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Developing a passive acoustic monitoring network for harbor porpoise in California

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Developing a passive acoustic monitoring network for harbor porpoise in California

A dissertation submitted in partial satisfaction of the
requirements for the degree
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in

Oceanography

by

Eiren Kate Jacobson

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2017

The dissertation of Eiren Kate Jacobson is approved, and it is acceptable in quality and form for publication on microfilm and electronically:

Co-Chair

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University of California, San Diego

2017

DEDICATION

To Dr. Easter Ellen Cupp (1904-1999) who was the first American woman to receive a doctorate in Oceanography.

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Chapter 3, in full, is a reprint of material as it appears in a NOAA Technical Memorandum: Jacobson, E. K., K. P. B. Merkens, K. A. Forney, and J. Barlow, 2017, NOAA-TM-NMFS-SWFSC-583. The dissertation author was the primary investigator and author of this paper.

Chapter 4, in full, is a reprint of material as it appears in the Journal of the Acoustical Society of America: Jacobson, E. K., K. A. Forney, and J. Barlow, 2017, volume 141, pages 219-230. The dissertation author was the primary investigator and author of this paper.

Chapter 5, in full, is currently in preparation for submission for publication and is printed here with the permission of co-authors K. A. Forney and J. Barlow. The dissertation author was the primary investigator and author of this paper.

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Jacobson, E. K., K. A. Forney, and J. Barlow. *In Prep.* PAMPower: Investigating the statistical power of passive acoustic monitoring networks to detect trends in cetacean abundance.

ABSTRACT OF THE DISSERTATION

Developing a passive acoustic monitoring network for harbor porpoise in California

by

Eiren Kate Jacobson

Doctor of Philosophy in Oceanography

University of California, San Diego, 2017

Jay Barlow, Co-Chair
Peter J. S. Franks, Co-Chair

Assessing the abundance of and trends in whale, dolphin, and porpoise (cetacean) populations using traditional visual methods can be challenging due primarily to their limited availability at the surface of the ocean. As a result, researchers are increasingly interested in incorporating non-visual and remote observations to improve cetacean population assessments. Passive acoustic monitoring (PAM) can complement or replace visual surveys for cetaceans that produce echolocation clicks, whistles, and other vocalizations. My doctoral dissertation is focused on developing methods to improve PAM of cetaceans. I used the Monterey Bay population of harbor porpoise (*Phocoena phocoena*) as a case study for methods development. In Chapter 2, I used passive acoustic data to document that harbor porpoises avoid bottlenose dolphins (*Tursiops truncatus*) in nearshore Monterey Bay. In Chapter 3, I investigated whether different passive acoustic instruments could be used to monitor harbor porpoise. I recorded harbor porpoise echolocation clicks simultaneously on two different passive acoustic instruments and compared the number and peak frequency of echolocation signals recorded on the two instruments. I found that the number of echolocation clicks was highly correlated between instruments but that the peak frequency of echolocation clicks was not well-correlated, suggesting that some instruments may not be capable of discriminating harbor porpoise echolocation clicks in regions where multiple species with similar echolocation signals are present. In Chapter 4, I used paired visual and passive acoustic surveys to estimate the effective detection area of the passive acoustic sensors in a Bayesian framework. This approach resulted in a posterior distribution of the effective detection area that was consistent with previously published values. In Chapter 5, I used aerial survey and passive acoustic data in a simulation framework to investigate the statistical power of different passive acoustic network designs and hypothetical changes in harbor porpoise abundance. As a whole, this dissertation used an applied approach to methods development to advance the use of PAM for cetaceans.

Chapter 1

Introduction

Preface

Here, I provide background information on cetacean population assessment, passive acoustic monitoring, and the case study population used in this dissertation. After outlining the objectives of the dissertation, I summarize the individual chapters of the dissertation. Each of the following chapters of this dissertation has been prepared as a standalone unit for publication. Therefore, information provided in the introduction and methods sections may be repeated across chapters. The summaries provided here are modified from the abstracts of each chapter.

Marine mammal abundance estimation

Marine mammal abundance is monitored to identify species of concern, to evaluate the success of conservation actions, and to calculate allowable removal of or incidental harm to individuals. It has also been suggested that marine mammals can serve as sentinels for ecosystem health and change (Moore, 2008). In practice, the U.S. Marine Mammal Protection Act (2008) requires federal agencies to prepare stock assessment reports, including a minimum population estimate, for all marine mammals found in U.S. waters. In general, marine mammal populations that spend time on or near land are better assessed than pelagic populations (Taylor et al., 2007). In some cases, currently or historically exploited populations are better assessed than unexploited populations, due to economic and management interests in accurate population estimation (Brownell Jr et al., 1989).

Because it is rarely possible to count all of the individuals within a population, statistical methods for estimating population size have been developed (Seber, 1982; Borchers et al., 2002). Typically, abundance estimation methods involve counting a portion of the population and using known or assumed population parameters to estimate the total population size. Methods for abundance estimation include distance sampling, mark-recapture, and harvest models (Buckland et al., 2000). These methods of abundance estimation have traditionally relied on visual observations of the species of interest. The abundance of marine mammal populations is particularly difficult to estimate because these animals spend much of their time underwater. In addition, inclement weather, poor visibility, and the logistical difficulty of surveying large sections of the ocean can impede the collection of visual survey data. Passive acoustic monitoring (PAM) is a promising alternative technology for the study of cetaceans (whales, dolphins, and porpoises) that produce distinctive vocalizations. PAM relies on passive listening to record the vocalizations of cetaceans and can be conducted in poor weather, at night, and under other circumstances where traditional visual observations are not possible (Marques et al., 2013).

Passive acoustic monitoring of harbor porpoise

Because harbor porpoise produce distinctive echolocation signals, they can be monitored using PAM. Harbor porpoises produce narrow-band, high-frequency clicks that are used primarily for foraging and navigation, though there is some evidence that they are also used for intraspecies communication (Clausen et al., 2011). These clicks are characterized by peak frequencies around 135 kHz, source levels around 175 dB re. 1 μPa, durations ranging from 50 to 125 usec, and -3 dB bandwidths from 6 to 26 kHz (Kyhn et al., 2013; Villadsgaard et al., 2007; Au et al., 1999; Madsen et al., 2005) and are extremely directional (Koblitz et al., 2012). Because of these click characteristics, harbor porpoises have an acoustically active radius of approximately 50-100 m for echolocation and 50-1000 m for communication (DeRuiter et al., 2010).

Due to the high frequency and rapid attenuation of their echolocation signals, monitoring harbor porpoise using traditional fixed passive acoustic systems with full-bandwidth recordings is prohibitively expensive. Chelonia Ltd. developed an automated click detector (the T-POD) to fill the demand for a cost-effective and easy-to-operate device for the passive acoustic monitoring of harbor porpoises. The T-POD and its successor the C-POD detect individual echolocation clicks and store digital summary information about each click. No waveform data are collected, and therefore data storage demands are low and long-term deployment (3-6 mo.) is possible. In post-processing, clicks are classified as belonging to NBHF echolocation trains using characteristics including the peak frequency and duration of clicks along with the inter-click interval (ICI). Since the introduction of the T-POD, this device and its successor the C-POD have been used to document harbor porpoise responses to anthropogenic disturbance (e.g., Teilmann and Carstensen, 2012) and to assess the abundance of harbor porpoise populations in Europe (e.g., Gallus et al., 2012).

To estimate animal density using data from a passive acoustic sensor, ancillary information is needed to convert the number of echolocation signals to a density of animals (Marques et al., 2009). Parameters needed include the echolocation rate of individual animals (a cue production rate), the proportion of false positives detected by the sensor, and the probability of detecting echolocation signals produced at varying distances from the sensor (a detection function). Obtaining these values can be difficult and time consuming, and estimates of cue production rates and detection functions are often imprecise due to variability in animal behavior, oceanographic properties, and sensor sensitivity. Currently, developing experimental and statistical methods for determining these parameters is an area of active research.

Harbor porpoise in Monterey Bay, California

For this dissertation project, I used the Monterey Bay population of harbor porpoise as a case study for the development of PAM methods. The harbor porpoise is a small coastal odontocete found in shallow waters of the temperate Northern hemisphere. The Monterey Bay population of harbor porpoise is relatively well studied and is accessible via boat or airplane from regional harbors and airports. This population of harbor porpoise occupies a nearshore area approximately 0-150 m deep and 2,500 km^2 in size and consists of approximately 3,700 individuals (Forney et al., 2014). The Monterey Bay population is distinct from other harbor porpoise populations along the U.S. West Coast (Calambokidis and Barlow, 1991; Chivers et al., 2002).

Since the late 1980s, the Monterey Bay population of harbor porpoise has been monitored using line-transect aerial surveys (Forney et al., 1991). Additionally, since 2000, line-transect aerial surveys targeting leatherback sea turtles have been conducted in the region using the same survey methodology, thereby also collecting data on cetaceans including harbor porpoise.

While fishery mortality is currently insignificant for this population (Carretta et al., 2015) the population is likely still recovering from bycatch in set gillnet fisheries for halibut that operated in the late-20th century (Jefferson et al., 1994; Forney et al., 2014) and earlier gillnet fisheries for white seabass (Barlow and Hanan, 1995). There have also been some deaths over the past decade due to bottlenose dolphin *(Tursiops truncatus)* attacks on harbor porpoise in this region (Cotter et al., 2012; Wilkin et al., 2012).

