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Acoustic monitoring reveals the times and tides of harbor porpoise (*Phocoena phocoena*) distribution off central Oregon, U.S.A.

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ABSTRACT

Harbor porpoises (*Phocoena phocoena*) are commonly observed in Oregon's nearshore marine environment yet knowledge of their ecosystem use and behavior remains limited, generating concerns for potential impacts on this species from future coastal development. Passive acoustic monitoring was used to investigate spatial and temporal variations in the presence and foraging activity of harbor porpoises off the Oregon coast from May through October 2014. Digital monitoring devices (DMONs) were deployed to record acoustic data (320 kHz sample rate) in two neighboring but bathymetrically different locations off the Oregon coast: (1) a site on the 30 m isobath in close proximity (<50 m) to a rocky reef, and (2) a site on the 60 m isobath in an open sandy environment. Data were analyzed with respect to two dynamic cyclic variables: diel and tidal phase. Porpoise presence at the rocky reef site was aligned with the ebb phase of the tidal forcing, while harbor porpoise presence and foraging at the offshore, sandy bottom site was associated with night-time foraging. The spatial and temporal patterns identified in this study suggest harbor porpoise habitat use is

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modulated by specific environmental conditions particular to each site that maximize foraging efficiency.

Key words: harbor porpoise, *Phocoena phocoena*, distribution, habitat use, foraging behavior, temporal patterns, Oregon, passive acoustics.

A combination of escalating pressures related to human activities is threatening almost all marine ecosystems worldwide (Halpern *et al.* 2008, Maxwell *et al.* 2013). Cetaceans are particularly vulnerable to incidental harm from anthropogenic activities, such as fisheries, noise and chemical pollution, shipping, and habitat loss, because they are long-lived with low fecundity (Heppell *et al.* 2005). Human activities vary in their spatial and temporal distribution across regions resulting in a wide range of ecological impacts for cetacean populations (Halpern *et al.* 2008). In particular, cetaceans that live in near-shore, shallow water environments are often exposed to elevated levels of anthropogenic activities (Barlow and Forney 1994). Furthermore, baseline information on the distribution and habitat usage of coastal species is often limited. Further, existing data are often only available at spatial and temporal scales much larger than what is needed to adequately inform regulatory decisions for fine-scale activities, including marine energy, seabed mining and point source pollution (Forney *et al.* 2017). Knowledge of cetacean distributions and habitat use at finer, site-specific scales is crucial to answer management questions and capture relevant habitat heterogeneity (Wiens 1989, Tett *et al.* 2013).

High-resolution spatial habitat-use data for marine mammals can be obtained through aerial or boat based visual surveys, with considerable cost and effort (Evans and Hammond 2004). Visual surveys typically have a wide spatial extent and are capable of covering a site-specific area, but are limited in temporal coverage to daylight hours and reasonable weather conditions. Furthermore, visual surveys are reliant on animals being identified at the surface, but cetaceans are often visible at the surface less than 10% of the time (Tyack and Miller 2002), limiting the visual detection time of observers. Passive acoustic monitoring (PAM) provides an alternate survey technique that can be used to examine patterns of movement and trends in behavior of vocalizing animals (Carlström 2005, Todd *et al.* 2009). Fixed passive acoustic recorders can detect vocalizing marine mammals during all hours, seasons, and sea states (Mellinger *et al.* 2007). Also, PAM allows for subsurface detection, is noninvasive, and unlikely to affect cetacean behavior, all the while providing information on animal presence and behavior at high temporal resolution.

In studying marine mammal distribution and foraging patterns, direct interactions with prey are often difficult to observe. In their absence, an indirect understanding of marine mammals and their prey can be beneficial. At fine temporal scales (<1 d) consistent diel and tidal patterns occur, which influence everything from primary production (Zamon 2002, 2003; Sharples *et al.* 2007) to marine top predators (Baumgartner *et al.* 2003, Hastie *et al.* 2004, Wang *et al.* 2015). Additionally, at fine

spatial scales (1–10 km), oceanic processes (upwelling, fronts, and eddies) can enhance biological production and consequently aggregate zooplankton (Scott *et al.* 2010). These fine-scale patterns in both time and space act to localize patches of food for marine predators. Furthermore, tidal currents can interact with bathymetry and aggregate prey vertically and horizontally (Zamon 2002), which results in spatially and temporally predictable prey patches (Riley 1976), which may attract marine predators (Hastie *et al.* 2004, Johnston *et al.* 2005). Preference by top predators for these brief yet predictable areas may be undetectable in larger-scale surveys, and failure to account for the distributions and habitat use of marine predators at fine spatial and temporal scales (<1 km, hours) may mask behavioral changes in response to anthropogenic disturbances.

New marine spatial planning and conservation initiatives have increased the need for finer-scale data regarding cetacean use of coastal and shelf waters (Rees *et al.* 2013). In the Pacific Northwest, the marine environment off Oregon has been considered for coastal development in recent years through potential development of wind and wave energy converters, vessel traffic, and fishing activities (Callaway 2007, Boehlert *et al.* 2008). The cumulative impact of a multitude of threats requires managers to understand how these activities affect the marine environment at fine-scales. Consequently, there is a need to provide managers and stakeholders with local population level information on species of concern within the management area. Although cryptic, harbor porpoises (*Phocoena phocoena*) are readily found along the Oregon coast and are a focal at-risk species (Henkel *et al.* 2014) that is highly sensitive to anthropogenic noise (Lucke *et al.* 2009; Tougaard *et al.* 2009, 2012, 2015; Dyndo *et al.* 2015). Harbor porpoises appear to be susceptible to auditory injuries at much lower levels than other studied cetaceans (Lucke *et al.* 2009, Tougaard *et al.* 2015), and if close enough to high-intensity sounds, harbor porpoise may suffer temporary or even permanent hearing loss as a result of exposure to human noise (Lucke *et al.* 2009, Kastelein *et al.* 2012). However, porpoises may also be threatened by noise at much larger distances from the sound source through responses such as increased stress levels (Wright *et al.* 2007), and behavioral changes (Richardson and Würsig 1997). In addition, noise exposure can lead to constrained acoustic communication through auditory masking (Kastelein *et al.* 2011) and broad-scale spatial displacement (Culik *et al.* 2001, Teilmann *et al.* 2008, Tougaard *et al.* 2009).

