AN ABSTRACT OF THE THESIS OF

Amanda Holdman for the degree of Master of Science in Wildlife Science presented on November 7, 2016.

Title: Spatio-temporal Patterns and Ecological Drivers of Harbor Porpoise (Phocoena phocoena) off the Central Oregon Coast, USA.

Abstract approved: ______________________________________________________

Leigh G. Torres

The marine environment is under increasing pressure from human activities worldwide, particularly in coastal waters, creating a need to better understand fine-scale distributions of highly mobile species that occur in the area, as they are frequently most threatened. Harbor porpoise (Phocoena phocoena) occur frequently in Oregon’s nearshore habitat, but due to limited survey data, the temporal and spatial distribution of these small cetaceans is not well understood. Sensitivity of harbor porpoise to anthropogenic noise and entanglement is well established, generating concerns for the spatial overlap between future coastal development projects and preferred coastal habitat. Passive-acoustic monitoring and standard line transect surveys were conducted from 2014 to 2015 providing information at a range of spatial and temporal scales of harbor porpoises distribution in Newport, Oregon’s neritic waters. The integration of visual and acoustic survey methods is advantageous in that it creates high spatial and temporal resolution, reduces methodology bias (acoustic surveys provide temporal coverage, visual survey provide spatial coverage), and results in a more robust data set. A total of 42 visual transect surveys were conducted in the study area resulting in over 65 individual sightings. Data collected from visual detections were compiled in 1 km bins relative to environmental conditions including bathymetry, distance to shore, distance to rocky reef, surface salinity, temperature, and fluorescence concentration. Acoustic survey efforts occurred May through October of 2014 using digital monitoring devices (DMONs) deployed at two
neighboring but bathymetrically different locations off the Oregon coast: (1) a site on the 30 m isobath in close proximity to an offshore rocky reef, and (2) a site on the 60 m isobath in an open sandy environment. Acoustic data were analyzed with respect to two dynamic cyclic variables (diel and tidal phase). Over 1500 echolocation click trains were detected and analyzed for patterns of occurrence and behavior, using inter-click intervals to differentiate between navigating and foraging activities. Using either acoustic or visual data, species distribution models were generated to describe harbor porpoise habitat use patterns. Visual surveys revealed harbor porpoise distribution in this area is likely to be influenced by nearshore rocky reefs and fine scale (1 Km) oceanographic conditions of temperature and salinity. Acoustic results revealed that porpoise presence at the nearshore reef was driven by tidal forcing, while harbor porpoise presence offshore was associated with night time foraging. Taken together, these results suggest harbor porpoise habitat use is modulated by specific dynamic environmental conditions that maximize foraging efficiency. Results of this study provide needed baseline data on harbor porpoise occurrence and movement patterns in Oregon, the ecological drivers of those patterns, and critical areas or temporal periods necessitating focused protection from current and developing anthropogenic activities along the Oregon coast.
Spatio-temporal Patterns and Ecological Drivers of Harbor Porpoise (Phocoena phocoena) off the Central Oregon Coast, USA

by

Amanda Holdman

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APPROVED:

________________________________________
Major Professor, representing Wildlife Science

________________________________________
Head of the Department of Fisheries and Wildlife

________________________________________
Dean of the Graduate School

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Amanda Holdman, Author
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 CHAPTER 1: GENERAL INTRODUCTION

Worldwide, the marine environment is under increasing pressure from human activities (Halpern et al. 2008, Witt et al. 2012, Maxwell et al. 2013, Waggitt & Scott 2014). Potentially damaging activities include, but are not limited to, fisheries interactions, vessel traffic, development of marine renewable energies, oil and gas extraction, shipping, naval training operations, recreation, and waste disposal. All of these activities can impact the habitat and availability of prey to apex marine predators. Cetaceans are often wide ranging and are found in diverse habitats from rivers and shallow coastal waters to abyssal canyons, and are likely to encounter a multitude of anthropogenic threats (Parsons et al. 2012).

However, cetaceans that occupy coastal environments are often amongst the most threatened to anthropogenic disturbance, as the majority of human activities occur within coastal zones. These highly mobile species are therefore in need of effective conservation measures to avoid long term decline in population and distribution (Thompson et al. 2000, Cañadas & Hammond 2006).

Marine ecosystems are dynamic and fluid, and temporal variability operates on diel to decadal scales, while spatial variability can be observed on scales from several meters to 1000s of kilometers. Therefore, knowledge of a species at a range of spatial and temporal distribution patterns is fundamental to understand the extent to which cetacean populations are impacted by a particular threat. Moreover, the need for detailed information on the fine scale occurrence and distribution of cetaceans has become more critical over recent years by marine resource managers who must select minimal-impact locations or temporal periods for an increasing number of human activities that have the potential to harm cetaceans (Rees et al. 2013).

Recent scientific advances provide an increasingly rich array of methods for understanding cetacean spatial ecology including vessel and aerial transect surveys, land-based surveys, satellite tracking, passive acoustics, remote sensing, photographic studies, strandings and citizen science data (Evans & Hammond 2004). All of these surveys vary in terms of invasiveness, spatial and temporal scale, cost and technical feasibility. Depending on the study area, target species, resources available, and conservation management questions, one or a combination of these methods may be preferred. All of the data collected from these methods can be linked to environmental conditions using the general species distribution model framework (Redfern et al. 2006, Austin 2007, Elith & Leathwick 2009).
Particular concerns of coastal development have been raised for one key species, the harbor porpoise. Although, known to occur in offshore shallow waters, harbor porpoises are predominately observed in coastal waters less than 200 m deep in the temperate northern hemisphere (Balcomb & Minasian 1984, Gaskin 1984). Being distributed in coastal waters, harbor porpoise are particularly vulnerable with respect to disturbance, injury or death from anthropogenic activities, including by-catch in fisheries, prey depletion, and vessel traffic or habitat degradation due to chemical pollution (Siebert et al. 2009, Herr et al. 2009). Noise, in particular, poses a large threat, as harbor porpoise have been shown to be sensitive to a range of human sounds at very low levels of exposure (Southall et al. 2007, Dyndo et al. 2015). Virtually all human activities lead to a generation of underwater noise, and the effects of possible biological significance from noise can be masking of echolocation sounds or calls from conspecifics, predator and prey, disturbance of natural behavior, hearing damage or physiological stress (Southall et al. 2000).

Despite their often coastal distribution, harbor porpoise have proven difficult to study. They typically go unnoticed in anything more than a Beaufort Sea State 2 (Teilmann 2003), due at least partly, to their low profile when breathing. Furthermore, they do not generally acquire markings on their dorsal fins, making photo-identification studies impractical. Vessel and shore based studies can provide some general indication of movement and surface behaviors for individuals over the short periods, but can only address populations in general over longer periods (Watson & Gaskin 1983). Passive acoustic monitoring (PAM) offers a means to monitor trends in echolocation use or distribution of a population (Carlström 2005, Todd et al. 2009), however, it can be difficult to differentiate between these two factors in a record of acoustic detections.

Harbor porpoise, while cryptic, are abundant in Oregon and Washington coastal waters with two stocks recognized in Oregon waters. The most recent abundance estimates conducted in 2010 and 2011 by Forney et al. (2013) are 21,487 in the Northern Oregon/Washington Coast stock and 35,769 in the Northern California/Southern Oregon stock. Their distribution is thought to vary seasonally by region off the coast of Oregon and Washington, with sightings most frequently observed in the fall (Dohl et al. 1983, Barlow et al. 1988) and it has been suggested that harbor porpoises occupy deeper, offshore waters during late winter (Dohl et al. 1983, Barlow et al. 1988). While periodic surveys have occurred off the Pacific Northwest coast (Carretta et al. 2009), survey efforts in Oregon waters were typically limited to a few weeks. Most recently, aerial surveys were conducted off Newport, Oregon that
targeted shelf waters in 2011 and 2012 but surveys were only conducted once per season (Adams et al. 2014). Results from these broad scale studies of harbor porpoise are of limited use when data are needed on a smaller and site-specific scale.