Summary of the dissertation

In this dissertation, I advanced methods for monitoring harbor porpoise in California using passive acoustics. The main objectives of this project were to:

1. Demonstrate the feasibility of installing passive acoustic sensors in the nearshore environment of California (Ch. 2, Ch. 3, Ch. 4)
2. Evaluate the ability of different passive acoustic sensors to accurately detect and measure properties of harbor porpoise echolocation clicks (Ch. 3)
3. Develop statistical methods for estimating the absolute density of harbor porpoise from passive acoustic data (Ch. 4)

4. Investigate the statistical power of different passive acoustic monitoring network designs to detect hypothetical changes in harbor porpoise abundance (Ch. 5)

Chapter 2

In Chapter 2, I used passive acoustic data to document that harbor porpoises avoid bottlenose dolphins (*Tursiops truncatus*) in nearshore Monterey Bay. In California and in other regions where harbor porpoises and bottlenose dolphins overlap in distribution, bottlenose dolphins have been observed attacking harbor porpoises. In this study, I investigated whether passive acoustic monitoring could be used to document nearshore habitat use of harbor porpoises and bottlenose dolphins in Monterey Bay, California. In particular, I was interested in whether this documented conflict between bottlenose dolphins and harbor porpoises affected harbor porpoise behavior within the nearshore environment, where habitat overlap occurs with bottlenose dolphins. I expected to find lower densities of harbor porpoises when bottlenose dolphins were present than when they were absent. To quantify the presence of harbor porpoises and bottlenose dolphins in the nearshore environment, I used data from a moored click detector (C-POD, Chelonia Ltd.) that we deployed at a single nearshore study site in northern Monterey Bay within a few kilometers of the sites where bottlenose dolphin attacks on harbor porpoises were observed in previous years. I found that when bottlenose dolphins are present, harbor porpoise acoustic activity is reduced by 52% at relatively low temperatures (during late fall and early winter) and by 82% at higher temperatures (during late summer and early fall) compared to when bottlenose dolphins are absent. I hypothesize that harbor porpoises passively detect bottlenose dolphin vocalizations and respond by reducing vocalization rates or by leaving the nearshore area, possibly resulting in reduced fitness due to exclusion from nearshore habitats.

Chapter 3

In Chapter 3, I investigated whether different passive acoustic instruments could be used to monitor harbor porpoise. Several sympatric species of cetaceans produce narrow-band, high-frequency (NBHF) echolocation clicks which are difficult to distinguish. On the U.S. West Coast, Dall's porpoise *(Phocoenoides dalli)* and harbor porpoise emit NBHF echolocation clicks and overlap in distribution. To determine whether different passive acoustic instruments could be used to monitor harbor porpoise in this region, I recorded harbor porpoise echolocation clicks simultaneously on an autonomous hydrophone recording system (SoundTrap, Ocean Instruments New Zealand) and on a commonly used passive acoustic monitoring device (C-POD, Chelonia Ltd., UK). I investigated whether the number and peak frequency of recorded echolocation clicks were consistent between the two instruments. I found that while the number of echolocation clicks recorded by the two instruments was highly correlated, the C-POD and SoundTrap measurements of the peak frequency of echolocation signals were not well-correlated. This suggests that while both instruments are capable of detecting harbor porpoise echolocation clicks, it may not be feasible to use C-PODs to discriminate harbor porpoise echolocation clicks in regions where multiple species with NBHF echolocation clicks are present. The use of calibrated hydrophones with full-bandwidth recording instruments may be required for this task.

Chapter 4

In Chapter 4, I used paired visual and passive acoustic surveys to estimate the effective detection area of the passive acoustic sensors in a Bayesian framework. Before passive acoustic monitoring can be implemented to estimate harbor porpoise abundance, information about the detectability of harbor porpoise is needed to convert recorded numbers of echolocation clicks to harbor porpoise densities. In this study, I used paired data from a grid of nine passive acoustic click detectors (C-PODs, Chelonia Ltd., United Kingdom) and three days of simultaneous aerial line-transect visual surveys in Monterey Bay. The focus of the study was estimating the effective detection area of the passive acoustic sensors, which was defined as the product of the sound production rate of individual animals and the area within which those sounds are detected by the passive acoustic sensors. Visually estimated porpoise densities were used as informative priors in a Bayesian model to solve for the effective detection area for individual harbor porpoises. This model-based approach resulted in a posterior distribution of the effective detection area of individual harbor porpoises consistent with previously published values. I concluded that this technique is a viable alternative for estimating the effective detection area of passive acoustic sensors when other experimental approaches are not feasible.

Chapter 5

In Chapter 5, I used aerial survey and passive acoustic data from Monterey Bay in a simulation framework to investigate the statistical power of different passive acoustic network designs to detect hypothetical changes in harbor porpoise abundance. I used aerial survey and passive acoustic data collected in Monterey Bay to simulate datasets for hypothetical passive acoustic monitoring network designs and changes in harbor porpoise abundance. I considered the number and geographic placement of sensors and scenarios of overall population decline as well as range contraction to a core habitat area. When the population declined uniformly over its geographic range, the placement of sensors did not impact power to detect a trend in abundance. However, scenarios in which animals contracted to core, high-quality habitat resulted in lower power to detect trends in abundance. This simulation study demonstrated that the effectiveness of PAM varies greatly depending on both survey design (number and placement of sensors) and manifestation of the change in the population (extent and spatial pattern of increase or decrease). When planning passive acoustic surveys, it will be important to consider different possible population responses so that power can be accurately assessed and an appropriate number and placement of sensors employed. While this simulation study was specific to the Monterey Bay population of harbor porpoise and employed a specific type of passive acoustic sensor, the results are generalizable to other regions, species, and types of passive acoustic surveys.

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Chapter 2

Acoustic evidence that harbor porpoises *(Phocoena phocoena)* avoid bottlenose dolphins *(Tursiops truncatus)*

Marine Mammal Science

Notes

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Acoustic evidence that harbor porpoises (*Phocoena phocoena*) avoid bottlenose dolphins (*Tursiops truncatus*)

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Along the West Coast of the United States, harbor porpoises (*Phocoena phocoena*) and coastal common bottlenose dolphins (*Tursiops truncatus*) overlap in distribution from Point Conception to San Francisco Bay in a narrow coastal band (Wells *et al.* 1990; Hansen and Defran 1993; Carretta *et al.* 1998, 2001). This overlap is relatively recent. Increased water temperatures in California during the 1982–1983 El Niño event prompted a northward range expansion of coastal bottlenose dolphins past Point Conception into central California (Hansen 1990, Wells *et al.* 1990). Harbor porpoises occur in distinct populations along the California coast (Calambokidis and Barlow 1991, Chivers *et al.* 2002, Carretta *et al.* 2009), whereas coastal bottlenose dolphins move throughout their range and comprise a single population (Defran *et al.* 1999, Hwang *et al.* 2014).

In California and in other regions where these species overlap, interspecies aggression has been observed (Ross and Wilson 1996, Dunn *et al.* 2002, Cotter *et al.* 2012). Between 1991 and 1993 in Moray Firth, Scotland, blunt force trauma associated with bottlenose dolphin attacks was the largest contributor to stranded harbor porpoise mortality (Ross and Wilson 1996). Bottlenose dolphin attacks on harbor porpoises have also been documented in Cardigan Bay, Wales (Jepson and Baker 1998) and in Monterey Bay, California (Cotter *et al.* 2012, Wilkin *et al.* 2012). The first documented stranding of a harbor porpoise killed by bottlenose dolphins in California occurred in July 2005. Between 2007 and 2009 researchers witnessed three bottlenose dolphin attacks on harbor porpoises in Monterey Bay (Cotter *et al.* 2012). These attacks involved 23 individual bottlenose dolphins, 21 of which were known

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to be males. Observed attacks occurred in the late summer and early fall, during the possible breeding season for bottlenose dolphins.

In Monterey and Santa Cruz counties between 2005 and 2011, 179 harbor porpoise strandings were documented. Of these, 43 of 68 stranded porpoises in which cause of death could be determined presented signs of blunt force trauma, at least 28 of which were consistent with attacks by bottlenose dolphins.[2] In California between 1998 and 2010, 54 of 216 stranded porpoises in which cause of death was determined presented signs of blunt force trauma consistent with attacks by bottlenose dolphins (Wilkin *et al.* 2012). In 2007 an apparent increase in harbor porpoise strandings in central California triggered the declaration of an Unusual Mortality Event (UME) and the stranding rate was more than twice the mean annual rate of the previous decade during 2008 and 2009. During this time, stranding rates were highest from June to November and blunt force trauma was the most common diagnosed cause of death (Wilkin *et al.* 2012). Taken together, the findings from California suggest that in this region a relatively sudden onset of aggression towards harbor porpoise was executed by a few male bottlenose dolphins.

Hypothesized drivers for bottlenose dolphin attacks on harbor porpoise can be broadly divided into ecological and behavioral explanations (Ross and Wilson 1996, Cotter *et al.* 2012). Possible ecological drivers include prey competition and feeding interference, whereas possible behavioral drivers include object-oriented play to practice fighting or infanticidal behaviors, with high levels of testosterone and a skewed sex ratio perhaps contributing to heightened aggression in male bottlenose dolphins (Ross and Wilson 1996, Cotter *et al.* 2012).

All of the proposed ecological explanations hinge on some form of competition for resources, for which evidence in California is weak. Spitz *et al*. (2006) reported qualitative similarities in diet composition of bottlenose dolphins and harbor porpoise in the Bay of Biscay, but quantitative examination found strong evidence that diet profiles were distinct between these two species. There has been no comprehensive comparative study of the diets of bottlenose dolphins and harbor porpoise on the U.S. West Coast (Cotter *et al.* 2012). The most relevant available data indicate that bottlenose dolphins in California feed primarily on surfperches (family *Embiotocidae*) and croakers (family *Sciaenidae*; Defran *et al.* 1999 and references therein), whereas harbor porpoises in this region feed mainly on market squid (*Doryteuthis opalescens*) and small forage fish (Cotter *et al.* 2012 and references therein). Harbor porpoise stomachs collected from stranded animals in Monterey Bay contained primarily northern anchovy (*Engraulis mordax*), spotted cusk-eel (*Chilara taylori*), rockfish (family *Sebastes*), and market squid (Dorfman 1990, Sekiguchi 1995, Byrd 2001). More recent analyses of stranded animals in central California confirmed northern anchovy, market squid, and sardine (*Sardinops sagax*) as harbor porpoise prey items.[3] Although not conclusive, these data indicate that harbor porpoise are generalists and may have seasonal or interannual variation in preferred prey types. The limited evidence for dietary overlap in combination with known differences in depth distributions for these two species indicate that competition for resources is an improbable explanation for the observed bottlenose dolphin aggression in California.