Harbor porpoises along the west coast of North America are predominantly observed in coastal waters <200 m deep (Minasian *et al.* 1984, Barlow *et al.* 1988, Carretta *et al.* 2001), and two stocks are currently recognized in Oregon (a northern and southern population with a separation area located near Lincoln City; Carretta *et al.* 2011). Seasonal changes in abundance along the west coast have been reported with a lower abundance during the winter (Barlow *et al.* 1988). Although it remains unclear whether reported movement patterns are related to seasonal inshore-offshore movements or because observation conditions are poor and it is harder to survey and detect them. Harbor porpoise populations in other regions display habitat-use patterns relative to

season (Simon *et al.* 2010, Gilles *et al.* 2011), diel cycle (Carlström 2005, Todd *et al.* 2009, Schaffeld *et al.* 2016), and tides (Johnston *et al.* 2005, Pierpoint 2008, Benjamins *et al.* 2016). However, the influence from diel and tidal cycles are region-specific, and this is likely related to the availability of dominant prey in the area. Harbor porpoises have high energy demands, due to their small body size and typically temperate water habitat, necessitating daily foraging to meet their basic energy requirements (Koopman 1998, Wisniewska *et al.* 2016). Porpoises feed at a daily rate of 10% of their body weight (Read and Gaskin 1985), and their distribution and movements are believed to be strongly connected to patches of prey aggregations (Sveegaard *et al.* 2012).

Studying the distribution patterns of harbor porpoises using visual methods has proven difficult due to their small size, small group size, cryptic behavior and minimal surface activity, as they are visible at the surface for less than 25% of the time (Laake *et al.* 1997). Furthermore, they are difficult to observe when sea conditions deteriorate above a Beaufort Sea State of 2 (Teilmann 2003), and photo-identification efforts are challenging due to a general lack of distinctive, natural markings on their dorsal fins (Koopman and Gaskin 1994). However, harbor porpoises are highly vocal animals and are thought to echolocate almost continuously (Villadsgaard *et al.* 2007, Linnenschmidt *et al.* 2013, Wisniewska *et al.* 2016), making passive acoustic surveys often a more successful approach for distribution and behavioral observations than visual methods (Teilmann 2003, Kyhn *et al.* 2008).

Harbor porpoise produce narrow-band, high-frequency echolocation clicks with a peak frequency of 130 kHz (Møhl and Andersen 1973, Villadsgaard *et al.* 2007). The mean source level (SL) has been estimated at 191 dB re 1 μ Pa p-p @ 1 m, ranging from 178 to 205 dB re 1 μ Pa p-p (Villadsgaard *et al.* 2007). Additionally, there is typically no energy below 100 kHz (Kyhn *et al.* 2012), enabling harbor porpoise clicks to be reliably discriminated from other odontocete (*e.g.*, delphinid) signals, as well as most other transient sounds. Harbor porpoise produce echolocation clicks for communicating, foraging, and navigation (Verfuß *et al.* 2005, 2009; Clausen *et al.* 2011). Foraging click trains (series of clicks) can be separated into different phases based on the interclick interval (ICI): the search phase is characterized by relatively stable ICIs around 50 ms, and the terminal phase is identified by a sudden and rapid shortening of ICI to levels below 10 ms (Linnenschmidt *et al.* 2012). Echolocation clicks that transition into a foraging click train with short and stable ICI of below 10 ms are called “buzzes” (DeRuiter *et al.* 2009, Verfuß *et al.* 2009, Madsen *et al.* 2013) and consequently buzzes recorded by acoustic data loggers have been used as a reliable proxy of foraging efficiency (Miller *et al.* 2004, Linnenschmidt *et al.* 2013, Wisniewska *et al.* 2016).

In order to obtain fine-scale data on harbor porpoise occurrence and foraging patterns in coastal Oregon waters, two passive acoustic monitoring devices (DMON, Baumgartner *et al.* 2013) were deployed and operated for an extended period. Unlike traditionally applied static acoustic recorders such as T-PODs and C-PODs (Chelonia Limited, Mousehole, U.K.) that employ an onboard, automated call detection

approach (Leeney *et al.* 2011, Wang *et al.* 2015), DMONs record full spectral waveforms within the high-frequency vocal range of harbor porpoise. T-POD and C-POD devices record continuously and rely on the performance of an algorithm to detect and classify click trains into categories (narrow-band, high-frequency clicks and nonnarrow band high-frequency clicks). In contrast, DMONs archive the acoustic data (typically on a duty cycle), which allows for supervised, visual detection and classification of echolocation activity by an analyst, leading to more robust estimates of true occurrence and behavior (Roberts and Read 2015). However, the DMON version used for this experiment is not well suited for long term studies due to limited battery and data storage capacity. In this study, we explore the influence of dynamic, fine-scale, cyclic environmental variables (tidal and diel forcing) on harbor porpoise distribution and foraging patterns at two neighboring but bathymetrically distinct habitats (nearshore reef *vs.* offshore sandy bottom).