Wave and wind energy resources along the Pacific Northwest coast presents a great opportunity for developing offshore renewable energy (Callaway 2007, Boehlert et al. 2008). In 2012, a six square mile area off the coast of Newport, OR was dedicated as a wave energy test-bed to be operated by the Northwest National Marine Renewable Energy Center. Wind resources in the United States are also available offshore in the Pacific Northwest (Thresher and Musial 2010). The need for fine scale data on the extent to which harbor porpoise use coastal and shelf waters in Oregon is becoming increasingly important to support growing conservation and marine spatial planning initiatives (Boehlert et al. 2008). Therefore, the aim of this thesis was to obtain information on the distribution and habitat use patterns of harbor porpoise in Newport, Oregon at fine spatial and temporal scales. To achieve this, data were collected and examined in a two-step process using two complementary survey techniques. First, the broad scale distribution of harbor porpoise was examined using ship-based surveys across the Oregon coast. Second, passive acoustic monitoring was used to examine the temporal patterns of harbor porpoise presence and foraging in two environmental contrasting sites: a nearshore rocky reef and an offshore sandy bottom. Both acoustic study sites are located within the vicinity of the visual transect surveys and consequently the study area. Together, these two approaches form a novel examination of harbor porpoise space use along the Oregon coast.
LITERATURE CITED

Dyndo M, Wiśniewska DM, Rojano-Doñate L, Madsen PT (2015) Harbour porpoises react to low levels of high frequency vessel noise. Scientific reports 5


CHAPTER 2: COMPARING THE USE OF FINE SCALE REMOTELY SENSED DATA AND IN SITU SPECIES DISTRIBUTION MODELS IN A HIGHLY DYNAMIC ENVIRONMENT

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Amanda K. Holdman¹* and Leigh G. Torres¹

¹ Marine Mammal Institute, Department of Fisheries and Wildlife, Oregon State University, 2030 SE Marine Science Drive, Newport, Oregon 97365, USA

*Corresponding author (Amanda.Holdman@gmail.com)

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ABSTRACT

Information on cetacean distribution plays an important role in developing management and monitoring programs to mitigate potential impacts from coastal development. The aim of this study was to investigate drivers of fine scale harbor porpoise habitat selection, to gain a better understanding of the spatial distribution of the species off of the central Oregon coast, where anthropogenic activities may occur. A total of 26 standard line transect surveys were conducted in 2014 and 2015, resulting in 1346 km of survey effort and 47 harbor porpoise sightings. We used negative binomial generalized additive models to model harbor porpoise abundance and distribution as a function of temporally and spatially variable oceanographic covariates and topographic features. Two separate models were created to assess the potential for in situ or remotely sensed environmental data to best describe harbor porpoise response to dynamic ocean conditions. Our results indicate that harbor porpoise distribution in this area is likely to be influenced by nearshore rocky reefs and fine scale oceanographic conditions that likely facilitate foraging: saline and mid-temperature waters (12-14°C) were favored over our study area. Also, the comparison of in situ and remotely sensed data revealed the benefits in using in situ environmental measurements to explain fine-scale cetacean distribution in coastal environments.
INTRODUCTION

Cetaceans are known for their wide-ranging habitats, yet, they often concentrate in spatially explicit areas for extended periods of time (Baumgartner et al. 2003). Their presence in these localized areas are thought to be based on foraging decisions made in response to meso (10s to 100s of km) and fine scale (1 to 10km) environmental cues (MacArthur & Pianka 1966, Sims et al. 2008). By examining species distributions at a range of scales, we can improve our understanding of the species interaction with its environment (Embling et al. 2012). This is particularly important for species conservation and management because information on spatial and temporal variation of occurrence will allow for detection of changes in abundance and distribution in response to anthropogenic activities (Forney 2000). However, knowledge of the abundance and distribution of cetaceans, and how they utilize their habitats at different scales, remains significantly limited for many populations.

The need for fine scale information of cetacean occurrence and distribution has become more critical for marine resource managers who must select minimal-impact locations or temporal periods for an increasing number of human activities that have the potential to harm cetaceans (e.g. vessel traffic, naval training, fisheries interactions, renewable energy devices). Along the northwest coast of the USA, the marine environment off Oregon has seen increased potential for coastal development in recent years (Callaway 2007, Boehlert et al. 2008), which has created a heightened sense of urgency to collect baseline data on marine mammal distribution and habitat use in this area. While there has been substantial regional survey effort to develop habitat-based predictions for cetaceans across broad geographic areas, such as the west coast region of the United States Exclusive Economic Zone at a resolution on X km (Carretta et al. 2009, Forney et al. 2013), these data provide a spatially and temporally patchy picture of cetacean distribution along the Oregon coast. Often previously surveyed areas are larger than operational areas where impacts may occur and fine scale information on the spatio-temporal distribution of marine mammals in Oregon’s neritic waters is incomplete. Therefore, it is important to fill these data gaps on the fine scale distribution patterns of coastal cetaceans with information from detailed baseline studies to guide policies addressing the location of potentially harmful anthropogenic activities.

Species distribution models (SDM) are increasingly used to provide a better understanding of the ecological processes underlying cetacean distributions (Redfern et al. 2006) and to inform conservation
and management decisions (Torres et al. 2003, Redfern et al. 2006, Gilles et al. 2011, Redfern et al. 2013). SDMs allow prediction of cetacean occurrence on variable scales because cetacean densities are estimated as continuous functions of habitat variables. Species distribution models typically use visual survey data to model distribution as a function of environmental variables and then predict over areas or time periods where data are sparse or absent, either through model interpolation or extrapolation (Mannocci et al. 2015). The distribution of marine mammals is often influenced by the distribution of their prey and their predators. However, data on prey and predator density is difficult to obtain, especially at appropriate temporal and spatial scales. Therefore, in their absence, species distribution models use indirect explanatory variables as proxies for prey abundance or availability. Environmental parameters have been shown to generate better models of cetacean habitat preferences than models derived from prey distribution data, due to the difficulty of accurately measuring prey data at fine scales (Torres et al. 2008).

Dynamic habitat data used to model cetacean distributions can be derived remotely sensed oceanographic data or may be collected in situ during cetacean surveys. Satellite data are readily obtainable and are often used in cetacean-habitat models (Baumgartner et al. 2003), as they provide near real time estimates of key environmental metrics (e.g. sea surface temperature and chlorophyll a concentration) known to influence distributions of cetaceans directly, or act as proxies for prey. Additionally, satellite data allow predictions derived from SDMs to wherever these habitat variables can be measured or estimated, allowing for geographical extrapolation within calibrated environmental conditions. However, satellite data are often patchy due to cloud cover, especially in coastal zones, and the available data at fine spatial and temporal resolutions (<1km, daily) is limited or unavailable for many variables pertinent to cetaceans (e.g., SSH, upwelling, fronts, salinity). In contrast, in situ data reflect environmental conditions at contemporaneous scales with cetacean survey data, but is restricted to the time and place where the study was conducted, which in turn constrains the ability to extrapolate and predict distributions, which could be crucial to conservation management. In this study SDMs for harbor porpoise *Phocoena phocoena* were constructed with both remotely sensed and in situ dynamic oceanographic variables.