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The prevailing hypothesis for bottlenose dolphin aggression towards harbor porpoises is that it is either a misdirection of infanticidal tendencies or a way of developing infanticidal behaviors (Patterson *et al*. 1998, Kaplan *et al.* 2009, Cotter *et al.* 2012). In Moray Firth, Scotland, stranded bottlenose dolphin calves presented internal and external injuries consistent with infanticide (Patterson *et al.* 1998) at the same time that harbor porpoise strandings were dominated by dolphin-inflicted blunt force trauma (Ross and Wilson 1996). Infanticide also has been observed in bottlenose dolphins in Virginia (Dunn *et al.* 2002) and Florida (Kaplan *et al.* 2009). It is likely that infanticidal behavior was previously observed in bottlenose dolphins but was documented by researchers as play rather than aggression (Dunn *et al.* 2002). In some of these instances, attacked individuals of both species have been similarly sized (100–150 cm; Ross and Wilson 1996, Patterson *et al*. 1998, Dunn *et al*. 2002). This link with infanticide is supported by some observations that aggressors are males (Kaplan *et al.* 2009, Cotter *et al.* 2012) who may use infanticide as a strategy to gain reproductive access to females (Kaplan *et al.* 2009). In California 92% of bottlenose dolphin aggressors in observed attacks were known or putative males, and there was 40% overlap in bottlenose dolphin identity between attacks (Cotter *et al.* 2012). However, there may be other explanations for the observed interspecies aggression since not all stranded harbor porpoises with dolphin-inflicted injuries fall within this size range (Wilkin *et al.* 2012), bottlenose dolphins have been observed attacking other delphinids (*e.g.*, Barnett *et al.* 2009), and infanticide has never been documented in bottlenose dolphins in California (Cotter *et al.* 2012).

In the present study, we investigated whether this documented conflict between bottlenose dolphins and harbor porpoises in California affected harbor porpoise behavior within the nearshore environment where habitat overlap occurs with bottlenose dolphins. We expected to find lower densities of harbor porpoises when bottlenose dolphins were present than when they were absent.

We used data from moored click detectors (C-PODs; Chelonia Ltd., http://www.chelonia.co.uk) which were deployed at a study site in Monterey Bay (Fig. 1) to quantify the relative presence of harbor porpoises as well as bottlenose dolphins. These data were collected as part of a separate study but provided an opportunity to examine the acoustic behavior of both species within a few kilometers of the sites where bottlenose dolphin attacks on harbor porpoises were observed by Cotter *et al*. (2012) in previous years. Our instruments were moored in Monterey Bay at 36°52′53″N, 121°50′31″W approximately 15 m deep and 6 m above the sea floor. We used a mooring design that required diver installation and retrieval but allowed C-PODs to be serviced by hand from a small boat. Our C-POD installation was active from 7 October to 30 December 2011, for a total of 2,016 one-hour sample periods. On 1 November we serviced the mooring and exchanged C-PODs.

C-PODs have been used in a variety of acoustic monitoring applications (*e.g.*, Gallus *et al.* 2012, Teilmann and Carstensen 2012, Benke *et al.* 2014). C-PODs record narrow-band high-frequency (120–140 kHz) porpoise echolocation clicks and mid-frequency (30–60 kHz) dolphin echolocation clicks. C-PODs detect and record only echolocation signals; therefore we have no information about other odontocete vocalizations, including whistles. Summary information for each echolocation signal detected is stored on a flash memory card. In postprocessing, the data were extracted using the C-POD software v. 2.024 and signal detections were classified into echolocation click trains using a manufacturer-supplied KERNO classifier (Tregenza 2012). The KERNO classifier identifies trains based on similarity of successive interclick intervals and the coherence of click parameters including peak frequency and

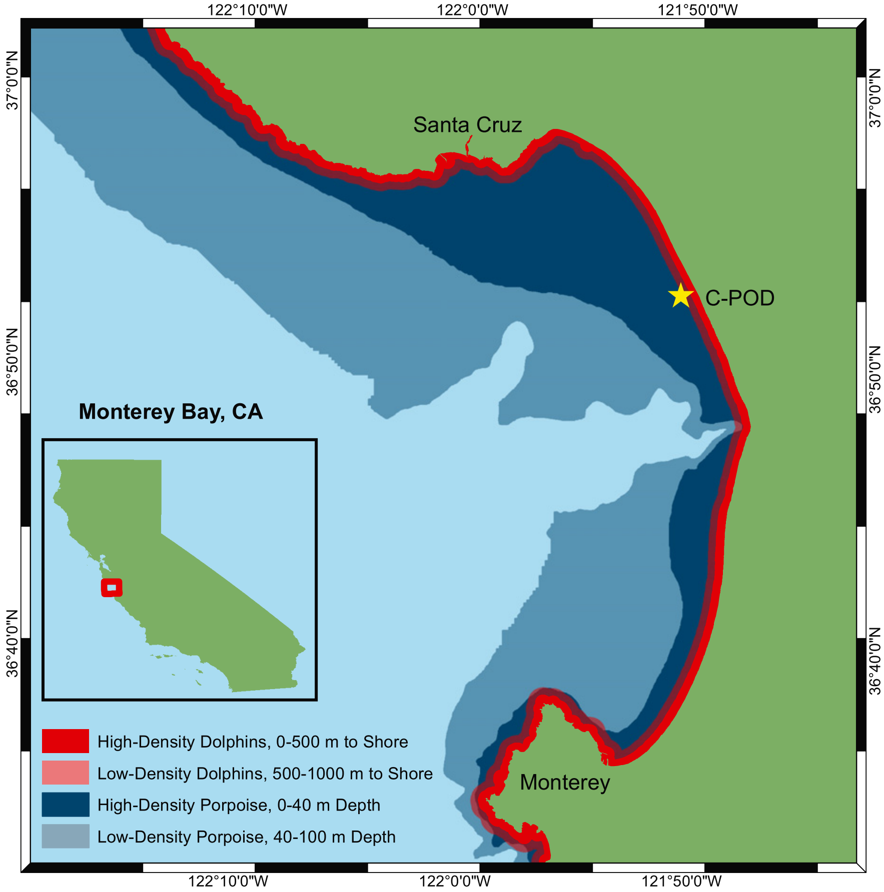

Figure 1. Study site in Monterey Bay, California. The yellow star indicates the position of the C-POD mooring. The approximate distribution of bottlenose dolphins is indicated in red (dark red: high density, 0–500 m from shore; light red: low density, 500–1,000 m from shore). The approximate distribution of harbor porpoises is indicated in blue (dark blue: high density, 0–40 m depth; medium blue: low density, 40–100 m depth).

duration. The inclusion of inter-click interval as a detection criterion reduces the false positive error rate since high-frequency noise from sediment or surf conditions is not patterned like cetacean click trains. For our analyses, we filtered the data to include only the highest quality echolocation click trains.

We used acoustic data exclusively to quantify harbor porpoise and bottlenose dolphin presence in the study area. At our study location, bottlenose dolphins and harbor porpoises are the only commonly encountered odontocetes. To confirm species identifications, we used data collected during six days of cliff-top observations and six days of aerial line-transect surveys that were conducted as part of a separate study. During both of these visual surveys we observed harbor porpoises and bottlenose dolphins in the vicinity of the C-POD and did not observe any other odontocetes. Therefore, we have attributed all narrow-band high-frequency click trains to harbor porpoise and all mid-frequency click trains to bottlenose dolphins. The maximum detection range of a C-POD for harbor porpoise is approximately 400 m, whereas bottlenose dolphins may be detected from more than 1,000 m (Chelonia Ltd. 2012).

Since the number of echolocation click trains increases nonlinearly with harbor porpoise density, we used a relative rather than absolute metric of echolocation activity. Before analysis, echolocation click trains were binned into one-hour periods. We chose hour-long sampling periods to reduce autocorrelation in the data set while also preserving the signal of bottlenose dolphin encounters, which occur on timescales of one to a few hours. Echolocation click trains were reported as either a Proportion of Positive Minutes (PPM) or as a count of positive minutes in each hour. A positive minute was defined as containing at least one echolocation click train. Additionally, in some analyses bottlenose dolphins were counted simply as absent or present for each hour. The C-PODs also recorded *in situ* temperature measurements every minute, which were averaged for each hour period. Because our instruments were moored successively rather than in tandem, we are unable to quantify possible instrumental differences in sensitivity. However, our chosen metric of PPM is robust to variation in instrumental sensitivity (Benke *et al.* 2014).

To validate our data set, we randomly selected a subsample of 1,000 min for manual confirmation. We calculated a false positive error rate for harbor porpoise positive minutes of 4% and a false positive error rate for bottlenose dolphin positive minutes of 0%. The false negative error rate is likely high for both species, however, for our application it is preferable to avoid false detections in the data set at the potential expense of missed detections.