MATERIALS AND METHODS

Study Sites and Instrument Deployments

DMONs were deployed at sites off the central Oregon coast for a 6 mo period from 13 May to 14 October 2014. Owing to the high sample rate (320 kHz) required for capturing harbor porpoise vocalizations, the recorders were programmed to record on a 10% duty cycle (first minute of every 10 min period) to conserve both battery power and memory storage space. The system features a noise floor 32 dB re $\mu\text{Pa}/\sqrt{\text{Hz}}$ and a system sensitivity of -203 dB re $\text{V}/\mu\text{Pa}$ (Baumgartner *et al.* 2013). The DMON was mounted with positively buoyant housing to avoid interference and suspended ~ 5 m above the seafloor along a mooring line attached to a surface buoy. The two instruments were operated on the 30 m isobath in close proximity (< 50 m) to a rocky reef and offshore on the 60 m isobath in an open sandy environment (Fig. 1). The reef and offshore sites were located 4 km and 12 km southwest of the Yaquina River inlet, respectively. Individual deployments were approximately two weeks in duration, limited by DMON battery and data storage capacity. Independence between moorings was assumed given the intermooring distance of > 8 km.

Acoustic Data Analysis

Data from the DMONs were offloaded *via* USB and were visually reviewed by an analyst using the MATLAB-based software package Triton developed by the Scripps Whale Acoustics Lab, San Diego, CA (Wiggins and Hildebrand 2007). All spectrograms were calculated with 1,024-point fast Fourier transform (FFT) with 50% overlap and a Hann window. The detection ranges for DMONs have not been investigated for harbor porpoises. However, estimates for other passive acoustic monitoring devices such as the T-POD are a few hundred meters (Villadsgaard *et al.* 2007; Kyhn *et al.* 2008, 2012; DeRuiter *et al.* 2010). All DMON data were analyzed at a temporal resolution of 1 min, with each minute classified as 1 or 0, denoting the presence or absence of harbor porpoise echolocation

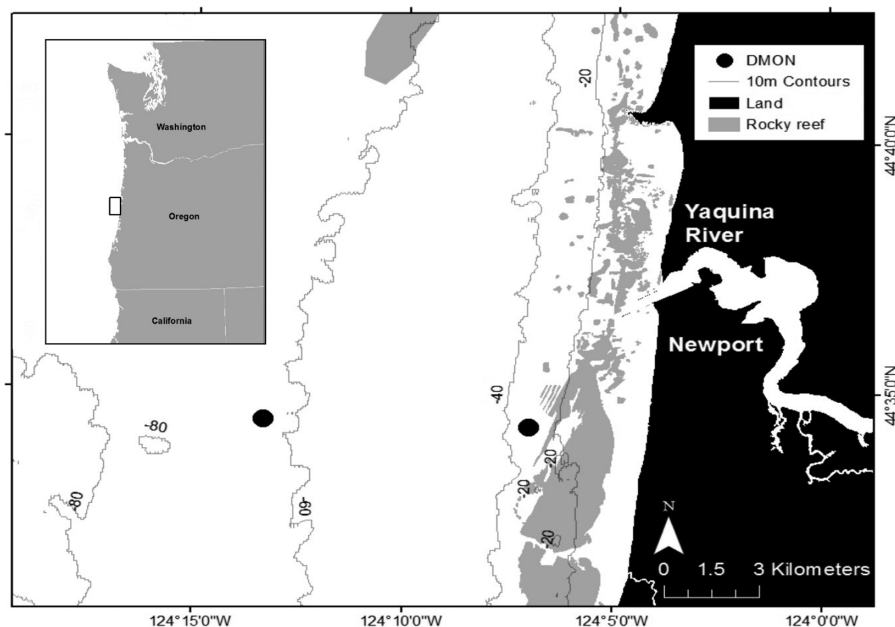


Figure 1. Bathymetric overview of study area in coastal Oregon (see inset) with acoustic instrumentation deployment sites displayed by the black dots.

click trains and buzzes. While Dall's porpoises (*Phocoenoides dalli*) also occur along the U.S. West Coast and produce very similar narrow-band, high-frequency echolocation signals, we are confident that our data set includes only harbor porpoise echolocation click trains because Dall's porpoises are typically found in much deeper offshore waters (Forney 2000). Previous studies have used a group of clicks separated by 10 min to define a separate encounter (Carlström 2005); in this study, each surveyed minute is a potential new encounter and not a continuation of the previous detection. A harbor porpoise encounter was defined as any recording minute that contained at least five visually confirmed clicks, and termed a porpoise positive minute (PPM). Click bouts consisting of less than 5 clicks were discarded from further analysis. In addition to presence patterns, individual harbor porpoise click trains were analyzed for feeding behavior through assessment of the ICI, which was used to differentiate between feeding buzz trains and all other trains. A minimum ICI (MICI) of <10 ms was used to identify terminal buzz vocalizations, a proxy of porpoise feeding (Carlström 2005, Todd *et al.* 2009). A click train that progressed into an ICI of <10 ms had to be recorded for the sequence to be recorded as a terminal buzz positive minute (BPM).

