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The influence of habitat and time of day on the occurrence of odontocete vocalizations in Onslow Bay, North Carolina

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Abstract

To determine whether the occurrence and duration of odontocete vocal events varied by depth or time of day in Onslow Bay, North Carolina, we analyzed acoustic data collected by five underwater recorders. These recorders were deployed in July 2008 at three depths: two in shallow (64–73 m), one in medium (236 m), and two in deep (~366 m) water. We found that habitat influenced the occurrence of odontocete vocalizations, with significantly greater daily vocal activity from delphinids on recorders in deeper waters and sperm whale clicks recorded only on the medium and deep recorders. These findings suggest that a greater diversity and occurrence of animals are located in waters beyond the shelf break in this area, a conclusion supported by visual surveys. We also found an increase in the occurrence of delphinid clicks at night on the shallow and deep recorders, likely reflecting nocturnal foraging activity, and a regular nocturnal occurrence of sperm whale clicks on the medium-depth recorder located near the shelf break, suggesting that one or more sperm whales moved into that area to feed at night. These observations improve our understanding of the occurrence and behavior of odontocetes in this region of the U.S. Atlantic seaboard.

Key words: odontocetes, delphinids, sperm whales, vocalizations, diel vocal patterns, depth-related distribution.

Distribution patterns of many odontocete cetaceans have been linked to habitat parameters that likely reflect the availability and distribution of prey (Baumgartner 1997, Davis *et al.* 1998, Cañadas *et al.* 2002). Such oceanographic and physiographic parameters can be used to differentiate habitats of species that occur in the same geographic region. To discriminate species-specific habitat preferences, researchers typically analyze data collected during visual surveys with synoptic information on habitat components, such as depth, sea surface temperature, *etc.*, to create mathematical descriptions of the physical environment used by each species (Redfern *et al.* 2006).

In the Gulf of Mexico, for example, Davis *et al.* (1998) found that it was possible to discriminate the distribution of 13 cetacean species using depth as the single

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habitat parameter. Atlantic spotted dolphins (*Stenella frontalis*) occurred in the shallow waters of the continental shelf and along the shelf break, in contrast to bottlenose dolphins (*Tursiops truncatus*), which were found most commonly over deeper waters of the upper slope. All other species were found in pelagic waters, with short-finned pilot whales (*Globicephala macrorhynchus*) and Risso's dolphins (*Grampus griseus*) occurring predominantly along the mid-to-upper portion of the slope and rough-toothed dolphins (*Steno bredanensis*) and sperm whales (*Physeter macrocephalus*) found in even deeper waters.

Time of day also can affect a species' distribution, although at a finer scale. For example, Hawaiian spinner dolphins (*Stenella longirostris*) move offshore late in the day to feed on the deep scattering layer (DSL) as it rises towards the surface at dusk (Norris *et al.* 1994, Benoit-Bird and Au 2003). Also, striped dolphins (*Stenella coeruleoalba*) in the northwestern Mediterranean Sea move inshore to feed at the shelf break at night and return offshore during the day (Gannier 1999).

In Onslow Bay, North Carolina, a consortium of academic institutions has conducted year-round aerial- and boat-based line-transect visual surveys since 2007. In general the density of cetaceans is quite low in Onslow Bay compared to nearby areas such as Cape Hatteras, North Carolina (Halpin *et al.* 2009). The most common odontocetes observed during these surveys are Atlantic spotted dolphins and bottlenose dolphins. Almost all spotted dolphin sightings have occurred over the shelf, but the distribution of bottlenose dolphins extends into deeper waters (Halpin *et al.* 2009). Thus, bottlenose dolphins inhabit a range of depths throughout the study area, but are found in larger group sizes beyond the 200 m isobath. A more diverse assemblage of odontocetes occurs past the shelf break, including Risso's dolphins, rough-toothed dolphins, short-beaked common dolphins (*Delphinus delphis*), short-finned pilot whales, and sperm whales (Halpin *et al.* 2009).

Insights into the occurrence and distribution of cetaceans from visual surveys are, of course, limited by weather and visibility. As a result, there is little information about the distribution of these animals during the winter and in other periods when visual survey conditions are poor. In addition, little is known about how their patterns of distribution may change over diel cycles, which may reflect variation in behavioral state or time-specific habitat preferences. However, many marine mammals vocalize frequently, and researchers have used passive acoustic techniques to monitor occurrence, distribution, and temporal patterns in the vocal activity of cetaceans in many areas (Stafford *et al.* 2001, Burtenshaw *et al.* 2004, Clark and Clapham 2004, Mellinger *et al.* 2004, Wiggins *et al.* 2005, Munger *et al.* 2008, Soldevilla *et al.* 2010). Autonomous passive acoustic recorders are being used with increasing frequency to monitor populations of marine mammals over extended periods (Mellinger *et al.* 2004, Oleson *et al.* 2007, Philpott *et al.* 2007, Stafford *et al.* 2007, Verfuß *et al.* 2007). Acoustic recorders provide long-term temporal records unmatched by visual surveys and can collect data in any type of weather or visibility. An important bias associated with the probability of making detections with passive acoustic monitoring is that only vocalizing animals are detected, so silent animals go undetected. Behavior, time of day, group size, and group composition have all been correlated with the degree of vocal activity for some species (Goold 2000, Gordon *et al.* 2000, Jones and Sayigh 2002, Cook *et al.* 2004, Carlström 2005, Quick and Janik 2008, Hawkins and Gartside 2010, Hernandez *et al.* 2010). In addition, if the desired goal is to monitor particular marine mammals, classification of calls to the species level is needed. Although it is possible to classify some vocalizations to the species level (*e.g.*, Oswald *et al.* 2003, Soldevilla *et al.* 2008), more work is needed in this area, especially to differentiate sounds produced by delphinids.