Preliminary examination of the data indicated a negative relationship between harbor porpoise presence and bottlenose dolphin presence. To explore this relationship, we examined changes in harbor porpoise PPM during discrete encounters with bottlenose dolphins using a boxplot (Fig. 2). Encounters were defined as single or consecutive hours with bottlenose dolphins present. We collated one- (n = 65), two- (n = 28), and three-hour (n = 7) bottlenose dolphin encounters and calculated harbor porpoise vocal activity before (T0), during (T1–T3), and after (T2–T4) these encounters. Qualitatively, we found that harbor porpoise acoustic presence at our study site decreased during bottlenose dolphin encounters. We performed a randomization test (Efron and Tibshirani 1993) to examine whether this observed pattern of lower mean harbor porpoise PPM when bottlenose dolphins were present (mean PPM = 0.06) compared with when they were absent (mean PPM = 0.18) could have occurred by chance (Fig. 3). This was accomplished by shifting the record of bottlenose dolphin presence to a new, randomly generated starting time and recalculating the mean harbor porpoise PPM when bottlenose dolphins were artificially present. We repeated this process 10,000 times to produce the distribution shown in Figure 3. Our randomization procedure was designed to preserve autocorrelation in the original time series. The randomization test results indicated that the observed harbor porpoise mean PPM was significantly less when bottlenose dolphins were present compared with the distribution of values expected by chance alone (P = 0.0002) thus the observed pattern was extremely unlikely to have occurred by chance.

Possible explanations for the observed decrease at our study site include niche partitioning (*i.e.*, habitat characteristics drive changes in species presence) and avoidance behavior (*i.e.*, harbor porpoises avoid potential aggression by bottlenose dolphins by either changing their distribution or their acoustic behavior).

Harbor porpoise and bottlenose dolphins have little diet overlap and different depth distributions, supporting a lack of competition for resources, and have

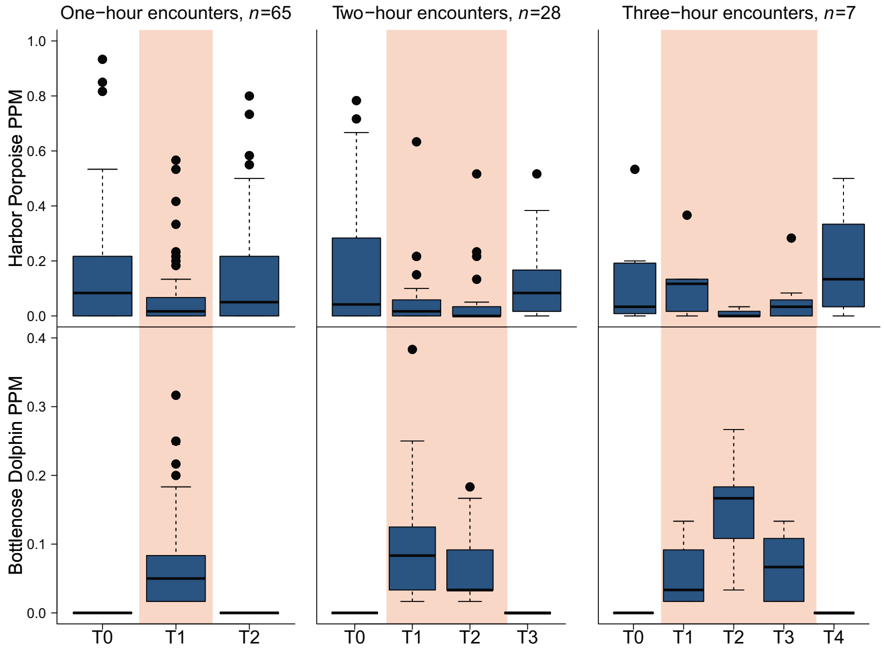

Figure 2. Box-and-whisker plots illustrating changes in the Positive Minutes (PPM) per hour for harbor porpoise (top panels) and bottlenose dolphins (bottom panels) before, during, and after all one-, two-, and three-hour bottlenose dolphin encounters in Monterey Bay. The black horizontal line indicates the median PPM value in each time period, while the blue shaded region represents the range between the first and third quartiles. The dashed lines show the range of the minimum and maximum values and the dots are outlier points that are more than 1.5 times the interquartile range beyond the first and third quartiles. T1 represents the onset of bottlenose dolphin presence and the red shaded regions indicate hours when bottlenose dolphins were present. At T0 and at the final period in each plot (T2, T3, or T4, depending on length of encounter), bottlenose dolphins were absent. Qualitatively, harbor porpoise PPM decreases when bottlenose dolphins are present and increases after they depart.

fundamentally different ecological niches. Best available data indicate that suitable habitat for both species is defined primarily in terms of depth, proximity to shore, and temperature (Fig. 1; Barlow 1988, Forney 1999, Carretta *et al.* 2001). Coastal bottlenose dolphins are found primarily within 1 km of shore (Hansen 1990, Defran *et al.* 1999), whereas harbor porpoise are less constrained by distance from shore and are more broadly distributed throughout waters 0–100 m deep, with greatest densities in depths from 0 to 40 m (Barlow 1988, Carretta *et al.* 2001, Forney *et al.* 2001). Because depth and proximity to shore are static, and temperature does not change rapidly enough to explain the observed changes in relative dolphin and porpoise presence, we do not believe that changes in habitat suitability could drive the observed periods of simultaneous increase in bottlenose dolphin presence and decrease in harbor porpoise presence in Monterey Bay.

Monterey Bay is at the northern end of the range of bottlenose dolphins (Hansen 1990, Defran *et al.* 1999). As water temperatures decreased during our study period the frequency of bottlenose dolphin encounters decreased. Bottlenose dolphin pres-

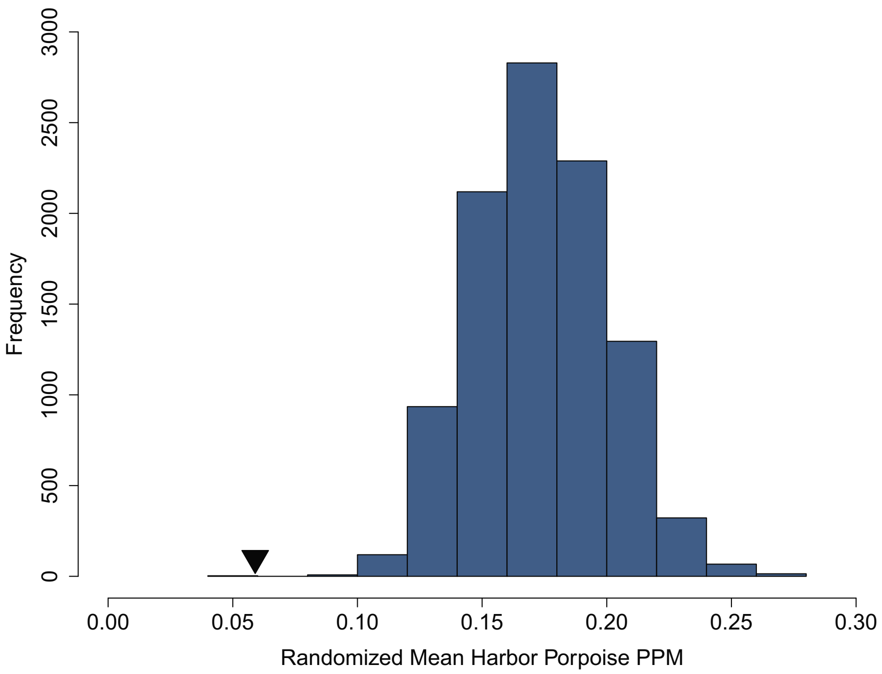

Figure 3. Blue bars indicate the randomization distribution of mean harbor porpoise Positive Minutes (PPM) during bottlenose dolphin encounters (mean = 0.18). The black arrow is the true mean harbor porpoise PPM during bottlenose dolphin encounters (mean = 0.06). There are no possible randomizations that result in a lower-than-observed mean PPM value when bottlenose dolphins are present.

ence at our study site could be considered as a stochastic occurrence moderated by temperature. We were interested in modeling the effect of bottlenose dolphin presence on counts of harbor porpoise positive minutes, but were concerned that changes in habitat might affect dolphin and porpoise presence. To explicitly include possible environmental influences, we included both dolphin presence and temperature as predictor variables of harbor porpoise positive minutes.

Because of the large proportion (29%) of zeros and overdispersion of counts in the harbor porpoise acoustic record, the data do not fit standard negative binomial or Poisson distributions. We tested for the goodness-of-fit of Generalized Linear Models specified with negative binomial and Poisson distributions using a chi-square test on the residual deviance and degrees of freedom. These tests indicated that models fitted using these distributions did not fit the data (chi-square tests, $P < 0.05$). Therefore, we chose a zero-inflated negative binomial (ZINB) model (Zeileis *et al.* 2008). This is a two-part model, with zeros generated by a binomial model with a logit link and counts generated by a negative binomial model with a log link. This model formulation allows zeros to be generated by either part of the model. Results of the ZINB model indicated that the data contained significantly more zeros than expected under standard distributions and that the data are overdispersed (Theta = 0.49). We use Akaike's Information Criterion (AIC) to choose between possible combinations of predictor variables in the ZINB model formulation (Table 1).

Table 1. Partial list of zero-inflated negative binomial (ZINB) model parameters for the binomial and negative binomial portions of the model with their degrees of freedom (DF) and AIC scores. A "+" indicates that both variables were included, whereas a "×" indicates that both variables and their interaction term were included in the model. The best model is in bold.