Temporal Patterns of Site Use

To analyze PPMs across the study period, a percent daily detection was calculated (PPM/Day) for the reef site and offshore site. Due to duty

cycling, a maximum number of 144 1 min data files could be recorded per day. Sampling effort across the study period varied in relation to vessel availability and how quickly DMONs could be recovered, refurbished, and redeployed. When devices were deployed at both the reef site and offshore site during the same time period, detections were compared to determine whether porpoises were selecting between the two locations during certain environmental conditions or spending equal time at both sites. For each synchronous recording period, a number was assigned to represent a discrete state of presence or absence for both sites. At the reef site, each minute of recording was assigned a one for presence or a zero for absence. At the offshore site, each minute of recording was assigned a two for presence or a zero for absence. Therefore, for each time period of acoustic monitoring overlap between sites, a sum of one represented a detection at the reef only, a sum of two represented a detection at the offshore site only, and a sum of three represented porpoises detected at the same time at both sites. Finally a sum of zero represented an absence of porpoises at both sites and we removed these absences from further analysis. For the remaining periods with porpoise detections we used contingency tables to compare the proportion of time the detections occurred at either the reef or offshore site to that when detections occurred at the same time at both sites.

Diel Phase Classification and Analysis

Harbor porpoise occurrence and presumed foraging patterns were investigated based on the change in PPM between diel phases of the diurnal cycle. Porpoise detections from each site were classified into four diel phases (morning, day, evening, and night) according to local civil twilight and sun-state tables obtained from the U.S. Naval Observatory (<http://aa.usno.navy.mil>). Definitions of diel phases were adapted from Carlström (2005): civil twilight start and civil twilight end refers to the time point in the morning and the evening where the center of the sun is geometrically 6° below the horizon. Sunrise and sunset refers to the times when the upper edge of the disk of the sun was on the horizon (see fig. 3 in Todd *et al.* 2009). Porpoise detection rates were computed as the proportion of PPMs relative to the whole period of investigation and diel phase. To investigate the proportion of time porpoises spent foraging, we calculated the percentage of PPMs that contained a terminal buzz (BPM) for each diel phase at each site. All train detections were nonnormally distributed (Shapiro-Wilk, $P = 2.2e-16$). Therefore, nonparametric Kruskal-Wallis one way ANOVAs and their appropriate *post hoc* tests, corrected for multiple comparisons, were used to assess differences in PPMs and BPMS between the diel phases at each site. All statistical analyses were carried out using the program R (R Development Core Team 2010).

Tidal Phase Classification and Analysis

To examine tidal influences on detection rates, the time dependent tidal phase (φ_t) was compared with PPM and BPM at each site. Due to

the complex nature of the mixed semidiurnal tides and range of amplitudes experienced in the study areas (-0.179 – 2.934 m, NOAA station 9435380), a simple comparison of the nearby-measured hydrostatic tidal amplitude is insufficient for determining linkages between barotropic tidal currents and harbor porpoise presence and behavior. Rather, using a calculated tidal phase parameter (ϕ_t) we make a more direct comparison of the velocity of tidally influenced currents relative to harbor porpoise presence and behavior. In this region of the northeast Pacific, the temporal dependency of the tidal phase parameter (ϕ_t) is dominated by the principal lunar semidiurnal constituent (M2), which has a period of 12 h and 25.2 min, exactly half a tidal lunar day. ϕ_t is calculated as the time dependent 2π modulus of the radial frequency of the tidal constituent M2 plus a constant phase delay C (Pond and Pickard 1983). This approach provides a direct link to dynamic physical processes related to tidally induced flow speeds and direction within each habitat, not just the changes in hydrostatic water levels.

Due to the cyclical nature of time and tides, we used the circular statistics toolbox, CircStat for MATLAB (Batschelet 1981, Berens 2009), to analyze PPM and BPM time series from each site with respect to the semidiurnal tidal phase. Temporal occurrences of PPM and BPM were transformed to angular values to describe their distribution relative to tidal phase. A Rayleigh test of uniformity was implemented to determine if the null hypothesis that the tidal phases of PPM and BPM were uniformly distributed, could be rejected. A Hartigan's dip test (Hartigan and Hartigan 1985) was performed to determine whether the distributions were unimodal or multimodal with respect to tidal phase.

Temporal Model

PPM and BPM were further analyzed and modeled using binomial generalized additive models (GAM) with a logit link function with respect to three temporal variables: Julian day, time of day, and tidal phase, along with their interactions. Data from the two sites were modeled separately to assess the effect of temporal variables for each site and each behavior. Tidal phase was determined by the tidal frequency of the M2 constituent. GAMs were generated in R package MGCV (Wood 2006), which contains integrated smoothness estimation. Nonlinear interactions in the model structure were allowed in order to capture any changes in preferences for one covariate as a function of another. Smooth functions for model covariates were specified using thin plate regression splines with shrinkage (Wood 2006). Interactions between covariates were modeled using tensor product (te) smooths. Hour of day was modeled with cyclic smoothers to account for the circular nature of time. In order to select the model that explained the most variation using the fewest number of variables, predictor variables were removed one at a time through manual backwards stepwise selection by removing variables not significantly influencing the model outcome. The model fit score Akaike's information criterion (AIC, Akaike 1973) was used to select the best model at each step. The AIC score must be reduced by a value of 2 or more for a covariate to be considered for

removal from the model. This method was repeated until no covariates could be removed from the model based on reduction of AIC.

RESULTS

Distributions Across Study Period

Ten total deployments were made over the 6 mo deployment period: five at each site at a variable rate of one to two deployments per month (Table 1). Moored DMONs collected approximately 43 d of acoustic data at the reef site and 60 d at the offshore site. This effort included 35 d of deployment overlap allowing for site comparison. DMONs at both sites logged data as programmed throughout deployments. During the fifth deployment, the DMON at the reef site was accidentally dragged by fisherman shortly after deployment.