During July 2008, we deployed five passive acoustic recorders in Onslow Bay as part of the U.S. Navy's marine species monitoring program in the Atlantic. Our goal was to examine the occurrence of odontocete vocal events. More specifically, we analyzed data from the recorders to determine (1) whether there were differences in the occurrence and duration of odontocete vocal events at different depths, and (2) whether the occurrence of odontocete vocal events showed diel patterns at any of the sites or depths.

METHODS

Study Area

We deployed acoustic recorders in Onslow Bay, North Carolina (Fig. 1), in the South Atlantic Bight. The Gulf Stream, a warm northward-flowing western boundary current, meanders over the shelf break and slope in this area.

Instruments

We deployed five archival passive acoustic recorders (Marine Autonomous Recording Units, Cornell Bioacoustics Research Program 2012), designed and

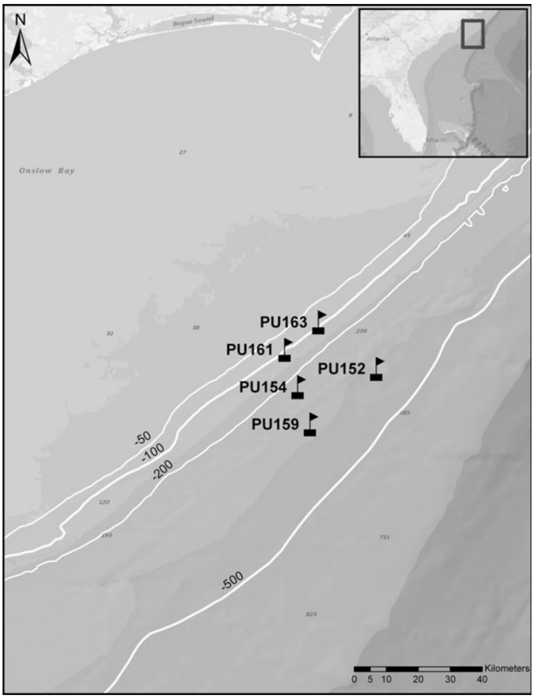

Figure 1. Onslow Bay study area showing locations of the five acoustic recorders (with recorder identification numbers to the left of the symbols).

manufactured by the Bioacoustics Research Program, Cornell Lab of Ornithology, in Onslow Bay (Fig. 1). The units sampled continuously at 32 kHz with 16-bit resolution from 6 July to 27 July 2008. Each recorder consisted of a single hydrophone (model HTI-94-SSQ, High Tech, Inc.) with a frequency response of 2 Hz to 30 kHz and sensitivity of −165 dB re: 1 Vrms/μPa. Each recording system had a 23.5 dB preamplifier and an overall flat frequency response (±3 dB) between 0.01 and 12.8 kHz. Due to the roll-off of the anti-alias filter, energy was present up to 16 kHz. The recorders were positively buoyant and deployed approximately 3 m from the ocean floor. They were each capable of recording up to 120 GB of acoustic data on an internal hard drive. Two (PU161 and PU163) were deployed in shallow water (64–73 m; "shallow" recorders), one (PU154) in medium-depth water (236 m; "medium-depth" recorder), and two (PU152 and PU159) in deeper water (~366 m; "deep" recorders). Once the recorders were retrieved, the hard drives were removed and the data were downloaded and converted from raw bin files to waveform audio files (.wav) using custom software from the Bioacoustics Research Program.