The harbor porpoise is among the most common cetacean in Oregon coastal waters and is predominately observed in waters less than 200 m deep (Balcomb & Minasian 1984). Sensitivity of
harbor porpoise to anthropogenic noise and entanglement is well established, generating concerns for the spatial overlap between present and future coastal development projects and preferred coastal habitat of this small cetacean. Harbor porpoise are sensitive to a range of human sounds at very low levels of exposure (Southall et al. 2007, Tougaard et al. 2012, Dyndo et al. 2015), and increase in noise from shipping traffic, coastal development and other human sources of disturbance, may impact their distribution and welfare. Harbor porpoise along the USA west coast show distinct variation in their distribution on seasonal and inter-annual scales. However, uncertainty over the factors influencing the distribution of harbor porpoise at fine scales can constrain efforts to develop targeted conservation policies and resource management strategies. Habitat modeling has been used successfully for harbor porpoise (Bailey & Thompson 2009, Embling et al. 2010), and their distribution in other regions has been indirectly linked to heterogeneous habitat variables such as sea temperature (Tynan et al. 2005), benthic topography (Baumgartner 1997, Cañadas et al. 2002) ocean currents and frontal systems (Johnston et al. 2005) and directly linked to prey distribution patterns (Read & Westgate 1997, Sveegaard et al. 2012).

In this paper, we present a fine-scale (1km) investigation of the key environmental drivers influencing the distribution of harbor porpoises on the central Oregon coast following the two stage approach of density surface modeling (Miller et al. 2013). Based on visual line transect surveys, generalized additive models (GAMs, Hastie & Tibshirani 1990) are used to relate harbor porpoise densities to static and dynamic environmental variables. Two separate models are created to assess the potential for in situ or remotely sensed environmental data to best describe harbor porpoise response to dynamic ocean conditions. We aim to understand the relative spatial distribution patterns of harbor porpoise along the Oregon coast and identify critical habitat features to help inform coastal development and management.

**MATERIALS AND METHODS**

**Survey data and field methodology.** We conducted visual transect surveys for cetaceans in 2014 and 2015 off the central Oregon coast opportunistically using a research vessel dedicated for another purpose (Fig. 1). Therefore, survey routes were not standardized across the study area, but trained observers followed rigorous survey and effort protocols, and data collection was broad enough to incorporate a range of habitat variability (Redfern et al. 2006). Thus data collected from transects in
this study are considered equivalent to data collected during designed transect surveys. Only surveys between April to October were analyzed due to low survey effort in the winter months caused by unfavorable weather conditions. This seasonal period generally corresponds to the major upwelling oceanographic season off the coast of Oregon (Mann & Lazier 2006), and includes the sensitive periods in the annual birth and mating cycle of harbor porpoise along the west coast of the U.S. (Balcomb & Minasian 1984).

All visual search effort for marine mammals was conducted from a 16.5 m oceanographic research vessel with an observational height of 3.5m and an average ship speed of 12 knots. Observations were only conducted during daylight whenever there was sufficient visibility (> 500 meters) and in Beaufort Sea state 3 or less. Occasionally conditions deteriorated during a survey and some small sections were surveyed in Beaufort Sea state 4. Observers experienced with field identification of marine mammals employed standard line transect methods. The primary observer scanned a 90 degree arc to one side of the vessel and used 7X50 binoculars to sight, identify, and estimate group size of all cetaceans encountered during transects. A second observer was responsible for data entry and recorded all mammal sightings into Seebird WinCruz software, which was interfaced to the ship’s Global Positioning System (GPS). For each cetacean sighting, the following data were recorded: GPS latitude and longitude, time stamp, species identification, number of individuals sighted, and reticle and bearing of cetacean position relative to the horizon and bow of vessel. In addition, variables related to survey conditions were recorded every hour, these included Beaufort sea state visibility, cloud cover and glare. Occasionally, the ship had to deviate from the planned trackline to avoid fishing gear or vessels, but otherwise the ship searched continuously in passing mode and did not approach sightings.

During line transect surveys, in-situ oceanographic data were collected including surface water conductivity, salinity, temperature, and florescence using a flow-through SeaCat21 thermosalinograph fitted with a Seapoint Ultraviolet fluorometer. Flow-through measurements were recorded continuously at 3 second intervals using SBE Seasave.

The study area was define post-hoc based on trackline distribution since survey effort was conducted according to other research objectives. A convex hull polygon was fitted around the tracklines where search effort occurred and within areas where coverage appeared reasonable (Figure 1).
**Data preparation.** Before fitting a detection function, we right truncated the sightings at a distance that removed any “long tail” of distance sightings (Buckland et al. 2001). We then evaluated detection functions that modeled the detectability of harbor porpoise according to distance from the trackline and other covariates. We considered both conventional distance sampling (CDS) and multiple-covariate distance sampling (MCDS) formulations. For CDS, we tested half normal (HN) and hazard rate (HR) key functions with no adjustments. For MCDS, group size, Beaufort sea state and the observer’s subjective estimate of the quality of observation conditions were considered as covariates. We did not attempt to correct our analysis for animals that may have been missed on the trackline. The appropriate detection function was chosen based on minimum Akaike Information Criterion (AIC), and goodness of fit using a Kolmogorov-Smirnov test (Buckland et al. 2004).

All vessel survey transect lines were divided into continuous-effort segments with a target segment length of 1 km, corresponding to the finest resolution of available remote sensed data. However, the lengths of continuous sections of survey effort were not evenly divisible by 1 km, and there was generally a “remainder” segment that was less than 1 km. If the remainder was less than 0.5 km long, each segment gained an equal fraction of the remainder, resulting in segments that are slightly larger than 1 km. If the remainder was greater than or equal to 0.5 km, then the number of segments was increased by 1 and the entire transect length was split into that many equal length segments, resulting in segments that were slightly smaller than 1 km. The final filtered dataset resulted in a total of 1,346 segments, with an average transect length of 999.1 m. The selected detection function was applied to these segments for density surface modeling and to estimate abundance using a Horvitz Thompson-like estimator (Hedley & Buckland 2004). All exploratory analysis of the sighting data and detection functions was conducted in R (cite; give version details) using the mrds package (cite; version 2.1.16).

**Spatial modeling.** The candidate set of static variables in each model included the spatial coordinates of x and y (in UTM projection system), depth, distance to coast, distance to river mouth and distance to rocky reefs. Dynamic environmental covariates included remotely sensed SST for the remotely sensed model and data collected during the line-transect surveys: SST, florescence, conductivity and sea surface salinity [SSS] for the in situ model. Bathymetry data and the benthic habitat data used to calculate distance from rocky reef was obtained from the Oregon Department of Fish and Wildlife Nearshore Ecological Data Atlas (NEDA). Habitat for NEDA was classified by the Active Tectonics Lab at
Oregon State University into coarse benthic sediment types: sand, rock or mud (Goldfinger 2010, Goldfinger et al. 2014). Daily estimates of SST for the remotely sensed model were obtained from the Multi-scale Ultra-high resolution Global SST dataset with 1 km resolution (NASA, MURSST). The value of all remotely sensed variables were taken from the midpoint of each trackline segment. To avoid bias introduced by cross-correlation between explanatory variables, Pairwise Spearman’s rank correlation was calculated between all candidate model covariates. Pairs of variables with high levels of correlation (rho >0.7) were identified and removed from subsequent analysis. Depth, distance to river mouth, and distance to shore were all found to be significantly correlated, therefore only depth was used for analysis.

The number of sightings per survey segment was modelled relative to the environmental covariates using Generalized Additive Models (GAM; (Hastie & Tibshirani 1990), using a negative binomial response with a log link function. All environmental covariates were modeled using thin plate regression splines as penalized smoothers, with the exception of the latitude and longitude that used a bivariate smoother. The natural logarithm of the segment area was included as the effort offset. AIC and deviance explained were used to measure model performance and used to select the best remotely sensed model and the best in situ model. Yet, the most parsimonious model in terms of number of predictors was always favored even in cases where the AIC was not reduced by 2. Predictors were usually removed when their approximate smooth significance test produced p-values > 0.05, and if their relative deviance explained was < 2%. GAM analysis were carried out in R using the ‘mgcv’ package (Wood 2006).

