolphin transmitting the sound and the local ambient sound conditions. This will likely vary the detection rate of signature whistles under differing ambient sound conditions and social contexts. The estimation of abundance based on signature whistle identification and determining any necessary correction factors could be improved through further research comparing the detection rate of known vocalizing dolphins under different conditions and behaviors and determining the number of signature whistles associated with different known group sizes. A recent study in Namibia, however, demonstrated close correspondence between a population abundance estimate based on acoustic detection of signature whistles (54–68 individuals) and an existing estimate derived from boat-based photo-identification of animals in a mark–recapture framework (54–76 individuals; Longden et al. 2020).

North of Maryland off New Jersey, USA, in 2003–2005, both seasonally resident and transient bottlenose dolphins were identified during photo-identification surveys (Toth et al. 2011). In, Toth et al. (2011) 205 individuals were identified and the discovery curve had not plateaued. There was a persistent influx of new individuals into the area with an average of 61% of new individuals in 2003 and 32% in 2004 (Toth et al. 2011). Re-sighting rates across photo-identification surveys were similarly low off Virginia, south of Maryland, USA (Engelhaupt et al. 2016). There were 878 individuals identified from

August 2012 to 2015, of which only 12.5% (*n* = 110) were seen on more than one occasion (Engelhaupt et al. 2016). This rate of re-occurrence is similar to that seen in our study, which was 11%. Off Virginia, only 2.4% (*n* = 21) of individuals were observed on three or more occasions, and most (89%) re-sightings were in the same calendar year (Engelhaupt et al. 2016). Our study indicated a similar pattern of signature whistle re-occurrence, the majority being in the same year (mean = 135 d). Both of the previous studies observed pulses in movement with an increase of new individuals in June and July (Toth et al. 2011, Engelhaupt et al. 2016), a trend which we also observed in the number of individual signature whistles (Table 3). Bottlenose dolphins likely move along the coast as a corridor, periodically returning or remaining in the region when the habitat and prey availability is favorable.

In contrast to the U.S. Mid-Atlantic Bight, the Chesapeake Bay, the largest estuary in the United States, has been generally well studied and the subject of major habitat restoration efforts (e.g., Hassett et al. 2005, Testa et al. 2017). Despite the considerable ecological research conducted, relatively little was known about bottlenose dolphin occurrence other than data from stranding records (Dunn et al. 2002, Schaffler et al. 2011) and a small number of surveys (Barco et al. 1999, Richlen et al. 2017). In 2015 and 2016, 303 dolphins were sighted during aerial surveys, and group sizes of up to 70 were observed from vessel surveys (Richlen et al. 2017). Acoustic detections of dolphins in the middle of the Bay mainly occurred between April and October with a peak in June and July (Richlen et al. 2017; Rodriguez et al. 2021). Surveys in the lower Bay in 1994 and 1995 had the largest number of dolphins in July and August (Barco et al. 1999). Sightings of bottlenose dolphins over the last few years indicate that they are frequent inhabitants of the Chesapeake Bay (Rodriguez et al. 2021). Similarly, although only one summer of acoustic recording data was analyzed in our study, dolphins were regularly detected at the mouth of the Rhode River in the upper Chesapeake Bay (Site 3) between June and August.

There were a total of 21 individual signature whistles detected in the Rhode River (Site 3), of which 19 were unique because one had

previously been identified at Site 1 and another was first detected at Site 2. A minimum of 21 individual bottlenose dolphins therefore visited this area during the summer of 2018. The total number of dolphins utilizing this habitat is likely much higher. The Rhode River is a small sub-estuary of the Chesapeake Bay, and larger group sizes have been reported within the larger tributaries and mainstem of the Bay (www.chesapeakedolphinwatch.org). In addition, because the acoustic recorder at Site 3 was in shallow water and close to the water's surface, recordings suffered from high background noise levels from waves, boats, and other animal calls, such as birds. This background noise occasionally masked the dolphin whistles or obscured the signal. This resulted in a low signal-to-noise ratio or only a single clearly detected whistle in a series, rendering us unable to consider it a part of a bout and classify it as a signature whistle. Acoustic recordings in deeper water and within larger tributaries or the mainstem of the Chesapeake Bay may improve our ability to detect signature whistles and, therefore, more accurately estimate of the number of individual dolphins present. Ideally, the same type of recorder and duty cycling (if any) would be used at all study sites, but this is not always possible with available resources.

Dolphin occurrence was most frequent at Site 1, and this trend was consistent across years. Bottlenose dolphins were present at this site year-round, but there was significant seasonal variation. The highest occurrence was between April and November with a peak between May and August, which concurs with previous studies in neighboring areas (Barco et al. 1999, Torres et al. 2005, Toth et al. 2011, Whitt et al. 2015). These bottlenose dolphins are likely from the Western North Atlantic Migratory Coastal Stock where the population is described as occurring coastally from Virginia to New York in the summer and migrating south in the fall to spend the winter in coastal waters off North Carolina (Garrison et al. 2017b). Based on the number of individual signature whistle re-occurrences, the highest site fidelity occurred at Site 1; dolphins that moved through this coastal area were more likely to return. There were fewer re-occurrences at Site 2, which was farther offshore and appeared to be at the fringe of the range for these coastal dolphins.