Harbor porpoise were acoustically detected on 96% and 93% of the total monitored days at the reef and offshore site respectively. All but 5 d had at least one detection of a harbor porpoise encounter across both locations. Peak harbor porpoise detections occurred between the months of June and July with a gradual decreasing trend in monthly presence through the fall, with the lowest PPMs in October (Fig. 2). The largest daily peak occurred in September with almost 70% PPM detection on the offshore station. During the entire 6 mo deployment period, a total of 13,318 (5,520 at the reef and 7,798 offshore) monitored minutes of the combined 2 sites resulted in 3,477 (26%) PPM. In 27% (964) of all PPM, foraging behavior was detected as defined by an MICI < 10 ms; this constitutes 7.2% of all analyzed minutes with buzz content.

Click train detection rates were higher at the reef site (2,057 of 5,520; 38%) compared to the offshore site (1,420 of 7,798; 18%). Relative foraging activity was a little higher, although not statistically significant, at the reef site where 30% of click trains were classified as buzzes (611 of 2,057) compared to 25% offshore (353 of 964).

DMONs were deployed at both the offshore site and the reef site during the same time period for a total of 4,461 min sampled, allowing for comparison between sites (Table 3). Of the monitored minutes when DMONs were recording simultaneously, 2,332 PPM and 796 BPM were recorded across both sites (Table 3). During 78% of these comonitored minutes, PPM occurred at either the offshore or the reef site, compared to 22% when PPMs were detected at both sites simultaneously. When both DMONs were recording, only 5% of BPMs were simultaneously detected at both sites compared to 95% of recordings where a BPM occurred at either the offshore site only or the reef site only.

Diel Patterns

The variation in the PPM showed significant difference across the four diel phases for the reef (Kruskal-Wallis ANOVA on ranks, χ^2 [df = 3, $n = 172$] = 9.91; $P = 0.02$; Table 3). However, *post hoc* pairwise, multiple-comparison, Tukey method procedures revealed no significant difference between phases for the reef site. The significant Kruskal-Wallis test

Table 1. Details of digital acoustic monitoring (DMON) deployment sites and recording times over the duration of the study.

Site	Coordinates	Deployment date	Recovery date	Deployment duration (time)	Recorded minutes
Reef	44°35.140 N, 124°07.120 W	16 May 2014	23 May 2014	6 d 20 h 00 min	985
	44°35.121 N, 124°07.000 W	12 Jun 2014	20 Jun 2014	7 d 21 h 30 min	1,138
	44°34.985 N, 124°07.117 W	26 Jun 2014	7 Jul 2014	10 d 14 h 40 min	1,529
	44°35.247 N, 124°06.815 W	29 Jul 2014	8 Aug 2014	9 d 21 h 40 min	1,427
Offshore	44°35.221 N, 124°06.859 W	16 Sep 2014	18 Sep 2014	2 d 13 h 20 min	441
	44°34.650 N, 124°13.218 W	12 Jun 2014	20 Jun 2014	7 d 21 h 40 min	1,138
	44°34.857 N, 124°13.419 W	26 Jun 2014	7 Jul 2014	10 d 23 h 10 min	1,580
	44°34.929 N, 124°13.215 W	29 Jul 2014	8 Aug 2014	10 d 0 h 30 min	1,444
	44°34.929 N, 124°13.215 W	16 Sep 2014	29 Sep 2014	12 d 17 h 40 min	1,835
	44°34.929 N, 124°13.215 W	20 Sep 2014	13 Oct 2014	12 d 12 h 00 min	1,801

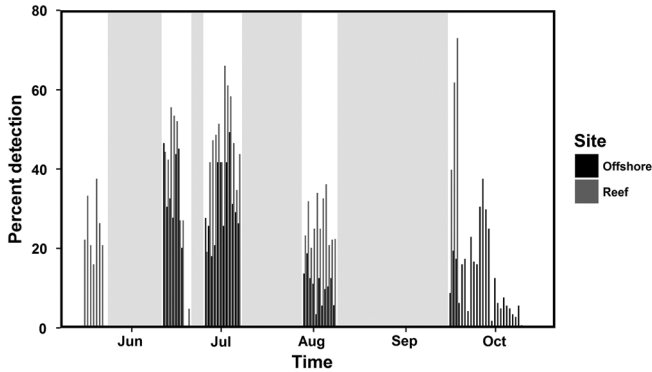


Figure 2. Percent of daily monitored minutes in which harbor porpoise were detected for the reef and offshore sites throughout the study period. The gray shaded areas represent data gaps between deployments.

was likely due to a nearly significant difference between night and day revealed by the Tukey test ($P = 0.05$). At the offshore site, no significant difference in PPMs across diel phase was detected (Kruskal-Wallis ANOVA on ranks, χ^2 [df = 3, $n = 228$] = 4.15; $P = 0.25$). For BPMs, no variation across the four diel phases was found at the reef site (Kruskal-Wallis ANOVA on ranks, χ^2 [df = 3, $n = 228$] = 3.01; $P = 0.39$). However, at the offshore site, the variation in BPMs showed significant variation across diel phase (Kruskal-Wallis ANOVA on ranks, χ^2 [df = 3, $n = 228$] = 29.775; $P < 0.001$); BPMs during the day was significantly lower than the BPMs in the morning ($P = 0.01$) and night ($P < 0.001$) (Fig. 3).