Binomial model (zeros)	Negative binomial model (counts)	DF	AIC
Temperature	Temperature	5	12,768.71
Dolphin Presence	Dolphin Presence	5	12,731.62
Temp × Dolphin	Temp × Dolphin	9	12,692.38
Temp × Dolphin	**Temp + Dolphin**	**8**	**12,692.48**
Temp + Dolphin	Temp × Dolphin	8	12,708.23

The best model includes temperature, dolphin presence, and their interaction to model the binomial process (probability of occurrence), and temperature and dolphin presence without their interaction to model the count (number of acoustic detections given occurrence). The model with interaction terms in both parts of the model had a slightly better AIC score ($\Delta AIC = 0.10$) but the interaction term was not significant in the count portion of the model (Z-test, $P = 0.14$). The best-fit model, with 95% confidence intervals, is shown in Figure 4. Both the presence of dolphins and temperature were significant in both parts of this best model (Z-test, $P < 0.05$ for all coefficients). The models including either only temperature or only dolphin presence performed poorly, indicating that neither is adequate to explain harbor porpoise acoustic activity.

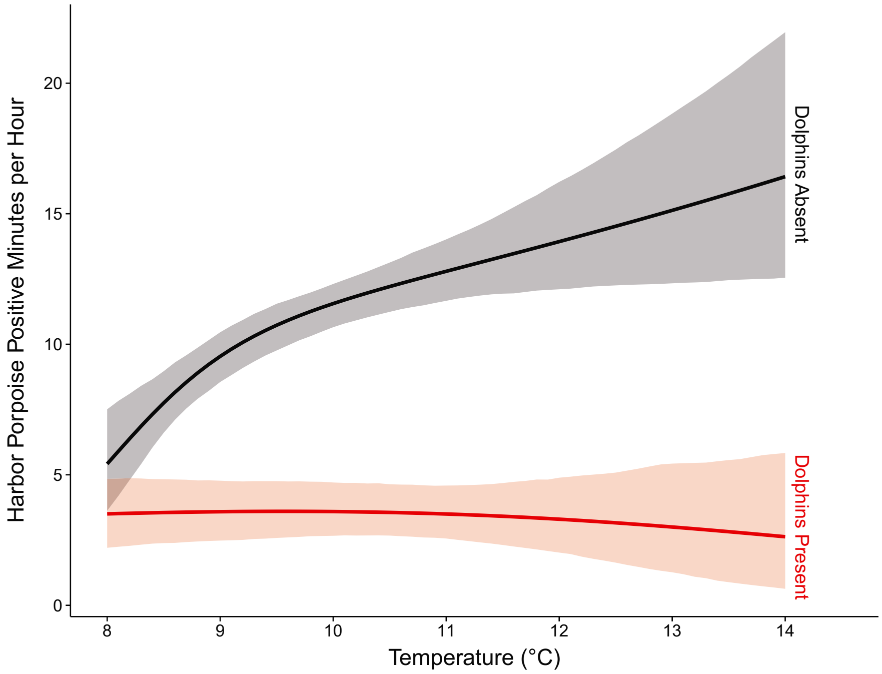

Figure 4. Fitted zero-inflated negative binomial (ZINB) model (red: dolphins present; black: dolphins absent) with 95% confidence intervals (shaded areas) indicating that harbor porpoise positive minutes per hour increased with temperature when dolphins were absent.

Our model predicts that when bottlenose dolphins are present, harbor porpoise acoustic activity is reduced by 52% at relatively low temperatures and by 82% at higher temperatures compared with when bottlenose dolphins are absent. Temperature decreased during our study, so this result may reflect seasonal changes in the relative abundances of harbor porpoises and bottlenose dolphins at our study site. Our data indicated that both species were relatively more abundant in October than in December. The magnitude of the harbor porpoise response to bottlenose dolphin presence may be heightened when both species are relatively more abundant.

We hypothesized that harbor porpoises passively detect bottlenose dolphin vocalizations in Monterey Bay and respond by reducing vocalization rates or leaving the area. The narrow-band high-frequency echolocation clicks of harbor porpoises have evolved independently in three odontocete lineages (Madsen *et al.* 2005). It has been suggested that use of these frequencies by harbor porpoises prevents passive acoustic detection by killer whales (Madsen *et al.* 2005, Rankin *et al.* 2013) whose hearing sensitivity declines above 100 kHz (Szymanski *et al.* 1999). Rankin *et al.* (2013) found that the vocal activity of dolphins decreased with proximity to killer whales, indicating that they used stealth to avoid passive detection and predation by killer whales.

Harbor porpoises have sensitive hearing in the range from 16 to 140 kHz (Kastelein *et al.* 2002), so they are able to hear echolocation clicks of bottlenose dolphins, which range in frequency from 30 to 110 kHz (Wahlberg *et al.* 2011). Bottlenose dolphin hearing is most sensitive in the range of 15–110 kHz (Johnson 1967, Brill *et al.* 2001, Popov *et al.* 2007) although they have limited hearing up to 150 kHz (Popov *et al.* 2007) and there is evidence that high-frequency hearing diminishes with age (Houser and Finneran 2006). Free-ranging harbor porpoise echolocation clicks are produced at a peak frequency of 129–145 kHz with a source level of 191 dB (Villadsgaard *et al.* 2007). Clicks with these parameters would attenuate in Monterey Bay seawater at a rate of approximately 40 dB per km (Fisher and Simmons 1977). Bottlenose dolphin hearing cutoff frequencies are 80 dB at 130 kHz (Popov *et al.* 2007). From these parameters, we might estimate that, bottlenose dolphins would be able to hear harbor porpoises echolocating within about 2 km. However, experimental work on the propagation of artificial harbor porpoise clicks in harbor porpoise habitats has found transmission loss of 61 dB at ranges of 200 m (DeRuiter *et al.* 2010) indicating that the true bottlenose dolphin detection range of harbor porpoise echolocation clicks may be <500 m. Since bottlenose dolphins could be passively or actively detecting harbor porpoises, we are unable to resolve whether harbor porpoises are responding to bottlenose dolphin presence by leaving the nearshore area or by reducing vocal activity to avoid detection.

In summary, our data indicated that harbor porpoise avoided bottlenose dolphins in Monterey Bay, possibly to reduce their risk of being attacked. There are two potential effects of bottlenose dolphin aggression on harbor porpoises in Monterey Bay. First, mortality that results from bottlenose dolphin attacks may directly impact harbor porpoise populations. The Monterey Bay population is approximately 3,715 individuals and appears to be increasing following past impacts from gill net bycatch (KAF, unpublished data). During the UME of harbor porpoises off central California, blunt force trauma was the most common identified cause of death (Wilkin *et al.* 2012), however, if this additional source of mortality was causing population declines, we would be unlikely to detect it given the frequency of past survey efforts and the precision of abundance and trends (Forney *et al.* 1991). The second potential impact of bottlenose dolphin aggression on harbor porpoises is a reduction in fitness as a result of exclusion from suitable habitat in the nearshore environment. This impact would be difficult to quantify. The population of coastal bottlenose dolphins in California is estimated to be 323 individuals (Dudzik *et al.* 2006). Cotter *et al.* (2012) reported the identities of 23 individual bottlenose dolphins that have participated in attacks, suggesting a minimum involvement of 7% of the bottlenose dolphin population. If this behavior continues to spread through the coastal bottlenose dolphin population in California, direct mortality and habitat exclusion could negatively impact harbor porpoise populations.

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Chapter 3

Comparison of harbor porpoise *(Phocoena phocoena)* echolocation clicks recorded simultaneously on two passive acoustic monitoring instruments

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U.S. DEPARTMENT OF COMMERCE
Wilbur L. Ross, Secretary of Commerce

National Oceanic and Atmospheric Administration
Benjamin Friedman, Acting NOAA Administrator

National Marine Fisheries Service
Chris Oliver, Assistant Administrator for Fisheries

Abstract

Passive acoustic surveys are a useful tool for long-term assessment of cetacean populations. However, the application of these methods requires that species of interest produce distinctive, well-characterized vocalizations. Several sympatric species of cetaceans produce narrow-band, high-frequency (NBHF) echolocation clicks which are difficult to distinguish. On the U.S. West Coast, Dall's porpoise *(Phocoenoides dalli)* and harbor porpoise *(Phocoena phocoena)* emit NBHF echolocation clicks and overlap in distribution. To determine whether different passive acoustic instruments could be used to monitor harbor porpoise, we recorded harbor porpoise echolocation clicks simultaneously on an autonomous hydrophone recording system (SoundTrap, Ocean Instruments New Zealand) and on a commonly used passive acoustic monitoring device (C-POD, Chelonia Ltd., UK) and investigated whether the number and peak frequency of recorded echolocation clicks were consistent between the two instruments. We found that the number of echolocation clicks recorded by the two instruments was highly correlated. However, the C-POD and SoundTrap measurements of the peak frequency of echolocation signals were not well-correlated. This suggests that while both instruments are capable of detecting harbor porpoise echolocation clicks, it may not be feasible to use C-PODs to discriminate harbor porpoise echolocation clicks in regions where multiple species with NBHF echolocation clicks are present. The use of calibrated hydrophones with full-bandwidth recording instruments may be required for this task.

Introduction

The use of narrow-band high-frequency (NBHF) echolocation signals (Au 1993, Au et al. 1999) has evolved independently in four odontocete lineages (Madsen et al. 2005, Kyhn et al. 2010, Miller and Wahlberg 2013). NBHF echolocation is relatively high-frequency (above 100 kHz), narrow-band (less than 15 kHz at -3 dB), long-duration (greater than 100 μsec), and weak (source levels less than 200 dB). This type of echolocation is used by at least four of the six species of porpoises (genera *Neophocaena*, *Phocoena* and *Phocoenoides*), dwarf and pygmy sperm whales (genus *Kogia*), at least four species of dolphins (genera *Lagenorhynchus* and *Cephalorhynchus*), and one species of river dolphin (genus *Pontoporia*). The convergent use of NBHF echolocation and the loss of whistles among this disparate group of small-bodied odontocetes has likely been driven by the need to avoid passive acoustic detection and predation by killer whales (*Orcinus orca*; Madsen et al. 2005, Morisaka and Connor 2007) which do not hear well above 100 kHz (Szymanski et al. 1999), as well as the need to maintain functional echolocation while avoiding increasing thermal noise and attenuation due to sound absorption at higher frequencies (Madsen et al. 2005, Kyhn et al. 2013). Though these highly stereotyped signals appear identical across species, it is possible that exploitation of different ecological niches or the need for intra-species communication have led to subtle differences in echolocation clicks between sympatric species (Kyhn et al. 2013).