Analysis

We detected vocal events between 1 and 16 kHz by viewing Long-Term Spectral Averages (LTSAs; Wiggins and Hildebrand 2007) generated in *Triton* (Scripps Whale Acoustic Lab, Scripps Institution of Oceanography, La Jolla, CA), a Matlab-based program (The MathWorks, Inc., Natick, MA). LTSAs allow visualization of minutes to weeks of data in the same figure, thereby allowing for rapid review of large data sets. We visually inspected 30 min LTSAs for high-energy vocal events containing whistles, clicks, and/or burst-pulse sounds (Richardson *et al.* 1995). Once a vocal event was identified, we visually inspected spectrograms to look at the event in more detail. We defined a vocal event as a series of whistles, clicks, and/or burst-pulse sounds separated by three minutes or less. Thus, if vocalizations were separated by more than three minutes, they were considered distinct vocal events. For each vocal event, we noted the start and end day and time (in GMT). For each vocal event, we also noted the start and end times of: (1) click events and (2) whistle and burst-pulse events. As with vocal events, we defined a single click event as a series of clicks separated by less than three minutes. We defined a single whistle and burst-pulse event as a series of whistles and burst-pulses separated by less than three minutes. Click events and whistle and burst-pulse events often overlapped in time. We grouped the vocal events into these two subcategories based on the probable function of the sounds. Clicks typically are used in navigation and foraging (Au 1993), whistles are used in communication (Caldwell and Caldwell 1965, Tyack 1986, Caldwell *et al.* 1990, Sayigh *et al.* 1990, Janik *et al.* 2006), and burst-pulse sounds are also likely involved in communication, as they are often produced during periods of social activity (Dawson 1991, Herzing 1996, Lammers *et al.* 2006). We then sorted the vocal events into two groups: delphinids and sperm whales. We were unable to differentiate delphinid vocalizations to the species level because our sampling rate allowed only the lower frequencies of clicks to be detected and we did not have recordings from all species known to occur in the study area, thereby making classification models for whistles incomplete. We were able to differentiate the highly distinctive clicks of sperm whales, which are lower in frequency than those of other odontocetes and have been well-described in the literature (Backus and Schevill 1966, Watkins and Schevill 1977, Weilgart and Whitehead 1988).

For the delphinid vocal events detected on each instrument, we calculated: (1) daily number of vocal events, (2) *daily vocal activity*, and (3) duration of individual vocal events (referred to as *vocal event duration*). The daily number of vocal events was calculated by summing the number of vocal events detected for each day. *Daily vocal activity* was calculated by summing the duration of all vocal events for each day. *Vocal event duration* was calculated by subtracting the start day and time of a single vocal event from the end day and time of that same vocal event. We used Wilcoxon rank-sum tests (Zar 1999) to determine if both recorders in the same depth category could be examined together (if results indicated they were not significantly different) for each of these three parameters. Once this was determined, we used a Kruskal-Wallis test (Zar 1999) to determine if there were significant differences between (1) the shallow and medium-depth recorders, (2) the shallow and deep recorders, and (3) the medium-depth and deep recorders. We performed multiple comparison tests using Bonferroni corrections to determine how these three parameters varied with depth. The recorders collected data for differing amounts of time on 6 July (when they were deployed) and on 27 July 2008 (when they were retrieved), so data from these two days were not used for the analyses of the daily number of vocal events or *daily vocal activity*.

We examined diel patterns in the occurrence of vocal events (separated into click events and whistle and burst-pulse events) for each recorder by dividing the recordings into one-minute bins. Bins with vocalizations were assigned a score of 1 and those without vocalizations were assigned a score of 0. Photoperiod (day *vs.* night) was assigned to each one-minute bin, using data obtained from the U.S. Naval Observatory website (http://aa.usno.navy.mil). Day was defined as between sunrise and sunset[2] and night was defined as between sunset and sunrise. For each calendar date within each photoperiod category (day *vs.* night), we summed bins with vocalizations to give the overall number of one-minute bins with vocal activity present per photoperiod. Also for each date and within each photoperiod, we calculated sampling effort by summing the total number of one-minute bins in which recordings were made. Finally, we corrected the overall duration of vocal events for effort (because photoperiod duration varies by day) by dividing by each photoperiod's sampling effort for each date. We examined diel variation in this effort-corrected overall duration of vocal events (or occurrence) for delphinid click events, delphinid whistle and burst-pulse events, and sperm whale click events using a Wilcoxon rank-sum test. We only included days with detections in the analysis. The recorders did not collect data during all photoperiods on the start date (6 July) or the end date (27 July), so we excluded these days from the analyses. All statistical analyses were performed using JMP software (SAS Institute Inc., Cary, NC).

RESULTS

Delphinids

We detected delphinid whistles, clicks, and burst-pulses on all recorders (Table 1). The daily occurrence and duration of these vocal events for each recorder are shown in Figure 2. Table 2 reports the mean (± SD) of the daily number of vocal events, *daily vocal activity*, and *vocal event duration* for each depth.

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[2] Sunrise and sunset are defined as the time of day when the sun is at 0°, at the horizon.

Table 1. Total number of days with and total number of vocal events, click events, and whistle and burst-pulse events for delphinids as well as total number of days with and total number of click events for sperm whales. Detections from 6 July and 27 July are not included.