Tidal Patterns

No significant pattern of PPM or BPM across tidal cycle was found at the offshore site (Rayleigh's test for circular uniformity, $P = 0.2495$, $P = 0.4065$, respectively). However, at the reef site, PPM were significantly different from a uniform distribution throughout the tidal phase (Rayleigh's test for circular uniformity, $P = 0.0078$) with the peak in mean PPM occurring during late flood (1.97 radians) (Fig. 4). Despite a visual bimodal pattern, BPM at the reef site were found to be uniformly distributed across the tidal phase (Rayleigh's test of uniformity, $P = 0.5067$) at the 95% confidence level. This results from a bimodal distribution with two peaks in BPM, observed at the reef site during the maximum ebb (3.05 radians) and flood (1.470) phases of the tides. Therefore, a Hartigan's dip test for unimodality was applied to test if the distributions were unimodal or multimodal (*i.e.*, at least bimodal, Hartigan and Hartigan 1985). Values < 0.05 indicate significant bimodality and values > 0.05 and < 0.10 suggest bimodality with marginal significance (Freeman and Dale 2013). The PPMs had a single mode evident (Hartigan's dip test, $P = 0.9539$), whereas BPMs had a bimodal distribution (Hartigan's dip test, $P = 0.05$).

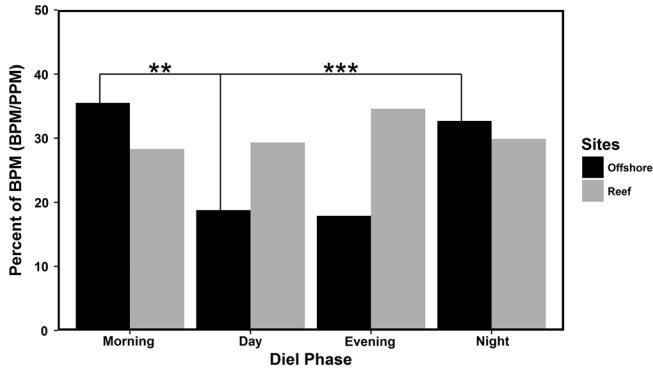


Figure 3. Percent of porpoise-positive minutes (PPM) that contained at least five click trains with minimum interclick intervals (MICIs) of < 10 ms, thus classified as a buzz-positive minute (BPM). The star symbols and brackets represent *post hoc* Tukey tests that gave significant results at the $P < 0.05$ level: Morning *vs.* Day and Day *vs.* Night for the offshore site.

GAM Modeling

The final GAM with PPM as a binary response variable representing porpoise presence/absence at the reef site included Julian day, diel phase, tidal phase, the interaction between Julian day and diel phase, and the interaction between Julian day and tidal phase (Table 2). The final GAM for PPM at the offshore site included the same variables as the reef PPM except for the interaction between Julian day and tidal phase. Oddly, tidal phase was a significant temporal covariate for PPM

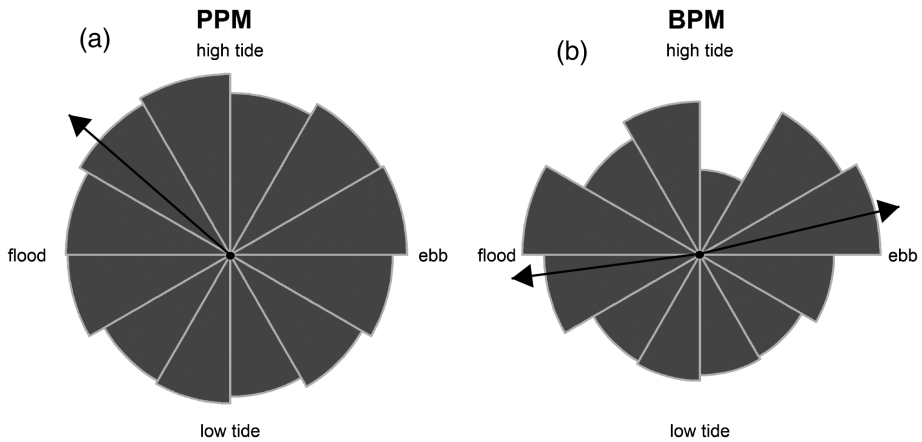


Figure 4. Distribution of harbor porpoise acoustic activity at the reef site measured as (a) porpoise positive minute (PPM) and (b) buzz positive minute (BPM) as a function of the tidal cycle. The length of the bars represents the binned presence of PPM or BPM during a given tidal phase. The black arrows represent the peak in mean PPMs and BPMs, respectively.

Table 2. Recorded data set for the entire time of investigation, separated for each station by diel phase and their totals. PPM: porpoise positive minute; BPM: buzz-positive minute.

Site	Diel phase	Recorded minutes	Porpoise positive minutes (PPM)	PPM (% per complete observation period)	Click only minutes	Buzz positive minutes (BPM)	BPM (% per PPM)
Reef	Morning	278	92	33.1	66	26	28.3
	Day	3,163	1,239	39.2	876	363	29.3
	Evening	286	104	36.4	68	36	34.6
Offshore	Night	1,793	622	34.7	436	186	29.9
	Morning	353	62	17.6	40	22	35.5
	Day	4,075	730	17.9	593	137	18.8
	Evening	351	78	22.2	64	14	17.9
	Night	3,019	550	18.2	370	180	32.7

Table 3. Simultaneous DMON site deployment data: For the periods when recording devices were present at both the reef and offshore sites and simultaneously recording, the number and percent of porpoise positive minutes (PPMs), and buzz positive minutes (BPMs) detected at each site are given, as well as the number and percent (displayed in bold) that were detected at both sites simultaneously during the same 10 min time period.