Along the U.S. West Coast, Dall's porpoise (*Phocoenoides dalli*), harbor porpoise (*Phocoena phocoena*), and dwarf (*Kogia sima*) and pygmy (*Kogia breviceps*) sperm whales produce NBHF echolocation clicks (Table 1). Harbor porpoise are found along the continental shelf mostly in water less than 100 m deep (Barlow 1988, Carretta et al. 2001) while Dall's porpoise have a more pelagic distribution and are found in relatively cold water hundreds to thousands of meters deep (Forney 2000). The distribution of dwarf and pygmy sperm whales is poorly characterized but they are thought to be deep-diving and to inhabit waters thousands of meters deep (Baird 2005). Given these depth distributions, some habitat overlap occurs between harbor porpoise and Dall's porpoise and between Dall's porpoise and dwarf and pygmy sperm whales. Therefore, recordings of NBHF clicks in these regions of overlap cannot currently be definitively attributed to a single species.

Harbor porpoise along the U.S. West Coast are monitored using aerial surveys, which are expensive, weather-limited, and therefore, infrequent. If harbor porpoise echolocation signals could be distinguished from Dall's porpoise echolocation signals, harbor porpoise populations along the U.S. West Coast could be assessed using passive acoustic monitoring (PAM), which requires that species of interest produce distinctive, well-characterized vocalizations (Marques et al. 2009). The development of PAM methods is of interest for both long-term monitoring of harbor porpoise populations and short-term impact assessments associated with offshore marine renewable energy projects.

At present, collecting full-bandwidth recordings of NBHF clicks is typically impractical in the context of long-term monitoring due to the prohibitive cost and limited storage capacity of available instruments. The C-POD (Chelonia Ltd.) is an alternative, inexpensive, commonly used echolocation click detector that has been successfully used to monitor the population decline of the critically endangered vaquita *(Phocoena sinus)* in the Gulf of California (Jaramillo-Legorreta et al. 2017) and to estimate the abundance of the critically endangered Baltic Sea harbor porpoise (Gallus et al. 2012). C-PODs detect individual echolocation clicks and store digital summary information about each click. No waveform data are collected, and therefore data storage demands are low and long-term deployment (3-6 mo.) is possible. In post-processing, clicks are classified as belonging to NBHF echolocation trains using characteristics including the peak frequency and duration of clicks along with the inter-click interval (ICI).

If C-PODs are to be used to monitor harbor porpoise populations along the U.S. West Coast, they must be shown to predictably record information about NBHF signals that could be used to discriminate harbor porpoise and Dall's porpoise echolocation clicks. The goal of the present study is to determine whether a C-POD can accurately or consistently record the number and peak frequency of echolocation clicks compared to a simultaneous full-bandwidth recording analyzed using a custom-written MATLAB (v. 2015a; The MathWorks Inc., 2015) click detection and spectra-based click measurement routine.

Table 1: Previously reported measurements (± standard deviation, when available) of echolocation clicks produced by Dall's porpoise, harbor porpoise, and dwarf and pygmy sperm whales. Region indicates whether the measured clicks were recorded from individuals in the Atlantic (A) or Pacific (P). Some measurements were not included in all publications and are reported as NA in those instances.

Species	**Region**	**Peak Frequency (kHz)**	**Source Level (dB *re.* 1 μPa)**	**Duration (μsec)**	**-3dB Bandwidth (kHz)**	**Source**
K. breviceps	A	130±0.7	175	119±19	8±2.3	Madsen et al. 2005
K. sima	A	129±2	NA	222±53	10±2	K.P.B.M unpublished data
K. sima	P	117±3	NA	241±70	11±4	K.P.B.M unpublished data
P. dalli	P	137±4	183±7	104±3	11±5	Kyhn et al. 2013
P. phocoena	A	127.5±7	157.2±6.9	NA	16.4±4.3	Au et al. 1999
P. phocoena	A	135	170	125	7	Madsen et al. 2005
P. phocoena	A	129-145	178-205	44-113	6-26	Villadsgaard et al. 2007
P. phocoena	P	140±1	178±4	88±29	8±3	Kyhn et al. 2013
P. phocoena	A	137±6	178±5	54±8	17± 5	Kyhn et al. 2013

Methods

Data Collection

We deployed a passive acoustic mooring including a SoundTrap 202HF autonomous hydrophone recording system[1] and a C-POD echolocation click detector[2] in Monterey Bay, California, USA on 24 August 2015. We selected a nearshore location in northern Monterey Bay for the mooring deployment (Fig. 1) in an area where harbor porpoise are known to be common (Jacobson et al. 2014, Forney et al. 2014). At this location, the only regularly observed cetacean species are harbor porpoise and bottlenose dolphins (*Tursiops truncatus*). The mooring location was approximately 10-m deep, and the instruments were suspended approximately 5-m below the sea surface. The instruments were attached to each other so that the respective hydrophones were as close as possible to one another (Fig. 2). The SoundTrap recorded continuously with a sampling rate of 576 kHz. The C-POD continuously monitored frequencies from 20 kHz to 160 kHz and recorded parameters associated with click events. The instruments were retrieved on 27 August 2015.

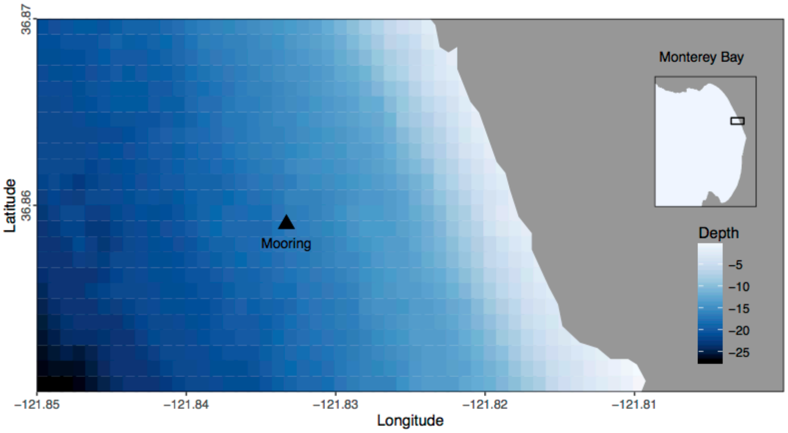

Figure 1: Map of SoundTrap/C-POD mooring location (black triangle) in northern Monterey Bay, CA.

Data Analysis

C-POD data were processed using the KERNO algorithm in the program CPOD.exe (Tregenza 2012) to detect and classify echolocation clicks. The exact algorithm used by the C-POD is proprietary, but in principle it uses a real-time energy detector to detect possible echolocation clicks and stores summary information about those clicks. In post-processing, the KERNO algorithm determines if those clicks are part of cetacean-like series or “trains” of clicks. Click trains are then assigned to a species class based on click characteristics including peak frequency, duration, and ICI, and are assigned a confidence rating based on the consistency of the click train and ambient noise conditions. We considered all narrow-band, high-frequency (NBHF) click trains as belonging to harbor porpoise, and included only clicks from high- and

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[1] Ocean Instruments New Zealand, www.oceaninstruments.co.nz.

[2] Chelonia Ltd., www.chelonia.co.uk

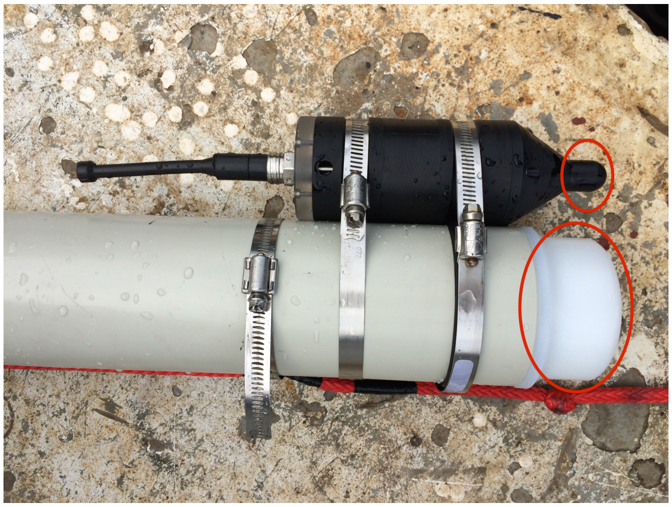

Figure 2: SoundTrap (black, top) and C-POD (white, bottom) attached for deployment. Red ovals indicate approximate hydrophone locations on each instrument. The instruments were attached to a nylon line with a surface float and 50-lb anchor weight for deployment.

moderate-quality click trains in our analyses. EKJ manually validated these click trains in the program CPOD.exe. Because no waveform data are collected by the C-POD, the program CPOD.exe uses a zero-crossings approach to calculate peak frequency. This technique uses the time between successive zero-crossings of the incoming waveform to calculate the frequency of the signal and ignores the amplitude envelope of the original signal (Parsons et al. 2000). Based on previously published peak frequency values for harbor porpoise echolocation clicks (Table 1) and for consistency with the analysis of SoundTrap data, we eliminated echolocation click detections with peak frequencies less than 120 kHz and greater than 150 kHz. Click details were exported from CPOD.exe to a text file for further analysis in R[3].