	# Days with delphinid			Total # of delphinid			Sperm whales	
Depth and recorder #	Vocal events	Click events	Whistle and burst-pulse events	Vocal events	Click events	Whistle and burst-pulse events	# Days with click events	Total # click events
Shallow PU161	16	5	16	51	11	50	0	0
Shallow PU163	15	11	15	79	22	77	0	0
Medium PU154	18	14	15	82	52	72	20	179
Deep PU159	19	18	18	144	80	136	3	22
Deep PU152	18	15	18	132	84	119	2	6

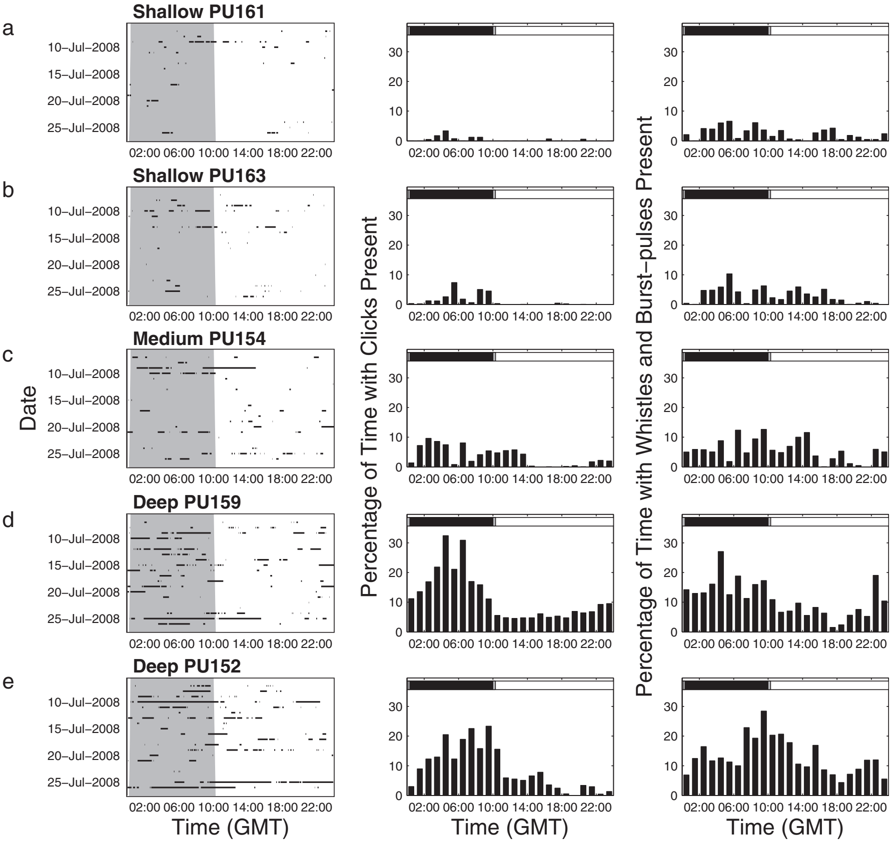

Figure 2. Daily occurrence of delphinid vocal events (left), percentage of entire recording time with delphinid click events (center), and percentage of entire recording time with delphinid whistle and burst-pulse events (right) by time of day (GMT) for (a) PU161 (shallow), (b) PU163 (shallow), (c) PU154 (medium-depth), (d) PU159 (deep), and (e) PU152 (deep). To calculate percentage of recording time with click events or with whistle and burst-pulse events, the total number of minutes with events was first summed, then divided by the total number of minutes of effort, and finally multiplied by 100. Shading in the figures on the left indicates periods of darkness. The black horizontal bars at the top of the center and right figures represent times of darkness, the white bars represent times of light, and the gray bars represent times that could be light or dark depending on the time of year. Photoperiods determined from the U.S. Naval Observatory website (http://aa.usno.navy.mil).

No significant difference in the daily number of vocal events (all call types combined) was found on recorders at the same depth (Wilcoxon rank-sum, shallow × shallow: $Z = 0.8$, $P = 0.404$; deep × deep: $Z = 0.6$, $P = 0.541$). Significant differences in the daily number of vocal events were found at different depths (Kruskal-Wallis, $\chi^2 = 14.4$, df = 2, $P < 0.001$), with a significantly greater number of vocal events per day on the deep *vs.* shallow recorders, but no significant difference between the medium-depth and deep recorders or the medium-depth and shallow recorders.

There was no significant difference in *daily vocal activity* (all call types combined) on recorders at the same depth (Wilcoxon rank-sum, shallow × shallow: $Z = 0.1$,

Table 2. Mean (± SD) daily number of vocal events, mean (± SD) *daily vocal activity*, and mean (± SD) *vocal event duration* for delphinids. Mean *vocal event duration* for the shallow recorders combined was N/A because there was a significant difference between the two shallow sites for this parameter and therefore these recorders were not combined for comparisons here. Detections from 6 July and 27 July are not included.

Depth and recorder #	Daily # of vocal events	Daily vocal activity (min/d)	Vocal event duration (min)
Shallow PU161	2.6 (± 2.8)	39.3 (± 66.0)	15.4 (± 15.4)
Shallow PU163	4.0 (± 4.1)	51.7 (± 74.4)	13.1 (± 21.3)
Shallow combined	3.3 (±3.5)	45.5 (± 69.7)	N/A
Medium PU154	4.1 (± 3.9)	102.1 (± 141.6)	24.9 (± 46.1)
Deep PU159	7.2 (± 5.1)	200.0 (± 201.1)	27.8 (± 58.8)
Deep PU152	6.6 (± 5.1)	226.4 (± 256.7)	34.3 (± 76.1)
Deep Combined	6.9 (± 5.0)	213.2 (± 228.0)	30.9 (± 67.6)

P = 0.913; deep × deep: Z = 0.1, P = 0.892). Significant differences in *daily vocal activity* were found among depths (Kruskal-Wallis, $\chi^2 = 21.2$, df = 2, $P < 0.001$), with significantly more vocal activity per day on the deep *vs.* shallow recorders, but no significant difference between the medium-depth and deep recorders or the medium-depth and shallow recorders.