To examine and compare the ability of remotely sensed and in situ data to capture the variability if oceanographic conditions across this dynamic coastal region, the median and range of SST values on each survey day from these two datasets were assessed using boxplots and ANOVA tests. Spatial predictions are not possible using in situ models due to a lack of predictive dynamic covariate spatial layers. Therefore, spatial predictions derived from GAMs were not generated and compared. However, harbor porpoise abundance was predicted in the study area using the remotely sensed model on a monthly basis using SST composites. These abundance estimates were constructed from the detection function, and thus accounted for survey effort and detection variability.
RESULTS

Survey effort totaled approximately 1,345 km and a total of 47 sightings of harbor porpoise groups were observed. The minimum number of sightings recommended for modeling detection probability is 60-80 schools (Buckland et al. 2001). However, a simulation study found that low bias can be achieved for some detection functions with just 30 sightings, the fewest number tested in that study (Miller & Thomas 2015). Exploratory data analysis suggested truncating the perpendicular sighting distances at 150 m, reducing the number of sightings used in the analysis to 45. This truncation distance was used to assess the fit of different candidate detection functions. The detection function model that fitted the resulting harbor porpoise sightings data best, as determined by AIC, was a hazard rate key function with no adjustment terms. There was no evidence in the data (based on AIC) to justify including sea state as a covariate. There was no significant relationship between visual group sizes and detection probability or distance from trackline. Group size of the 47 sightings ranged from 1 to 6, with a mean of 1.2 (SE = 0.07). Using the XYZ, Total estimated abundance in the study area was estimated at 92 animals (CV =0.36; 95% CI= 45-188).

Spatial Models.

The selected remotely sensed GAM explained 12.4% of the deviance. SST had a significant effect on harbor porpoise occurrence, as well as latitude and longitude modelled with a bivariate smooth (Fig. 2, Table 1). Harbor porpoise occurred more in the observed SST mid-range and peaked around 14°C. Distance to rocky reef was nearly significant (P = 0.067) and harbor porpoise occurrence decreased with distance from a reef structure. The selected in situ GAM explained 29.4% of the deviance and retained SST, salinity, and distance to rocky reef as significant variables covariates (Fig. 2, Table 1). SST for the in situ GAM showed a similar functional response curve as the remotely sensed GAM in terms of range and trend, however finer scale variation is apparent with two slight peaks occurring at 11.5 and 13.5 °C. Similar to the remotely sensed model, the occurrence of harbor porpoise decreased with increasing distance from a reef. Additionally, salinity significantly affected harbor porpoise occurrence in the in situ model, revealing a linear preference for higher salinity waters.

DESCRIPT BOXPLOT AND ANOVA RESULTS HERE FOR COMPARING ABILITY TO DESCRIBE DYNAMIC HABITAT. The monthly predictions of harbor porpoise abundance gradually increased in the spring, peaked during summer months, and then decreased into the fall (Figure 2).
We aimed to identify habitat preferences of harbor porpoise off the Oregon coast, an area that has previously seen little scientific attention, using species distribution models. Using models based on remotely sensed and in situ environmental data, we highlight significant relationships between harbor porpoise and topographic and dynamic features, which are proxies for the underlying drivers of harbor porpoise prey distributions.

The covariate with the highest relative importance for both the remotely sensed and in situ habitat model was SST. It is thought that SST relates directly to species physiology and anatomy through adaptations of diving and thermoregulation (Koopman 1998). Additionally, this physiologically based preference for a given range of SST may be reinforced by structures of prey density. Phytoplankton and zooplankton accumulate in frontal zones offering a localized area of concentrated food particles for feeding organisms (Bakun 2006). The increased productivity in those areas attracts a wide variety of fish, bird, and mammal predators (Hoefer 2000, Ainley et al. 2009). In the Oregon coastal upwelling region, cross-shelf zonation in the spatial distribution of zooplankton is typically associated with SST fronts (Reese et al. 2005). Zooplankton concentrations are spatially patchy, with highest concentrations nearshore in cooler upwelled water (Reese et al. 2005).

Consequently, SST is one of the most tested variables in marine species distribution models and significant correlations of marine mammal distribution and species richness with SST have been demonstrated across many regions and taxa (Baumgartner et al. 2001, Hamazaki 2002, Rasmussen et al. 2007). In addition, SST is one of the most accessible environmental parameter through remote sensing: it is available at high resolution (1km), has worldwide coverage and is easily obtainable from online databases, which could explain its frequent use in habitat models. However, other potential environmental drivers of species distribution might go unnoticed simply because they are not available at such fine resolution using remote sensing.

In situ data sampling allows collection of variables that are either not available at an appropriate small scale, or not available at all from remote sensing. For example, in this study, salinity was found to be an important driver of porpoise distribution in our in situ model. Other studies using in situ methodology have shown Harbor porpoise distribution to be closely related to sea surface salinity in the California current (Tynan et al. 2005), the Marsdeip area of the Netherlands (IJsseldijk et al. 2015), and the Baltic Sea (Mikkelsen et al. 2016) with more detections occurring during higher salinity levels.
It is unlikely that salinity directly impacts porpoise, as they are observed in much less saline waters such as the Eastern Schelte (Jansen et al. 2013). Therefore, the relationship with salinity is most likely driven by the behavior preference of their prey.

The final model for using the remotely sensed data included SST and a bivariate smooth of X and Y, with distance from rock reef being nearly significant, and this model explained only 12.4% of the deviance. In contrast, the in situ model included temperature, salinity, and distance to rocky reef and explained up to 29.4% of the deviance. The basic functional form of SST in our remotely sensed model and our in situ model was similar. This is consistent with Becker et al. (2010) findings that remotely sensed measures of SST can be used effectively in place of in situ measures. However, in the present study, the modeling using in situ data had more explanatory power than the model using satellite data. This apparent contradiction to Becker et al. (2010) may be due to the size and scale of the study. Indeed, data from satellite are gridded at a medium or low resolution at a daily to monthly scale, whereas in situ data can be collected at any discrete geographical location in time. It is likely the processes that drive the distribution of harbor porpoise along the Oregon coast occur at such a fine scale that they are not likely to be captured using remotely sensed oceanographic conditions. As a result, for understanding the distribution patterns of small cetaceans highly mobile at fine scales we advocate the use of in situ environmental data in combination with remote sensing.

Rocky reef habitat was also found to be a significant predictor variable for harbor porpoise in situ model and nearly significant for the remotely sensed model. Complex topographic features have been described as key foraging grounds for many marine predators (Scott et al. 2010, Bouchet et al. 2015). Such areas probably interrupt the water flow, particularly in coastal waters, causing convergence zones that lead to accumulation of plankton and secondary consumers (Smith et al. 1984). These features consequently create predictable, localized aggregations of prey. Taking advantage of these locations would enable species to maximize their foraging efficiency, which is a strategy clearly important for highly mobile marine species with high energy demands, such as the harbor porpoise (Read & Westgate 1997).

Harbor porpoise habitat relationships explored previously found depth to be a significant variable for explaining distribution patterns (Isojunno 2010, Wier et al. 2007, Marubini 2009, Embling 2010). Our transects, and consequently our harbor porpoise sightings never extended out past 200 meters, which
is the upper limit of the extent of their environmental range in the literature. As a consequence, all of the survey effort was concentrated within harbor porpoise preferred depth conditions, which could explain why depth was not significant in this study. Finally, our models were improved when a smooth interaction of X and Y coordinates were included. In some studies, latitude or longitude are included and used as proxies for ecological variables that could not be measured such as primary productivity. In the present study, the relationship between X and Y was likely due to the survey effort, where more survey effort occurred towards the north of end our study area. Since our coordinates were fit in the model with a bivariate smoother and their influence is highly linear, we could include the coordinates in our final model.