Sound files collected using the SoundTrap were processed using a custom-written MATLAB click detection and measurement routine[4] modified from Soldevilla et al. (2008) and Roch et al. (2011). SoundTrap data were not corrected for frequency-specific sensitivity; however, we calibrated the SoundTrap relative to a Reson TC4014 reference hydrophone and found the response to be flat ($\pm$ 1 dB re. 1 μPa/V) from 75 to 150 kHz. In summary, the MATLAB detection and measurement routine uses an energy detector to detect possible echolocation clicks and generates spectra from which click parameters are calculated. Candidate clicks are pruned according to user-specified parameter ranges for the species of interest including minimum and maximum peak frequency; we pruned candidate clicks with peak frequencies below 120 kHz and above 150 kHz. Concatenated spectrograms of resulting click detections were visually validated (see Fig. 3 for example). Data were exported from MATLAB for further analysis in R.

We calculated the total number of harbor porpoise echolocation clicks recorded by the C-POD and by the SoundTrap/MATLAB routine as well as the average peak frequency of recorded echolocation clicks. We also plotted the distribution of peak frequencies recorded by each instrument. For each hour during which the instruments were deployed, we calculated the number of echolocation clicks recorded by each instrument and the corresponding proportion of seconds during which harbor porpoise were detected (porpoise-positive seconds; PPS) per

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[3] version 3.2.2, www.r-project.org

[4] An archived version of the code used can be found at http://doi.org/10.5281/zenodo.164881.

hour.

In addition to comparing average click characteristics recorded by the two instruments, we were also interested in examining whether and how individual echolocation clicks were simultaneously recorded by both instruments. Directly matching timestamps between clicks detected on the two instruments is not possible because of clock drift in both instruments. To align the data sets, we divided the first 24 h of data into 5-min bins. Within each bin, we tested clock offsets between the instruments of -2 sec to +2 sec in increments of 1 ms. We used the number of clicks matched between instruments with each offset as an indicator of the offset accuracy. To be considered a match, click timestamps on the two instruments had to be within 0.5 ms of each other after offset correction. These parameters are stringent in the context of harbor porpoise echolocation clicks; reported ICIs are on the order of 50 ms (Villadsgaard et al. 2007) and click durations on the order of tens of μsecs (Table 1). An optimal offset (defined as the offset producing the highest number of matched clicks) was selected for each 5 min bin. After offset, at least 5 clicks within each 5-min bin had to match between instruments to be considered valid. Data from bins which did not meet this criterion were discarded. We used the optimal offsets to correct timestamps within each 5-min bin, then matched individual clicks between instruments, and finally, compared the peak frequency recorded by each instrument for each matched click. Because of the computer-intensive nature of this procedure, only the first 24 h of data were analyzed.

Results and Discussion

The C-POD and SoundTrap were co-deployed for 75 h in northern Monterey Bay, California, USA. At the time of deployment, tens of harbor porpoise were present and appeared to be foraging near the mooring site. Over the 75-h deployment period, the MATLAB routine detected 229,376 harbor porpoise echolocation clicks in the SoundTrap recording (Fig. 3). The C-POD detected 202,390 echolocation clicks during the same time period. Qualitatively, patterns of harbor porpoise echolocation activity were similar between instruments (Fig. 4) and correlations between the number of echolocation clicks or the PPS recorded by each instrument per hour were high ($R^2 = 0.95$ for both; Fig. 5). The mean peak frequency of clicks recorded by the SoundTrap/MATLAB routine was 139.13 kHz (SD = 6.08) while the mean peak frequency of clicks recorded by the C-POD within the range of 120–150 kHz was 135.93 (SD = 5.62). The distribution of peak frequencies recorded by the C-POD appears to be unimodal around the mean, while the distribution of peak frequencies recorded by the SoundTrap/MATLAB may be bimodal, with peaks at 136 kHz and 141 kHz (Fig. 6). A Kolmogorov-Smirnov test rejected the null hypothesis that these distributions could have been drawn from a single overlying distribution (p-value < 0.001). The only published estimate of Pacific harbor porpoise echolocation click peak frequency (Tab. 1; Kyhn et al. 2013) is 140 kHz, which is closer to the average peak frequency calculated by the SoundTrap/MATLAB than to the average peak frequency calculated by the C-POD. Kyhn et al. (2013) used only on-axis echolocation clicks to calculate peak frequency, resulting in a much more precise estimate (mean = 140 kHz, SD = 1 kHz) than our SoundTrap measurements (mean = 139.13 kHz, SD = 6.08 kHz).

Previous studies (e.g., Kyhn et al. 2013) have recorded thousands and analyzed tens or hundreds of clicks; we recorded and analyzed more than 200,000 echolocation clicks. The C-POD and SoundTrap/MATLAB did not record the same number of echolocation clicks, probably due to different sensitivities of the hydrophones and of the echolocation click detection algorithms (e.g., threshold amplitudes for click detection were not identical). The two instruments reported similar patterns in echolocation click activity over the 3-day period (Fig. 4) and the number of echolocation clicks recorded was highly correlated between instruments (Fig. 5),

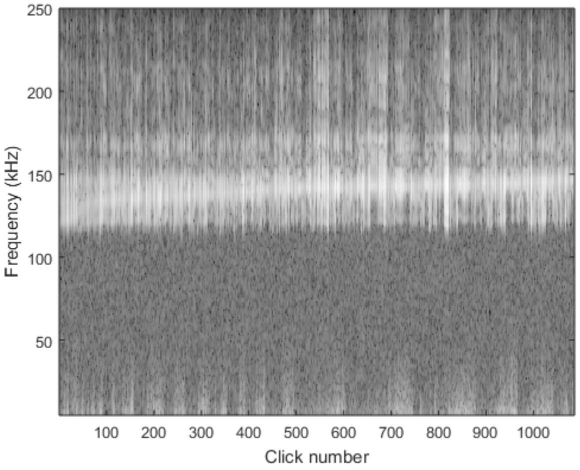

Figure 3: Representative concatenated spectrogram of 1086 harbor porpoise clicks detected by the MATLAB routine in a 30 min SoundTrap recording and sorted by peak frequency.

indicating that the instruments are probably similarly reliable for the purpose of monitoring harbor porpoise presence. Visual examination of detected echolocation clicks indicated no false positives in either dataset, though the instruments may have detected multipath arrival of single echolocation clicks in some instances.

Within each 5-min bin used to test instrument timestamp offsets (Fig. 7) the range of optimal offsets was between -0.56 and +1.9 sec (Fig. 8). The consistency of optimal offsets from one time bin to the next gives us confidence that this matching technique was successful. Drift in the clocks of both instruments are apparent and non-linear over time, with periods of stability or gradual drift followed by large shifts in the clock alignment (e.g., the approx. 1-sec jump in alignment at 00:00 on 25 August). Due to the nonlinearity of the observed instrument clock drift, simply correcting instruments relative to synchronization at the start and end of a deployment would not be sufficient to match individual echolocation clicks recorded on two instruments. Regular synchronization of the two instruments during the deployment period (e.g., with a pinger programmed to ping every minute) would allow for a better and echolocation-independent alignment of the two datasets.

Within the first 24-h period, 19% of individual echolocation clicks were successfully matched between the two instruments (N = 17,825). This relatively low match rate could be due to the extremely high directionality of harbor porpoise echolocation clicks resulting in few simultaneous arrivals at the two instruments, or to overly stringent matching criteria that excluded “true” matches from the data set. It is also possible that the instruments shadowed one another so that some clicks arrived at only one instrument.

The mean peak frequency of echolocation clicks recorded by the C-POD was lower than that of those recorded by the SoundTrap/MATLAB when averaged over the entire deployment period (C-POD mean = 135.93, SoundTrap/MATLAB mean = 139.13 kHz) but very similar when individual echolocation clicks were matched between instruments (C-POD mean = 137.10 kHz, SoundTrap/MATLAB mean = 137.74 kHz). However, the peak frequencies of individual matched clicks were not well-correlated ($R^2 = 0.27$; Fig. 9).

Our MATLAB routine used an FFT-based method to calculate peak frequency of echolocation clicks, while the C-POD used a zero-crossings approach. The FFT-based method calculates the peak frequency by weighting the different frequencies present in a signal by their

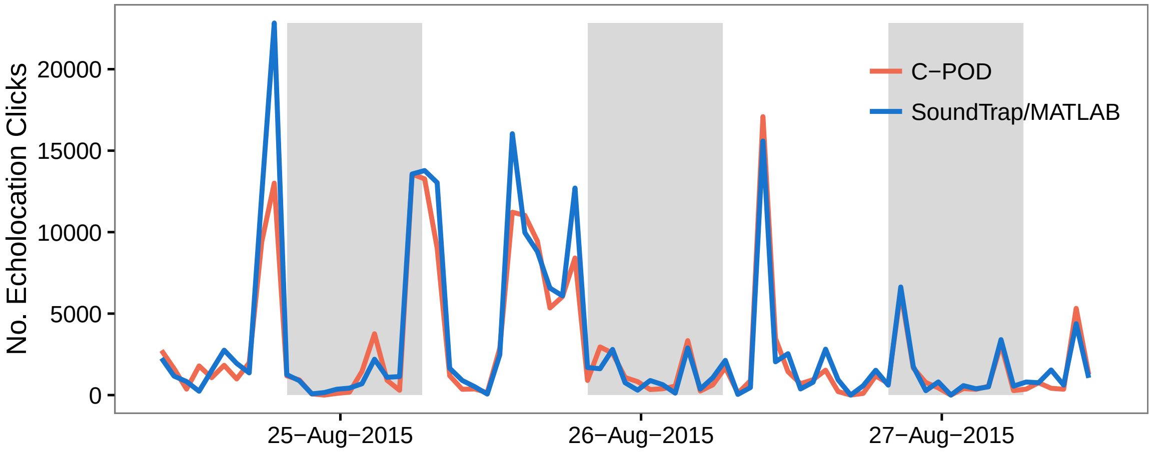

Figure 4: Number of harbor porpoise echolocation clicks recorded per hour by the C-POD (orange line) and the SoundTrap/MATLAB detector (blue line) over the 3 d deployment period. Gray shading indicates local nighttime (time between sunset and sunrise).