There was a significant difference in *vocal event duration* (all call types combined) between the two shallow sites (Wilcoxon rank-sum, $Z = 2.3$, $P = 0.024$), with significantly longer vocal events found in the PU161 recordings. Thus, we did not combine the shallow recorders for the comparisons of *vocal event duration* between different depths because they were significantly different. No significant difference in *vocal event duration* was found between the two deep recorders (Wilcoxon rank-sum, $Z = 1.1$, $P = 0.290$). Significant differences were found in *vocal event duration* at different depths (Kruskal-Wallis, $\chi^2 = 10.9$, df = 3, $P = 0.012$). The *post hoc* tests revealed significantly longer vocal events on (1) the medium-depth recorder *vs.* PU163 (a shallow recorder) and (2) the deep recorders *vs.* PU163. No significant difference was found between (1) the medium-depth and deep recorders, (2) the medium-depth recorder and PU161 (a shallow recorder), or (3) the deep recorders and PU161.

As shown in Figure 2, both deep recorders (PU152: $Z = 3.3$, $P = 0.001$; PU159: $Z = 3.2$, $P = 0.002$) and one shallow recorder (PU163: $Z = 2.4$, $P = 0.014$) showed significant nocturnal increases in delphinid click activity. The medium-depth recorder showed no significant difference in the occurrence of click events during day *vs.* night ($Z = 1.3$, $P = 0.187$). The sample size for the other shallow recorder (PU161) was too small for statistical analysis.

Analysis of diel variation in whistle and burst-pulse events (Fig. 2) revealed that none of the recorders showed significant differences in the occurrence of such events during day *vs.* night (PU161: $Z = 1.0$, $P = 0.333$; PU163: $Z = 1.1$, $P = 0.270$; PU154: $Z = -0.2$, $P = 0.835$; PU159: $Z = 1.9$, $P = 0.064$; PU152: $Z = 0.9$, $P = 0.367$).

Sperm Whales

Sperm whale clicks were detected only on the medium-depth (PU154) and deep recorders (Fig. 3). Analysis of diel variation in sperm whale clicks for the medium-depth

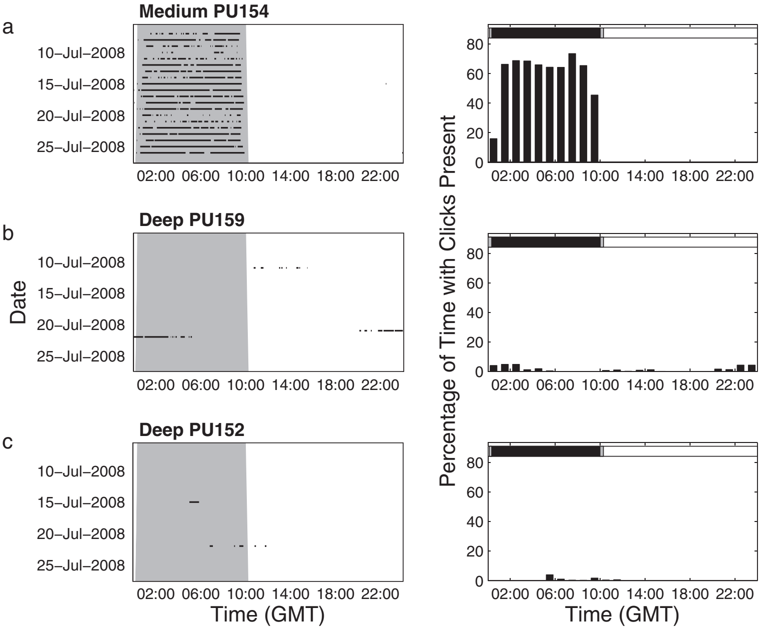

Figure 3. Daily occurrence of sperm whale click events (left) and percentage of entire recording time with sperm whale click events (right) by time of day (GMT) for (a) PU154 (medium-depth), (b) PU159 (deep), and (c) PU152 (deep). To calculate percentage of recording time with sperm whale click events, the total number of minutes with click events was first summed, then divided by the total number of minutes of effort, and finally multiplied by 100. Shading in the figures on the left indicates periods of darkness, determined from the U.S. Naval Observatory website (http://aa.usno.navy.mil). The black bars at the top of the figures on the right represent times of darkness, the white bars represent times of light, and the gray bars represent times that could be light or dark depending on the time of year.

recorder (PU154), which had numerous detections, showed a significant nocturnal increase in sperm whale clicks (Wilcoxon rank-sum, $Z = 5.6$, $P < 0.001$), with clicks occurring during 64% of the one-minute bins at night compared to only 0.04% of the one-minute bins during the day (Fig. 3a). Sperm whale clicks were detected during the night on a regular basis on this recorder (Fig. 3a). Many of these click bouts appeared to have been made by a single animal at a time, as on most occasions we did not detect overlapping click bouts. The deep recorders only had detections on two or three days (Table 1, Fig. 3b, c), so the sample sizes were not sufficient for statistical analysis.