Two standard assumption of line transect sampling, is that all animals on the transect line are detected and that animals remain stationary or move little before they are detected. This is unlikely for small cetaceans in general and certainly not for harbor porpoise due to possibility that animals might respond to the survey ships. Several studies of harbor porpoise have indicated on the basis of perception bias, that the probability of detecting a harbor porpoise on the trackline, \( g(0) \), is less than one (Barlow 1988; Calambokidis ). Using an independent team of three observers, Barlow (1988) reported an estimated 22% of harbor porpoise that surface on the trackline were missed by a team of five observers (perception bias) traveling on a vessel at 18.5 km/h. We assumed \( g(0) \) was one during our study because we were unable to determine availability or perception bias stratified by sea state due to low sample size. Total estimated abundance in the study area was estimated at 92 animals, although, it is probable that some porpoises did avoid the vessel, were submerged, and went undetected. Therefore, it is likely that harbor porpoise abundance in this study is underestimated. Our predicted monthly abundances estimates revealed peak harbor porpoise occurrence during summer months (June-September). This is consistent with previous reports, which have found the largest concentrations of harbor porpoise in summer and early fall in the northern San Juan Islands (Osborne et al. 1988).

Surveys from this study provide only a ‘snapshot’ of the distribution of harbor porpoise. Indeed, different study scales, both spatially and temporally may reveal species-environment relationships at different levels in a resource that is structured hierarchically in space, where small, high density patches are nested within large, low density patches (Wiens 1989, Embling 2008, Marubini et al. 2009).
To disentangle these processes that occur at different scales, more continuous intensive monitoring (of relatively long duration and frequent sampling periods) is required at a high spatial resolution. Acoustic methods could provide further insights into these patterns and would be particularly suited to often challenging ocean conditions in Oregon coastal waters. Although the direct applicability of our results is limited to harbor porpoises off the coastal waters of Oregon, we highlight that the incorporation of in situ measurements into habitat models can improve model accuracy at small spatial scales. Nonetheless, this study fills data gaps on the small scale drivers of harbor porpoise distribution in Oregon coastal waters and can be used as a baseline for potential impacts of present and future anthropogenic activities.

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**TABLES**

Table 1: Comparison of the approximate significance of smooth terms included in the final models built with remotely sensed and in situ data (p-values and total deviance explained).

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Remotely Sensed</th>
<th>In Situ</th>
</tr>
</thead>
<tbody>
<tr>
<td>x and y</td>
<td>0.02931</td>
<td>0.08045</td>
</tr>
<tr>
<td>Depth</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Distance to Rocky Reef</td>
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<td>0.01598</td>
</tr>
<tr>
<td>SST</td>
<td>0.00283</td>
<td>7.19E-05</td>
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<tr>
<td>Florescence</td>
<td>NA</td>
<td>-</td>
</tr>
<tr>
<td>Salinity</td>
<td>NA</td>
<td>0.00413</td>
</tr>
<tr>
<td>Deviance Explained</td>
<td><strong>12.40%</strong></td>
<td><strong>29.40%</strong></td>
</tr>
</tbody>
</table>
Figure 1: Map of the Oregon coast study area (inset, Oregon, USA) and visual survey effort. Black lines represent transect lines and gray shaded area show rocky reef.
Figure 2: Predicted abundance with 95% upper confidence level across study area from the remotely sensed model
Figure 3: Partial response plots from remotely sensed and *in situ* GAM models. Y axis shows probability of presence function to each smooth term. 95% confidence interval are represented by gray shaded area. Non-significant terms are not presented.
LITERATURE CITED


Baumgartner MF (1997) The distribution of Risso’s dolphin (Grampus griseus) with respect to the physiography of the northern Gulf of Mexico. Marine Mammal Science 13:614-638


CHAPTER 3: THE TIMES AND TIDES OF HARBOR PORPOISE (PHOCOENA PHOCOENA) OFF CENTRAL OREGON, USA

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Amanda K. Holdman¹, Joseph H. Haxel², Holger Klinck²,³, Leigh G. Torres¹

¹ Marine Mammal Institute, Department of Fisheries and Wildlife, Oregon State University, 2030 SE Marine Science Drive, Newport, Oregon 97365, USA

² NOAA Pacific Marine Environmental Laboratory, Cooperative institute for Marine Resources Studies, Oregon State University, 2030 SE Marine Science Drive, Newport, Oregon 97365, USA

³ Cornell Laboratory of Ornithology, Bioacoustics Research Program, Cornell University, 159 Sapsucker Woods Road, Ithaca, New York 14850, USA

*Corresponding author (Amandaholdman@gmail.com)

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ABSTRACT

Harbor porpoise (Phocoena phocoena) are commonly observed in Oregon’s nearshore habitat, yet knowledge of their preferred 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 porpoise off of 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 an offshore 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 nearshore reef 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 modulated by specific environmental conditions particular to each site that maximize foraging efficiency.
INTRODUCTION

In the face of increasing anthropogenic disturbance in coastal waters (Halpern et al. 2008, Maxwell et al. 2013), the marine environment is subject to a range of threats. Cetaceans are particularly vulnerable to incidental harm from human activities, such as fisheries, noise and chemical pollution, shipping, and habitat loss because they are noise sensitive and long-lived with low fecundity (Forney et al. 2000, Taylor 2002). These human activities vary in their spatial distribution across the seascape and in their intensity of impact on the ecological condition of cetacean populations. Cetaceans that live in near-shore, shallow water environments are particularly exposed to an array of anthropogenic impacts and often baseline information on the distributions of these species and how they use their coastal environment is limited. Furthermore, existing data for marine mammal distributions 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. Often cetacean distribution and habitat use at finer, site specific scales is more appropriate to answer management questions and capture relevant habitat heterogeneity (Wiens 1989, Tett et al. 2013).

High resolution spatial distribution for marine mammals can be obtained through aerial or boat based visual surveys, with considerable cost and effort (Evans & 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. However, cetaceans are only visible at the surface between 1 to 10% of the time (Tyack & Miller 2002), limiting the visual detection time of observers. Passive acoustic monitoring (PAM) provides an alternate survey technique that can be used to examine movement patterns and behavioral trends 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 and can be deployed at lower costs than visual surveys or mobile, towed acoustic arrays (Mellinger et al. 2007). Also, PAM allows for sub-surface detection, is non-invasive and unlikely to affect cetacean behavior, all the while providing information on animal presence and behavior at higher temporal resolutions.
In studying marine mammal distribution and foraging patterns, direct interactions of prey are often unobservable. In their absence, an indirect understanding of marine mammals and their prey can be beneficial. At fine temporal scales (< 1 day) 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. 2003a, Hastie et al. 2004, Wang et al. 2015). At fine spatial scales (1 to 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. Studies have shown that tidal currents over complex bathymetry acts to aggregate prey both vertically and horizontally (Zamon 2002, Hastie et al. 2004, Johnston et al. 2005), resulting in spatially and temporally predictable patchy prey distributions (Riley 1976) toward which marine predators are positively distributed. Preference by top predators for these short-lived yet predictable areas may go undocumented in large-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 anthropogenically induced 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 2013). Along the northwest coast of the USA, the marine environment off Oregon has seen increased potential for coastal development in recent years through marine energy, vessel traffic and fishing activities (Callaway 2007, Boehlert et al. 2008). The cumulative impacts of such activities pressures managers to make fine-scale management efforts to reduce harm to the marine environment. Consequently, there is a need to provide managers and stakeholders with local fine-scale population level information on species of concern within the management area. Although cryptic, harbor porpoise *Phocoena phocoena* are readily found along the Oregon coast and are a focal at-risk species that is highly sensitive to anthropogenic noise (Lucke et al. 2009, Tougaard et al. 2009, Tougaard et al. 2012, Dyndo et al. 2015, Tougaard et al. 2015). When exposed to various types of anthropogenic noise, harbor porpoise may experience temporary threshold shifts (Lucke et al. 2009) that can interrupt normal activities such as resting, feeding, or social interactions (Richardson & Würsig 1997) or they may exhibit spatial displacement (Culik et al. 2001, Teilmann et al. 2008, Tougaard et al. 2009).
Harbor porpoise along the west coast of North America are predominately observed in coastal waters less than 200 m deep (Balcomb & Minasian 1984), and two stocks are currently recognized in Oregon. Distinct seasonal changes in abundance along the west coast have been noted, with possible shifts in distribution to deeper offshore waters during late winter (Barlow et al. 1988), however, seasonal movement patterns are not fully understood. 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). 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 porpoise have high energy demands, due to their small body size and temperate water habitat, necessitating daily foraging to meet their basic energy requirements (Koopman 1998). Porpoises feed at a daily rate of ten percent of their body weight (Read & Gaskin 1985), thus restricting long distance travel and habitat range. Therefore, the distribution and movements of harbor porpoises are believed to be strongly connected to patches of prey aggregations (Sveegaard et al. 2012).