Site 2 is 30 km offshore, which would overlap this stock's distribution range with that of the Western North Atlantic Offshore Stock of bottlenose dolphins. This offshore population is generally found more than 34 km from land in water depths greater than 34 m, although they have also been observed closer to shore (Torres et al. 2003, Hayes et al. 2018). The re-occurrence of individuals between Sites 1 and 2 indicates that at least a portion of Site 2 detections were likely members of the Western North Atlantic Migratory Coastal Stock; however, some of the signature whistles solely detected at Site 2 could have been from the Western North Atlantic Offshore Stock.

There was significant seasonal variation in the occurrence of dolphins at Site 2, but this variation was less pronounced than at Site 1. During the winter, this may indicate either the presence of bottlenose dolphins from the Western North Atlantic Offshore Stock at Site 2 or common dolphins (*Delphinus delphis*). Common dolphins cannot be distinguished from bottlenose dolphins using the C-POD click classifier (Robbins et al. 2016) and may also produce signature whistles (Caldwell and Caldwell 1968). Common dolphins and other dolphin species occasionally occur in the study area in winter and spring (Jefferson et al. 2009, Barco et al. 2015). In the Pacific Ocean, an odontocete call classification algorithm, ROCCA, was developed to allow species identification of different delphinids (Oswald et al. 2007). This algorithm performed poorly in the Northwest Atlantic based on concurrent visual and passive acoustic observation data and has not yet been updated for dolphin calls from this region (S. Van Parijs, *personal communication*). Re-training ROCCA, or developing a similar algorithm, for this and other locations would be a useful tool to assist in discriminating acoustically among dolphin species where or when multiple species can co-occur. Acoustic recordings at a site farther offshore than Site 2 would allow us to identify signature whistles and confirm whether there are any matches with Site 2 that would indicate those whistles likely belonged to bottlenose dolphins from the Western North Atlantic Offshore Stock. Although this offshore stock is estimated to number approximately 26,766 animals between central Virginia and the lower Bay of Fundy (Palka 2012), it is challenging to conduct traditional survey methods in this

offshore habitat, resulting in very little being known about their seasonal movements and population structure.

The habitat-based model we developed for Sites 1 and 2 indicated a relationship between the relative abundance of dolphins and environmental conditions. This model included sea surface temperature, a measure that is readily available. This allows our dynamic model of dolphin abundance to be used in an operational, near real-time tool to inform and assist in management of this protected species (e.g., Hazen et al. 2017). In addition, knowing the identity and frequency of individuals visiting a particular area using this non-invasive approach could improve our understanding of individual responses to specific anthropogenic activities and whether the same or different (naïve) animals occur after such events. This would give further insights into how to improve environmental assessments and characterize responses to anthropogenic activities (Bailey et al. 2014, Harris et al. 2018, Southall et al. 2019).

The Chesapeake Bay is an urban, estuarine habitat with a watershed population of over 17 million people and economically important fisheries, tourism, and recreation, as well as the largest naval base in the world. In the Western North Atlantic, there are proposals for the development of multiple offshore wind farms (Bailey et al. 2014, www.boem.gov), with two offshore wind turbines installed in the Mid-Atlantic Bight approximately 43 km off Virginia in 2020 (https://www.boem.gov/renewable-energy/state-activities/coastal-virginia-offshore-wind-project-cvow), and proposals for seismic surveys (Bureau of Ocean Energy Management 2014). Construction and other anthropogenic activities within these environments could cause harm and disturbance to bottlenose dolphins. By quantifying the occurrence, abundance, and density of these animals, we can understand the movements and residency patterns of individuals within affected areas. This understanding can aid in determining the exposure risk and disturbance effects at an individual and population level (Warton and Aarts 2013, Farmer et al. 2018).

While our study focused on the bottlenose dolphin, other marine mammals, terrestrial mammals, birds, and amphibians (Bee et al. 2001, Sousa-Lima et al. 2002, Darden et al. 2003,

Petrusková et al. 2016), many of which are at risk or poorly surveyed, are known to have identity-specific calls. Given individual acoustic-cue recognition is prevalent across a range of taxa, species likely utilize these cues to acoustically identify mates, offspring, relatives, and predators (Tibbetts and Dale 2007). Such communication has provided valuable insight into animal behavior, but has been relatively under-utilized in further understanding their ecology. For species in which vocal individuality has been determined a reliable survey technique (Terry et al. 2005), the application of PAM can non-invasively identify individual and group calls. These calls can then be used to track the number and identity of animals at high temporal resolution (e.g., hourly or daily) and can provide a valuable tool for single and multi-species management and conservation (Terry et al. 2005, Jacoby and Freeman 2016). Fully automated recognition of calls would also greatly enhance the speed and accuracy of large acoustic recording dataset analysis (Stowell et al. 2019). Passive acoustic monitoring is a relatively cost-effective method for long-term monitoring of vocalizing species, particularly in remote locations, such as offshore, where surveying can be logistically challenging and expensive. The use of PAM to detect individually identifiable calls has the capability to greatly enhance our ability to track individuals in more remote locations, farther from shore, and over larger areas.

ACKNOWLEDGMENTS

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3685/full