DISCUSSION

Odontocete vocal activity varied with depth in Onslow Bay, with significantly more vocal events (defined here as vocalizations separated by three minutes or less) per day and significantly greater *daily vocal activity* occurring in deep water than in shallow water. The greater number of vocal events on the deep recorders drove the greater *daily vocal activity*, because *vocal event duration* was similar for all sites but one.

This increased number of vocal events could be due to greater vocal activity in delphinid groups in deeper waters, more groups of delphinids in deeper waters, or a combination of both factors. Diel trends in delphinid clicks also were found to vary with depth, with nocturnal trends observed at some, but not all, sites. Sperm whale clicks were rarely detected on the deep recorders but were detected every night on the medium-depth recorder, suggesting that one or more sperm whales moved onto the shelf break to forage at night during the recording period.

Delphinid vocal events were detected on each of the passive acoustic recorders. Most of these delphinid vocal events were likely produced by Atlantic spotted or bottlenose dolphins, as these two species are by far the most commonly sighted cetaceans in boat-based and aerial surveys in the area (Halpin *et al.* 2009).

The shallow recorders were located at depths of 64–73 m. Atlantic spotted dolphins and bottlenose dolphins are the only two delphinid species that have been sighted in these depths in Onslow Bay (Halpin *et al.* 2009). The finding of significantly shorter *vocal event durations* on one of the shallow recorders in comparison to all other recorders was somewhat surprising. One explanation for these shorter *vocal event durations* may come from the observation of smaller group sizes of bottlenose dolphins in shallower waters (AJR, unpublished data). Other studies have found that bottlenose dolphin vocal rates vary with group size in some locations, with fewer vocalizations produced by smaller groups (Jones and Sayigh 2002, Hernandez *et al.* 2010). One must remember, however, that of the two shallow sites, only one had shorter *vocal event durations*. Another explanation for these shorter *vocal event durations* could result from the behavioral state of groups, which, if different at this shallow site, may play a role as some studies have found that vocal rate and occurrence are correlated with behavioral state (Jones and Sayigh 2002, Cook *et al.* 2004). In general, these studies found more whistles during social activity and fewer during traveling (Jones and Sayigh 2002, Cook *et al.* 2004). Jones and Sayigh (2002) also found more echolocation clicks during foraging. Vocal activity budgets may vary for different groups as well depending on species, population, or group composition (such as the presence and/or number of calves). Thus, it is possible that groups at this shallow site were silent for a greater proportion of time due to either group size, behavioral state, or species or group composition. We found no significant difference in the daily number of vocal events between the two shallow recorders, but we did find a greater number of total vocal events (1.6 times as many) on the shallow recorder with significantly shorter *vocal event durations* (PU163). Some of the shorter vocal events detected on PU163 occurred close together in time to other short vocal events (Fig. 2b). It is possible that such events were counted as multiple vocal events when in fact they were produced by the same group that either was silent much of the time that it was within range of the recorder or was moving into and out of detection range of the instrument.

The medium-depth recorder had almost twice the number of vocal events than the shallow recorder that exhibited similar *vocal event durations* (PU161). The medium-depth recorder was located along the shelf break, an area often associated with increased biological activity (Mann and Lazier 1996). This recorder may also have been influenced by the front created by the western edge of the Gulf Stream, which runs through the survey area. The meanders of this front, along with Gulf Stream frontal eddies (Lee *et al.* 1981), cause upwelling to occur at the shelf break (Atkinson 1977, Mann and Lazier 1996). This upwelling can lead to an increase in productivity (Yoder *et al.* 1981), which in turn can lead to aggregation of prey, and may explain the increase in total number of vocal events on the medium-depth recorder.

Lastly, the deep recorders, which had the greatest *daily vocal activity* and most vocal events (both in terms of the total number of vocal events and the daily number of vocal events), were located on the upper continental slope, in approximately 366 m. Sperm whale clicks were the only type of vocalization identified to species in this study, but calls similar to those produced by pilot whales (included in the delphinid species category here) were present in the recordings (Fig. 4). The mean maximum frequency for pilot whale calls is typically reported in the 6–10 kHz range (Rendell *et al.* 1999, Oswald *et al.* 2003, Baron *et al.* 2008) although calls with higher frequencies are also produced (Sayigh *et al.* 2012; Fig. 4b, d). Compared to bottlenose and spotted dolphins, the calls of pilot whales are generally lower in frequency (see Rendell *et al.* 1999, Oswald *et al.* 2003, and Baron *et al.* 2008) and may include nonlinear phenomena (Sayigh *et al.* 2012). Such calls were only detected on the deep recorders, which agrees with the sighting data (Halpin *et al.* 2009) and the findings of deep water prey in the stomachs of short-finned pilot whales stranded in North Carolina (Mintzer *et al.* 2008). The presence of these calls only on the deep instruments and the presence of sperm whale clicks only at the medium-depth and deep sites suggest the existence of a more diverse cetacean assemblage at these depths in comparison to the shallow sites. This is in agreement with the results of aerial and shipboard surveys in this area (Halpin *et al.* 2009) and the findings of Davis *et al.* (1998) from the Gulf of Mexico. A more diverse assemblage of species at these greater depths also could explain the significantly greater number of vocal events observed on the deeper recorders if some of these species are more vocal than Atlantic spotted dolphins and small groups of bottlenose dolphins, or if there is a higher density of cetaceans in these waters.