Studying the distribution patterns of harbor porpoise using visual methods has proven difficult due to their small size and negligible respiratory blow, and are difficult to observe when sea conditions deteriorate above a Beaufort Sea State 2 (Teilmann 2003). Additionally, harbor porpoise are shy natured and do not generally acquire markings on their dorsal fins (Koopman & Gaskin 1994), making photo identification studies impractical. However, harbor porpoise are highly vocal animals and are known to echolocate almost continuously (Villadsgaard et al. 2007, Kyhn et al. 2012) making acoustic surveys of porpoise activity based on their vocalizations often a more successful approach for distribution and behavioral observations than visual methods (Teilmann 2003, Kyhn et al. 2008).

In order to obtain fine-scale data on harbor porpoise presence and foraging patterns in coastal Oregon waters, passive acoustic monitoring devices were deployed at two sites using programmable digital acoustic monitoring instruments (DMON, Baumgartner et al. 2013). Unlike traditionally applied static acoustic recorders such as T-PODs™, or more recently C-PODs™ (by Chelonia Limited, UK) that employ an onboard, automated call detection approach, (Leeney et al. 2011, Wang et al. 2015), DMONs record full spectral wave forms within the high frequency vocal range of harbor porpoise. T-PODs and C-PODs devices do not archive passive acoustic data and are limited to the performance of the algorithm for
confirmation of species and behavior, while DMONs allows for confirmed classification of echolocation activity rather than relying on an odontocete classification algorithm and thus reduces the amount of false positive sequences. 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 (near shore reef vs offshore sandy bottom).

**MATERIALS AND METHODS**

**Brief description of harbor porpoise acoustics:** Harbor porpoise produce narrow band high frequency echolocation clicks with source levels (SL) ranging from 178 to 205 dB re 1 µPa peak-to-peak, a mean SL of 191 dB re 1 µPa p-p @ 1 m (Villadsgaard et al. 2007) with a peak frequency of 130 kHz (Møhl & Andersen 1973, Villadsgaard et al. 2007). Additionally, there is little energy below 100 kHz (Kyhn et al. 2012), enabling harbor porpoise clicks to be reliably discriminated from other odontocete signals, as well as most other transient sounds. Harbor porpoise produce echolocation for communicating, foraging and navigation and are known to emit specific click patterns for each (Verfuß et al. 2005, Verfuß et al. 2009, Clausen et al. 2011). Foraging trains can be separated into different phases based on the inter-click interval (ICI), with the search phase characterized by relatively stable ICIs around 50 ms and the terminal phase being marked by a sudden and rapid shortening of ICI to levels below 10 ms (Linnenschmidt et al. 2012). Click sequences with a 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).

**Study sites and instrument deployments:** DMONs were deployed at sites off of the central Oregon coast for a six month period from May 13th, 2014 to October 14th, 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 minute period) to conserve both battery power and memory storage space. The system has a noise floor 32 dB re µPa/VHz with a response sensitivity of -203 dB re V/µPa at 10 kHz. The DMON was mounted on a positively buoyant housing to keep it suspended 5 m from the seafloor along a mooring line attached to a surface buoy at two sites off the Oregon coast: (1) a reef site on the 30 m isobath in close proximity (< 50 m) to an offshore rocky reef, and (2) an offshore site 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. Deployment periods were approximately two weeks in duration, limited by DMON battery power and memory capacity.

**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, USA (Wiggins & Hildebrand 2007). The detection ranges for DMONs have not been investigated for harbor porpoise. However, estimates for similar devices such as the T-POD are a few hundred meters (Kyhn et al. 2012, Kyhn et al. 2008, Villadsgaard et al. 2007). All DMON data were analyzed at a temporal resolution of one minute, with each minute classified as 1 or 0 denoting the presence or absence of harbor porpoise echolocation click trains. Previous studies have used a group of clicks separated by 10 minutes to define a separate encounter (Carlstrom 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 <10ms 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 less that 10ms 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/D) for the reef site and offshore site. Due to duty cycling, a maximum number of 144 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 re-deployed. When devices were deployed at both the reef site and offshore site during the same time period, detections were compared to determine if porpoises were selecting between the two locations during certain environmental conditions or spending equal time at both sites.

Diel phase classification and analysis.
Harbor porpoise occurrence 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 US Naval Observatory (http://aa.usno.navy.mil). Definitions of diel phases were adapted from Carlstrom (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). The encounter rate per diel phase was calculated as the number of PPM in each diel phase divided by the mean duration of each diel phase across the study period multiplied by the number of recording days at each site. Since day, night and civil twilight vary with season, average durations of each diel phase across the study period were used in calculations. The binary classification of PPM and BPM was used to create a feeding buzz ratio (FBR), which was generated for each phase of each day by dividing the number of trains with MICIs of <10ms (BPM) by those with MICIs of >10ms (PPM), creating a ratio of possible feeding buzz trains to all other trains. FBRs were then averaged across all study days for each site. A high ratio suggests more time spent producing buzz trains and therefore possible feeding behavior. All train detections were non-uniformly distributed (Shapiro-Wilk, p-value = 2.2e-16). Therefore, non-parametric Kruskal-Wallis one way ANOVAs and their appropriate post hoc tests, corrected for multiple comparisons, were used to assess differences in FBR 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 ($\varphi(t)$) was compared with PPM and BPM at each site. Due to the complex nature of the mixed semi-diurnal tides and range of amplitudes experienced in the study areas (-0.179 to 2.934 meters, 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, by using the temporal signature of the tidal forcing afforded by the tidal phase parameter ($\phi_t$) we make a more direct comparison of the speed and direction of tidally influenced currents relative to harbor porpoise presence and behavior. Furthermore, the temporal dependency of the tidal phase parameter is
dominated by the principle lunar semi-diurnal constituent (M2), simplifying the calculation of the tidal phase \( \phi_t \) to the expression in equation 1.

\[
\omega t + C \equiv \varphi_t \pmod{2\pi}
\]  

(1)

\[
\omega = \frac{2\pi}{12.42 \text{ hours}}
\]  

(2)

The tidal phase parameter \( \phi_t \) is calculated as the time dependent \( 2\pi \) modulus of the radial frequency \( \omega \), eq. 2) of the tidal constituent M2 plus a constant phase delay C. The principle lunar semi-diurnal tidal constituent (M2), has a period of 12 hours and 25.2 minutes, exactly half a tidal lunar day, and C is the phase delay between the high tide hour and the start of the tidal phase time series at \( t = 0 \). This approach provides a direct link to dynamic physical processes relating tidally induced flow speed and direction within each habitat, not just the changes in hydrostatic water levels. Independence between moorings was assumed given the inter-mooring distance of >8km.

Using the circular statistics toolbox for MATLAB (Batschelet 1981, Berens 2009), PPM and BPM time series were analyzed with respect to the site specific, modeled mixed, semi-diurnal tidal cycle. 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. In addition, from the circular transformation of PPM and BPM times to tidal phases, we calculated the mean angle and used it to describe the distributions of PPM and BPM as a function of the tidal phase. To test whether the mean phase of PPM and BPM differed significantly at each site, we performed a parametric Watson-Williams multi-sample test for equal means (Zar 1984) with the null hypothesis being that the distribution of BPM and PPM are the same.