Detection type	Location	Number of detections	Percent of total detection type
PPMs	Reef	1,297	55.6%
	Offshore	514	22.0%
	Present at both	521	22.3%
BPMs	Reef	546	68.6%
	Offshore	207	26.0%
	Present at both	43	5.4%

at the offshore site. It was found to be nonsignificant ($P = 0.054$) for PPMs at the reef site. However, at the reef there were more PPMs during low tide, while offshore had more PPMs during high tide. Diel phase was significant at both sites, with more PPMs occurring during the day at the reef site and during the evening and night at the offshore site. The deviance explained for the GAMs of PPM at the reef and the offshore sites, was 6.9% and 11.5%, respectively.

The GAM of BPMs at the reef site included the same variables as the GAM of PPMs at the reef site. However, diel phase was not significant for foraging at the reef site, similar to the diel analysis. The final GAM of BPMs at the offshore site included Julian day, diel phase, and their interaction; no tidal phase parameters were included in the model for BPM. The deviance explained for the GAMs of BPM at reef site and the offshore site was 13.7% and 13.2%, respectively.

DISCUSSION

This study provides first insights towards the fine scale spatial and temporal patterns of habitat use by harbor porpoises off the central Oregon coast during the summer months. Our results indicate a regular use of our study area by harbor porpoises with almost daily presence at both sites. Presumed feeding, *i.e.*, buzzes, was detected in 27% of all PPMs, additionally highlighting this area as a regular feeding spot. Overall, echolocation activity indicative of presence and foraging at the reef site was higher, and likely reflective of prey availability. Harbor porpoise foraging activity was also prevalent at the offshore site where feeding buzzes were more correlated with diel patterns, whereas foraging activity at the reef site was influenced by tidal phase. Harbor porpoises were rarely present at both the reef site and the offshore site at the same time. This may suggest that harbor porpoises in this region move between the

Table 4. Predictor environmental variables in generalized additive models (GAM) of harbor porpoise echolocation activity and their significance, with deviance explained of entire model.

Predictor	Reef PPM	Reef BPM	Offshore PPM	Offshore BPM
Julian day	<0.001 ^c	<0.001 ^c	<0.001 ^c	<0.001 ^c
Diel phase:				
Morning	—	—	—	—
Day	—	—	—	—
Evening	—	—	0.003 ^b	—
Night	0.01 ^a	—	0.04 ^a	<0.001 ^c
Tidal phase	0.05	—	0.05	—
Julian day × Diel phase:				
Morning	—	—	—	<0.001 ^c
Day	—	0.04 ^a	<0.001 ^c	<0.001 ^c
Evening	<0.001 ^c	0.001 ^b	<0.001 ^c	—
Night	<0.001 ^c	<0.001 ^c	<0.001 ^c	—
Julian day × Tidal phase	0.02 ^a	<0.001 ^c	—	—
Diel phase × Tidal phase	—	—	—	—
Deviance explained	6.9%	13.7%	11.5%	13.2%

^aSignificant at the 0.05 probability level.

^bSignificant at the 0.01 probability level.

^cSignificant at the 0.001 probability level.

two nearby study sites. This temporal habitat use pattern may increase foraging opportunities that are enabled by fine-scale oceanographic patterns driven by tidal and diurnal forces. More research is needed to describe the mechanisms by which these environmental forces increase prey availability for harbor porpoises at these two sites, but harbor porpoise spatial distribution appears to vary temporally relative to cycles (*e.g.*, tidal phase, time of data) at small spatiotemporal scales (<10 km, hours).

The location of these two deployment sites and their surrounding habitat may offer an explanation for this temporal difference in space use. The reef site is located in a bathymetrically complex 30 m depth area only 4 km from shore, while the offshore site is 12 km from shore and in deeper (60 m) water over a flat sandy bottom. Tidal flows are likely much stronger at the reef site, due to the shallow nature and complex bathymetry in that area and proximity to the Yaquina River mouth. Whereas, in the open water of the offshore site, tidal flows are more reduced and likely do not have a strong impact on the environmental conditions. The interaction of bathymetry and tides and subsequent attraction of cetaceans has also been demonstrated in the Bay of Fundy, Canada, where the movement of strong tidal flow around islands and across variable bottom topography produced numerous fine scale tidal fronts and eddy systems (Smith *et al.* 1984). In our study, PPMs were

detected more often at the reef site during peak ebb and flood flow. Studies show that variables, such as tidal height, tidal speed, or tidal phase have a direct influence on the distribution (Marubini *et al.* 2009, Jones *et al.* 2014, Benjamins *et al.* 2016) and behavior (Johnston *et al.* 2005, Pierpoint 2008) of porpoises. However, no consistent pattern has emerged and it seems the preferred tidal height, speed or phase for porpoises is site specific. In agreement with our results, porpoises in Land's End, Cornwall, U.K. and southwest Wales, U.K., were also found to prefer strong ebbing tidal flows for foraging (Pierpoint 2008, Jones *et al.* 2014). Benjamins *et al.* (2016) hypothesized that peak tidal flows may disrupt the ability for fish to stabilize their position in the water, therefore creating opportunities for predators to take advantage of disoriented prey. In addition, Jones *et al.* (2014) suggested porpoises had adopted a foraging strategy of intercepting or "ambushing" prey during ebb tide that was concentrated on coastal and benthic topography. Studies have also shown that porpoises are attracted to reef structures (Todd *et al.* 2009, Mikkelsen *et al.* 2013), likely due to increased prey. Taken as a whole, harbor porpoise may select a range of current and tidal regimes that interact with local topography to enhance relative vorticity (Johnston *et al.* 2005) and thus provide a consistent and predictable foraging resource.