Significantly more click activity was observed at night than during the day on both deep recorders and on one shallow recorder (PU163). Click activity of the other shallow recorder (PU161) could not be examined statistically due to the small sample size ($n = 5$ d with clicks present), but Figure 2a suggests that more click activity occurred at night than during the day. Also, while no significant pattern emerged for the medium-depth recorder, there was more click activity at night and during the morning hours than during the middle and end of the day (Fig. 2c). Odontocetes use clicks to navigate and find prey (Au 1993) and possibly in communication (Watkins and Schevill 1977, Dawson 1991, Benoit-Bird and Au 2008). Possible explanations for a nocturnal increase in click activity include diel changes in behavior, such as an increase in foraging activity at night, or an increase in the number of animals in the area.

Some studies have found a correlation between echolocation click activity and behavioral state, with greater activity occurring while animals are foraging (Jones and Sayigh 2002, Nowacek 2005). At least two species detected in deeper waters during visual surveys in Onslow Bay forage on prey in the DSL (common dolphin: Overhotlz and Waring 1991, Evans 1994, Pusineri *et al.* 2007; Risso's dolphin: Clarke 1996). Studies suggest that both of these species forage at dusk or at night when their prey are undertaking vertical migrations (common dolphin: Evans 1994, Pusineri *et al.* 2007; Risso's dolphin: Shane 1995). Soldevilla *et al.* (2010) showed that Risso's dolphins, a deep-water species, show a nocturnal trend in clicking behavior that is likely associated with foraging on squid in the DSL. Unfortunately, however, given the sampling rate employed for the present study, only clipped clicks of Risso's dolphins would be detected on these recorders, because the lower end of this species' clicks typically begin at a higher frequency than we were able to record.

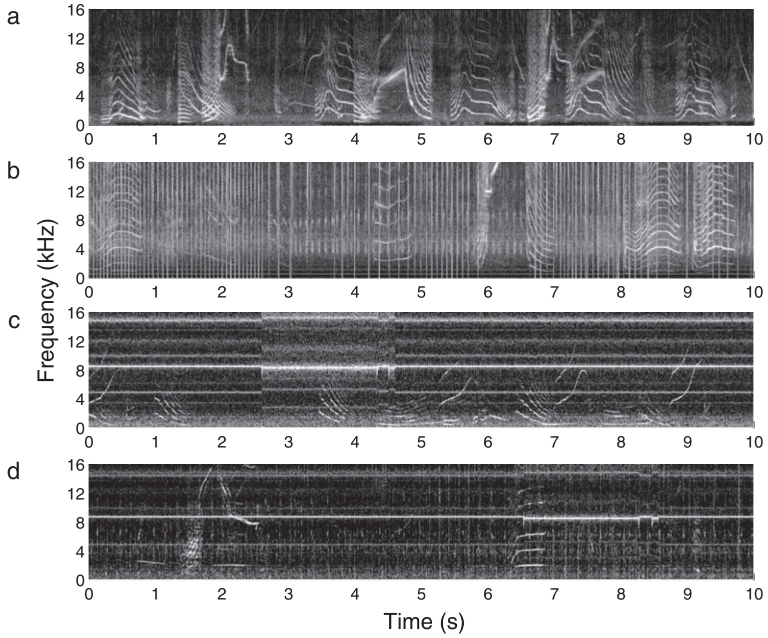

Figure 4. Pilot whale calls recorded off Hatteras, North Carolina, using (a) a digital acoustic recording tag (DTAG, Johnson and Tyack 2003) that was attached to a pilot whale and (b) a towed hydrophone array (with visual confirmation of species). (c), (d) Calls thought to be produced by pilot whales found in the acoustic data of one of the deep recorders (PU159).

Other species (with poorly known prey preferences) may also be responsible for the observed increase in click activity at night. The nocturnal increase in click activity was noted at both the deep and shallow recorders, which suggests an increase in foraging at night by Atlantic spotted and/or bottlenose dolphins. Atlantic spotted dolphins feed on a variety of fish, small cephalopods, and benthic invertebrates (Perrin 2009) and, thus, might not be expected to exhibit such a diel pattern, although very little is known about the foraging behavior of this species. Knowledge of the foraging activity of offshore bottlenose dolphins in this area is also limited, although Barros and Odell (1990) found ommastrephid squids in the stomach contents of one individual. These squid inhabit the epipelagic zone and exhibit diel vertical migrations. Thus, if offshore bottlenose dolphins exhibit diel feeding patterns and wait for their prey to move towards the surface before foraging, a nocturnal trend in click activity would be expected.