Temporal model. PPM and BPM were further analyzed and modelled 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 modelled 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 constitute. GAMs were generated in R package MGCV (Wood 2006), which contains integrated smoothness estimation. Non-linear interactions in the model structure were allowed in order to capture any changes in preferences for one covariate as a function of another covariate. Smooth functions for model covariates were specified using thin plate regression splines with shrinkage (Wood 2006). Interactions between covariates were modelled using tensor product (te) smooths. Hour of day was modelled 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 Criteria (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 six months deployment period: five at each site at a variable rate of one to two deployments per month (Table 1). Moored DMONs collected approximately 43 days of acoustic data at the reef site and 60 days at the offshore site. This effort included 35 days 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 accidently dragged by fisherman and later recovered; data analysis revealed harbor porpoise detections during the 3 days of that 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 days had at least one detection of a harbor porpoise encounter; two of those days were the final two days of the last deployment in October. 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 percent PPM detection. During the entire six month deployment period, a total of 13,248 monitored minutes of the combined 2 sites resulted in 3,473 (26%) PPM. In 27% (n=964) of all PPM, foraging behavior was detected as defined by an MICI < 10ms; this constitutes 7.2% of all analyzed minutes with buzz content.

Click train detection rates were higher at the reef site (n = 2057; 38%) compared to the offshore site (n = 1420; 18%) (Fig. 3). Relative foraging activity was also higher at the reef site where 30% of click trains were classified as buzzes (n=611) compared to 25% offshore (n=353) (Fig. 3).

DMONs were deployed at both the offshore site and the reef site during the same time periods for a total of 4,461 minutes, allowing for comparison between sites. Of the monitored minutes, 2,332 PPM and 796 BPM were recorded across both sites. During 78 percent (n=1811) of these co-monitored minutes, PPM occurred at either the offshore or the reef site, compared to 22 percent (n=521) when PPMs were detected at both sites simultaneously. Only 5% of BPM were simultaneously detected at both sites compared to 95% of asynchronous recordings at either the offshore site or the reef site. These results infer that this is the same population of porpoises moving between the different DMON deployment sites.

Diel patterns

The variation in the FBR showed significant difference across the four diel phases for both reef (Kruskal-Wallis ANOVA on ranks, $X^2(3) = 8.29, P = 0.04$) and offshore (Kruskal – Wallis ANOVA on ranks, $X^2(3) = 16.233, P = 0.001$) (Fig. 4). However, post hoc pairwise, multiple-comparison, Tukey method procedures revealed no significant difference between phases for the reef site. The significant Kruskal-Wallis test was likely due to a nearly significant difference between night and morning revealed by the Tukey test ($P = 0.054$). However, at the offshore site, the FBR during the evening was significantly lower than the FBR in the night ($P < 0.0001$) (Fig. 4).

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 maximum ebb flow (1.719 radians) (Fig. 5). 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. The two peaks for BPM at the reef site occurred at early and late ebb. At the reef site, the distribution of PPM and BPM significantly differed from each other relative to tidal phase associations with peak click and buzz train detection rates (pairwise Watson-Williams test, $P = 0.0010$).

**GAM modelling**

The final GAM with PPM as a binary response variable of 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. The final GAM for PPM at offshore site included the same variables as reef PPM except for the interaction between Julian day and tidal phase. Tidal phase was a significant temporal covariate for PPM at the offshore site, and similarly it was found to be nearly significant ($p = 0.054$) 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 PPM at reef and the offshore site, was 6.85% 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. 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 BPM at reef site and the offshore site was 13.7% and 13.2% respectively.

**DISCUSSION**

To our knowledge, our study provides the first insight towards the fine scale spatial and temporal patterns of habitat use by harbor porpoise off the central Oregon coast during the summer months. Our results conclude that this study area is an important habitat for harbor porpoise with almost daily presence at both sites. Feeding was detected in 27 percent of the
total encounters, additionally highlighting this area as a regular feeding spot. Overall, presence and foraging at the reef site was higher, and it is likely that this increased presence is due to prey availability. Yet, harbor porpoise foraging was also prevalent at the offshore site, and appears to be driven by diel patterns, unlike the reef site where foraging activity correlated with tidal phase. Harbor porpoise in this region appear to move between the two nearby study sites to exploit increased prey availability enhanced by fine-scale temporal patterns. The overall variation between the sites in the number of PPM and BPM in relation to cyclic temporal patterns suggests different levels of use and importance to these animals. Porpoises used the two sites differently, with their main period of activity at the two sites being influenced by different environmental forcing cycles, suggesting that harbor porpoise distribution can be highly heterogeneous at small spatiotemporal scales.

The location of these two deployment sites and their surrounding habitat may offer an explanation for this difference. 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. Whereas, the open water of the offshore site, tidal flows are much 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 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 flow. Previous studies show that tidal variables, such as tidal state, tidal speed, or tidal height have an important influence on both the distribution (Marubini et al. 2009, Jones et al. 2014, Benjamins et al. 2016) and behavior (Johnson 2005, Pierpoint 2008) of porpoises. However, the preferred tidal phase or speed appears to vary across areas. In agreement with our results, porpoises in Land’s End, Cornwall UK and south-west Wales, UK 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 (2014) suggested porpoises had adopted a foraging strategy of intercepting or ‘ambushing’ prey during ebb tide that was concentrated on coastal and benthic topography. Overall, it is likely that harbor porpoise select a range of current regimes and topography that enhance relative vorticity (Johnston et al. 2005) and thus provide a foraging resource that occurs at regular and predictable intervals governed by a tidal rhythm.

Meanwhile, harbor porpoise at the offshore site displayed increased feeding from sundown to sunrise. This is concurrent with other PAM studies which have reported that porpoises appear to shift their distribution, to different depths and/or habitats at night, perhaps to take advantage of changing prey availability (Carlstrom 2005, Todd et al. 2009). Furthermore, Brandt et al. (2010) found that water depth had a significant impact on porpoise diel rhythms, with more nocturnal porpoise echolocation activity occurring in deeper waters. 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 porpoise suggest active selection of habitat through tidal and diel mediated foraging intensity, likely due to maximizing their foraging opportunities. This is supported by the probability of a harbor porpoise feeding at the reef or the offshore site (95%) compared to when harbor porpoises are detected at both sites at the same time (5%). The small percentage of PPM and BPM at both sites at the same time suggests this is the same population of porpoises moving between the different foraging locations dependent on diel or tidal forced environmental conditions linked with prey availability at each site. Therefore, it appears that harbor porpoise in this region exhibit prey switching between the two monitored habitats as a function of times and tides. The high energetic demands and limited storage capacity of this species require them to spend a high proportion of their time foraging (Read & 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 & Read 1989) and feed on a diversity of both pelagic and demersal fish. Harbor porpoise in west coast waters are known to feed on juvenile rockfish, mackerel, sardines, squid, and shrimp but prefer schooling fishes such as Pacific herring, smelt walleye Pollock, and Pacific whiting (Leatherwood & 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 area are known to spend time near the surface in other areas, especially during the night (Cardinale et al. 2003), and could likely be the targeted prey offshore.

The gradual increase of detections in May and peak detections occurring between summer and fall observed in this study is consistent with the hypothesis that harbor porpoise move nearshore in relation to large scale temperature changes likely for increased 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 porpoise occur in summer and early fall, specifically September (Calambokidis & Barlow 1987, Barlow et al. 1988). However, our temporal coverage is limited and limits our ability to address this knowledge gap of winter distribution patterns.

Results indicate the presence and foraging behavior of harbor porpoise 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 cetaceans. Being able to view the full acoustic repertoire of high-frequency species removes biases associated with visual descriptions of behavior, ultimately facilitating comparisons of data between studies and across regions. However, recording at these high frequencies is technologically challenging with the accompanying increase in data storage requirements and power. While we were able to capture valuable behavioral information about harbor porpoise through detection of foraging events, 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. In the future, a recording device capable of capturing high frequency species repertoires and a long battery life is recommended so that year round presence of harbor porpoise 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 create effective spatially selected conservation and management strategies. This data set may serve as a starting baseline from which to identify critical habitats, 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 vital component in future conservation efforts.