Meanwhile, harbor porpoise at the offshore site displayed increased feeding from sundown to sunrise. This is concurrent with other PAM studies that reported porpoises appear to shift their distribution to different depths and/or habitats at night, perhaps to take advantage of changing prey availability (Carlström 2005, Todd *et al.* 2009, Mikkelsen *et al.* 2013). Furthermore, water depth has a significant impact on porpoise diel rhythms, with more nocturnal porpoise echolocation activity occurring in deeper waters (Brandt *et al.* 2014, Wisniewska *et al.* 2016). In deeper waters, porpoises may be feeding pelagically on prey species that vertically migrate up into the water column at night, such as herring (Cardinale *et al.* 2003).

Occurrence patterns of harbor porpoises suggest active selection of habitat through tidal and diel mediated foraging intensity, likely due to maximizing their foraging opportunities. This is supported by the high probability of a harbor porpoise feeding event detected at either the reef or the offshore site (95%), compared to detection of a feeding event at both sites during the same 10 min period (5%). The small percentage of PPM and BPM at both sites simultaneously suggests this is the same population of porpoises moving between the different foraging locations dependent on diel or tidal forced environmental conditions that is likely linked with prey availability at each site. The high energetic demands and limited energy storage capacity of this species require them to spend a high proportion of their time foraging (Read and Gaskin 1985) and their ability to react to predictable drivers of prey can greatly reduce foraging costs. Porpoises worldwide are reasonably opportunistic in their foraging ecology (Recchia and Read 1989) and feed on a diversity of both pelagic and demersal fish. Harbor porpoise in west coast waters of the United States are known to feed on cephalopods and shrimp but prefer schooling nonspiny fishes such as herring (*Clupea pallasii*), smelt

(*Osmeridea* spp.), mackerel (*Trachurus symmetricus* and *Scomber japonicus*), sardines (*Sardinops sagax*), pollock (*Gadus chalcogrammus*) and whiting (*Merluccius productus*) (Leatherwood and Reeves 1983). In our study, we have no empirical assessment on harbor porpoise prey off the Oregon coast. However, at least two prey species for porpoises (herring and whiting) that are found in this region are known to spend time near the surface, especially during the night (Cardinale *et al.* 2003), and could likely be the targeted prey offshore.

The gradual increase of detections from May to June, and peak detections between summer and fall, observed in this study is consistent with the hypothesis that harbor porpoises move nearshore in relation to large scale temperature changes, which may increase prey availability and mating and calving opportunities (Dohl *et al.* 1983, Green *et al.* 1992). Our results correspond to previous reports documenting the largest concentrations of harbor porpoises along the west coast of the United States occur in summer and early fall, specifically September (Calambokidis and Barlow 1987, Barlow *et al.* 1988). However, our temporal coverage is limited and constrains our ability to address this knowledge gap of winter distribution patterns.

Our final GAM models had a relatively poor fit to the data the model was built upon (<15%), suggesting that most of the variability driving harbor porpoise distribution in this area is due to factors not measured and included in our study. However, results from the GAMs that assess all three temporal variables (day of year, time of day, tidal phase parameter) simultaneously provide largely comparable results to our analysis of the individual relationships between these factors and harbor porpoise presence. Due to the static nature of our recording stations, we are unable to incorporate spatial drivers of porpoise presence or behavior (*i.e.*, temperature, productivity, salinity) and thus our models were simply constructed using the available temporal variables. It is likely that our models would improve with the inclusion of information on dynamic environmental conditions and the distribution and abundance of prey species. Regardless, it is common for GAMs modeling cetacean occurrence at high resolution to explain only a small portion of the deviance (Best *et al.* 2012, Forney *et al.* 2012), and this is particularly true for temporal models (de Boer *et al.* 2014, Temple *et al.* 2016, Wingfield *et al.* 2017).

Nevertheless, recognizing and understanding the temporal drivers of harbor porpoise distribution can better inform the location and timing of management actions to allow more effective risk mitigation and population monitoring of harbor porpoise. Results from this study indicate that presence and foraging behavior of harbor porpoises in this area is related to seasonal, diel and tidal factors relative to local habitat. These highly resolve temporal patterns can only be achieved effectively by PAM. High frequency passive acoustic recording devices like DMONs offer great promise for the study of the ecology, behavior, and conservation of small, acoustically active cetaceans. However, recording at these high frequencies is technologically challenging due to the accompanying increase in data storage requirements and power. While we were able to capture valuable data on harbor porpoise presence, the limited battery

life and memory storage of the DMONs is particularly challenging for long-term monitoring studies. Moreover, bottom-trawling and ship traffic in general produce large amounts of background noise and are a threat to moored devices. An ideal recording device for future studies should be capable of capturing high frequency species repertoires with a long battery life so that year round presence of harbor porpoises can be determined.

This study begins to fill information gaps needed to understand the temporal variations in harbor porpoise distribution and behavior in order to apply effective spatial management and conservation strategies. This data set may serve as a baseline from which to identify critical areas, refine current conservation efforts, and compare future trends for monitoring harbor porpoise off the Oregon coast. Continued and expanded monitoring of porpoise occurrence and behavior will be a critical component in future conservation efforts.

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