An alternate hypothesis to explain the nocturnal increase in click production is that delphinids are found within detection distance of the instruments more frequently at night than during the day due to fine-scale daily movements. As noted previously, some species make daily horizontal movements as a result of their foraging strategies (*e.g.*, actively following prey or moving from a resting location to a foraging location). Such horizontal movements have been described for Hawaiian spinner dolphins (Norris *et al.* 1994, Benoit-Bird and Au 2003) and striped dolphins (Gannier 1999). Thus, it is possible that animals move into the area from either shallower or deeper waters during the night, although the lack of a nocturnal increase in whistle and burst-pulse events does not seem to support such movement.

The lack of a diel trend in click activity on the medium-depth recorder was surprising given that all other recorders with a large enough sample size had a nocturnal trend. A period of low click activity was evident during the middle of the day on this instrument (Fig. 2c) although whistles and burst-pulses continued. At present, it is not possible to interpret this finding without more information on the specific identity of cetaceans recorded on this recorder.

Sperm whale click events were recorded only on the medium-depth and the deep recorders. Sperm whale clicks were detected during the night on the medium-depth recorder for long periods of time (Fig. 3a). Sperm whales have not been visually observed in such shallow waters in Onslow Bay, so it was surprising to find such a regular pattern of sperm whale clicks each night on this instrument. It is possible that one or more sperm whales moved to the shelf break in Onslow Bay to feed at night. In fact, many of the clicks detected on the medium-depth recorder appeared to have been produced by a single animal, suggesting that the same individual may have been consistently foraging at night near the waters of the upper slope during July 2008. The lack of sperm whale clicks on the deep recorders was not necessarily surprising given that aerial- and boat-based line-transect visual surveys between 2007 and 2011 yielded only one sighting of a sperm whale, which was in very deep water (offshore of the deep recorders). The few click events that were detected on the deep recorders may have been from animals far away, as the high amplitude (Møhl *et al.* 2003) and lower frequency of sperm whale clicks allow them to potentially be detected at great distances (>10 km).

There are several important caveats to our interpretation of the results presented here. First, we acknowledge that our definition of a vocal event could influence our results. We attempted to capture all vocalizations of a single group of animals without incorporating long periods of silence, so we defined a single vocal event as a series of calls separated by less than three minutes. This definition may have resulted in occasional separation of vocalizations from one group into multiple vocal events (rather than a desired single vocal event), which would increase the total number of vocal events while decreasing the *vocal event duration*.

Second, we only had less than one month of data from which to draw conclusions. During this time period, there were days with high levels of vocal activity and other days with fewer calls. In addition, we assumed that a day without vocal events meant that no animals were present during that entire day, even though silent animals may have been present. Including days without detections into the diel analyses would lower the mean and median values for both periods and could have resulted in fewer findings of significance.

Finally, it is important to note that our detection distances were unknown. Sound transmission and acoustic detections on recorders vary as a function of various factors, including: propagation conditions; source level of the call; ambient noise level; and receiver (in this case, instrument) sensitivity (Richardson *et al.* 1995). Propagation efficiency is affected by depth (of both vocalizing animal and recorder), seafloor bottom type, bottom slope, the frequency range of the call, temperature (and thus season), and salinity (Richardson *et al.* 1995). For directional calls (such as odontocete clicks), detection distances are also dependent upon an animal's orientation and location in relation to the hydrophone. In addition, as mentioned above, the source level and frequency of the call can affect its detection distance. Odontocete clicks may have high source levels (Zimmer 2011), but they typically (except for sperm whale clicks) occur at relatively high frequencies (Nakamura and Akamatsu 2004), for which absorption has a greater effect on transmission loss and, thus, detection ranges. Odontocete whistles, on the other hand, are lower in frequency and, therefore, less affected by absorption, but these calls have lower source levels (Richardson *et al.* 1995). As mentioned above, sperm whale clicks, with lower frequencies and high amplitudes, could potentially be detected at significant distances (>10 km). Future research should investigate at what distances these odontocete vocalizations were detected.

In summary, we found that depth and time of day influence the occurrence of odontocete vocalizations in Onslow Bay during at least one month of the year. Specifically, we found that delphinid vocal events occurred most often in deeper waters, likely due to a greater diversity and occurrence of animals. The finding that click occurrence increased at night at the shallow and deep sites likely reflects behavior, with animals foraging as the DSL rises to the surface. The classification of delphinid calls to the species level will add to our understanding of which species are found at different depths and which species show diel variation in vocalizations. The regular nocturnal occurrence of low-frequency clicks on the recorder near the shelf break suggests that one or more sperm whales moved into that area to feed at night throughout the present study. Despite these patterns in the occurrence of vocal events, it is important to remember that this study gives a conservative portrait of the true presence of odontocetes, as silent animals will not be detected using this method. In addition, these results only represent the occurrence of odontocete vocalizations during one month of the year. Seasonal differences in the vocal behavior of different species may exist, but could not be explored in this study. Therefore, future research should include collecting data at different times of the year.

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