Acknowledgments.
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TABLES

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

<table>
<thead>
<tr>
<th>Site</th>
<th>Coordinates</th>
<th>Deployment date</th>
<th>Recovery date</th>
<th>Deployment duration (days)</th>
<th>Recorded minutes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reef</td>
<td>44 35.140 N, 124 07.120 W</td>
<td>05.16.2014</td>
<td>05.23.2014</td>
<td>6d 20h 00m</td>
<td>985</td>
</tr>
<tr>
<td>Reef</td>
<td>44 35.121 N, 124 07.000 W</td>
<td>06.12.2014</td>
<td>06.20.2014</td>
<td>7d 21h 30m</td>
<td>1138</td>
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<tr>
<td>Reef</td>
<td>44 34.985 N, 124 07.117 W</td>
<td>06.26.2014</td>
<td>07.07.2014</td>
<td>10d 14 h 40m</td>
<td>1529</td>
</tr>
<tr>
<td>Predictor</td>
<td>Reef PPM</td>
<td>Reef BPM</td>
<td>Offshore PPM</td>
<td>Offshore BPM</td>
<td></td>
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<tr>
<td>--------------------------------------</td>
<td>------------</td>
<td>-----------</td>
<td>--------------</td>
<td>--------------</td>
<td></td>
</tr>
<tr>
<td>Julian Day</td>
<td>&lt; 2e-16</td>
<td>1.08E-06</td>
<td>1.14E-08</td>
<td>&lt; 2e-16</td>
<td></td>
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<tr>
<td>Diel Phase: Morning</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Day</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Evening</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Night</td>
<td>0.01</td>
<td></td>
<td>0.043</td>
<td>1.47E-06</td>
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<td>Tidal Phase</td>
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<td>Julian Day x Diel Phase: Morning</td>
<td></td>
<td></td>
<td></td>
<td>0.007</td>
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<td>Day</td>
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<td>0.035</td>
<td>&lt; 2e-16</td>
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<td>Evening</td>
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<tr>
<td>Night</td>
<td>1.29E-07</td>
<td>7.08E-05</td>
<td>&lt; 2e-16</td>
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<td>Julian Day X Tidal Phase</td>
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<td>Diel Phase X Tidal Phase</td>
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<tr>
<td>Deviance Explained</td>
<td>6.85%</td>
<td>13.70%</td>
<td>11.50%</td>
<td>13.20%</td>
<td></td>
</tr>
</tbody>
</table>
Figure 1: Bathymetric overview of study area in coastal Oregon (see inset) with acoustic instrumentation deployment sites displayed by the black dots.
Figure 2: Percent daily detection of harbor porpoise for the reef and offshore sites throughout the study period. The gray shaded areas represent data gaps between deployments.

Figure 3: Percent of click trains with MICIs greater than 10 ms (porpoise positive minutes, PPM) and the percent of click trains with MICI less than 10 ms (buzz positive minutes, BPM) for each site.
Figure 4: Feeding Buzz Ratios (FBRs) calculated as the number of trains with minimum inter-click-intervals (MICIs) of <10ms divided by the number of trains with intervals of >10ms, in each diel phase. The star symbols and brackets represent post hoc Tukey tests that gave significant results at the p < 0.05 level: Evening vs Night for the offshore site.
Figure 5: Distribution of harbor porpoise acoustic activity measured as (a) porpoise positive minute (PPM) and (b) buzz positive minute (BPM) as a function of the tidal cycle at the reef site. The length of the bars represents the binned presence of PPM or BPM during a given tidal phase.

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CHAPTER 4: GENERAL CONCLUSION

Robust data on the population size and distribution of cetaceans are required to support a wide range of management and conservation measures (Evans & Hammond 2004). Data on spatio-temporal patterns of the distribution of cetacean populations are often unavailable at the scales required to assess current management issues. In this study, I used visual and acoustic methods that provide complimentary data sets to build our knowledge of harbor porpoise presence, habitat use, and foraging behavior on the central Oregon coast. The combined acoustic and visual methods proved to be practical and cost effective for monitoring the distribution of harbor porpoise. Although the quantity and scale of data collected by each method differs, together, these databases fill gaps in our knowledge of harbor porpoise space use, particularly adding knowledge to their fine scale (< 1km, hours) occurrence patterns in coastal waters.

Both, visual line transects and static acoustic monitoring are well established methods of studying cetaceans (Evans & Hammond 2004, Bailey & Thompson 2009). Clearly both techniques have weaknesses as well as strengths: visual surveys provide wide spatial coverage, but are limited temporally as transects can only be conducted during daylight hours and passive acoustics provide high temporal coverage, but are limited spatially since they rely on animal’s echolocating in the vicinity of the devices to be detected. For cryptic species such as harbor porpoise, the likelihood of acoustic detection compared to visual detection is high as they have been shown to produce echolocation almost constantly, particularly when foraging (Akamatsu et al. 2007, Linnenschmidt et al. 2013). Visual survey are reliant on porpoises being visible at the surface, which is affected by sighting conditions as well as the length of time they are under the water, whereas, acoustics can detect subsurface species independent of an observer. Finally, visual surveys are often unfeasible due to adverse weather conditions which is common in Pacific Northwest waters, but PAM devices can be deployed in all weather conditions. The relative strengths and weaknesses of visual surveys and acoustic monitoring data are complementary and the integration of these approaches have provided robust data on the spatio-temporal patterns of harbor porpoise on the Oregon coast.
Harbor porpoise were detected across the entire study area and during all hours of the day, which suggest this area provides important habitat for harbor porpoise. Visual and acoustic survey detections were modelled with respect to a range of environmental and oceanographic data, which revealed a preference for specific topographic features, such as rocky reefs, and highly dynamic oceanographic conditions driven by tidal, diel, and seasonal cycles. While each method provided their own insights into harbor porpoise ecology, both approaches demonstrated how dynamic harbor porpoise distribution are in relation to fine scale spatial and temporal drivers. Furthermore, a few patterns emerged consistently in both methods. Both visual transect surveys and acoustic surveys revealed a similar summer seasonal pattern of harbor porpoise abundance with a distinctive increase in detection in June to September, and then decreases in the fall. This period corresponds with the harbor porpoise breeding and birthing periods (Barlow et al. 1988), and this habitat could provide necessary resources in this energetically demanding stage. Overall, the consistent preference for rocky reef in both analysis emphasizes the importance of this static oceanographic feature for porpoises.

Additional data may be required to assess the potential impacts of proposals for new human activities within the area, and to advise on mitigation of the impact of such development. Given the findings from this study, it could be valuable to cross examine results from one method with the other. For example, while visual surveys are already limited to daylight hours, it could be advantageous to standardize transects against tidal cycle. Additionally or alternatively, acoustic monitoring devices could be equipped with in situ oceanographic measuring devices to allow for better correlative analysis of occurrence with environmental conditions.

Finally, future work should aim to achieve year-round representative coverage of the Oregon coast and surrounding areas so that broad scale survey data can be integrated with more detailed work in areas of particular interest of concern (Hastie et al. 2003). Visual surveys for cetaceans during the winter months is inherently difficult due to rough seas and short days, therefore, methods may be limited to PAM during this time. Recent developments have made it possible to measure temporal and spatial distribution of high frequency marine mammals with PAM techniques, but current devices have limited battery life and require frequent servicing. A device capable of monitoring high frequency species for an extended period of time could help to inform data gaps on how harbor porpoise use this area over winter.
In summary, the results presented here help to fill one of the key information gaps hindering assessment of the impact of coastal development to harbor porpoise populations in Oregon. There now exists baseline estimates of harbor porpoise abundance and habitat patterns off the coast of Newport, Oregon that can serve as a reference point for the future and upon which a framework for management and monitoring can be founded.

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