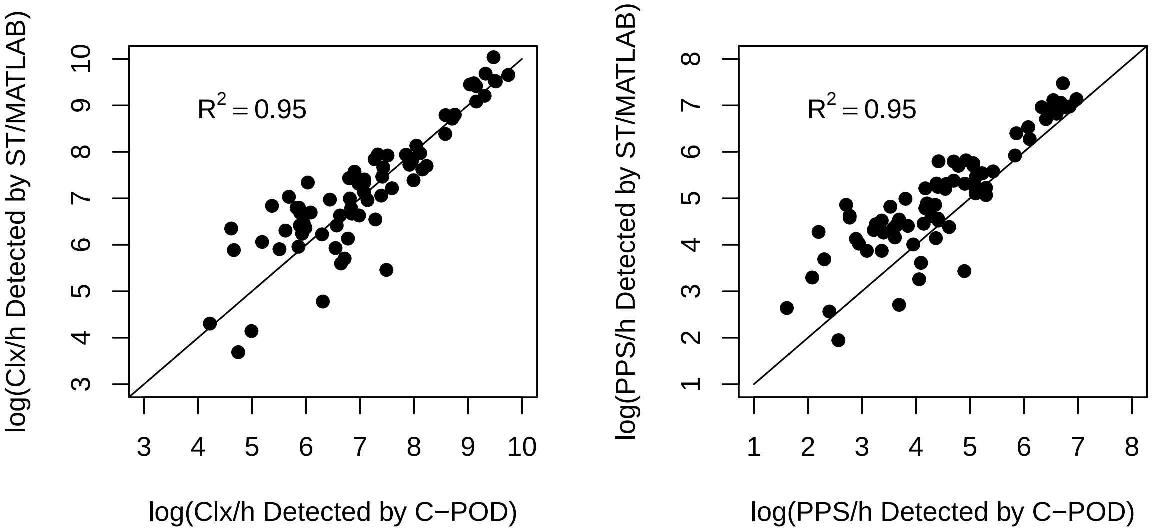

Figure 5: Log-transformed comparison of the number of echolocation clicks detected by each instrument per hour (left panel) and the number of porpoise positive seconds (PPS) detected by each instrument per hour (right panel) with correlations for each comparison and a one-to-one line (black) indicating perfect agreement.

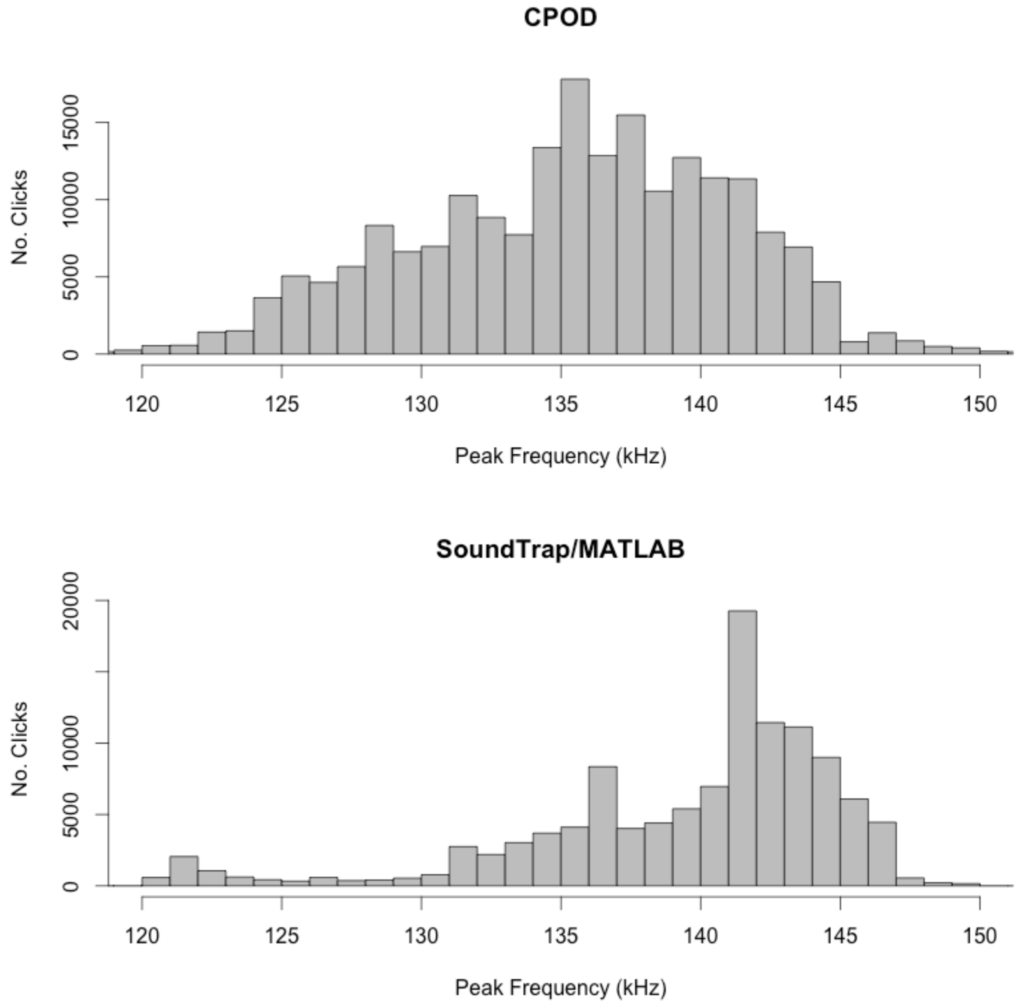

Figure 6: Histograms illustrating the distribution of click peak frequencies recorded by the C-POD (top panel) and the SoundTrap/MATLAB (bottom panel) within the range of 120-150 kHz.

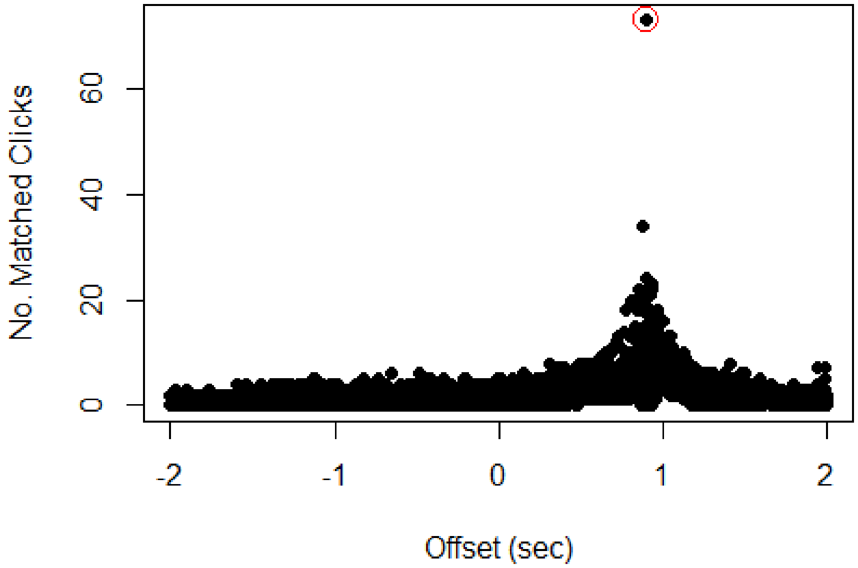

Figure 7: Example of tested offsets between the SoundTrap and C-POD (*x*-axis) and the number of matched clicks resulting from that offset (*y*-axis) within a single 5-min bin. The offset which produced the highest number of matches within this bin is indicated by a red circle.

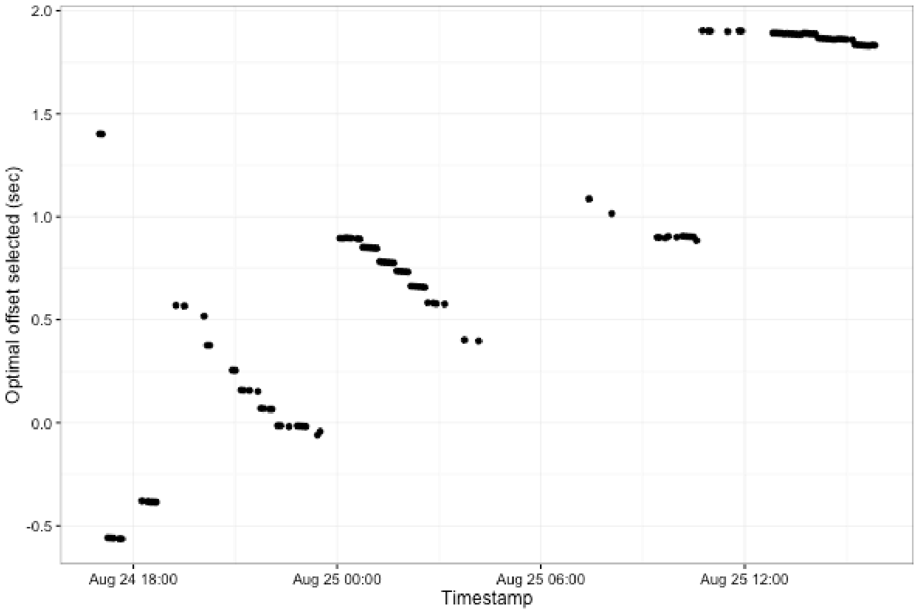

Figure 8: Time series of optimal offsets (*y*-axis) calculated within each 5 min bin over a 24-h period (*x*-axis).

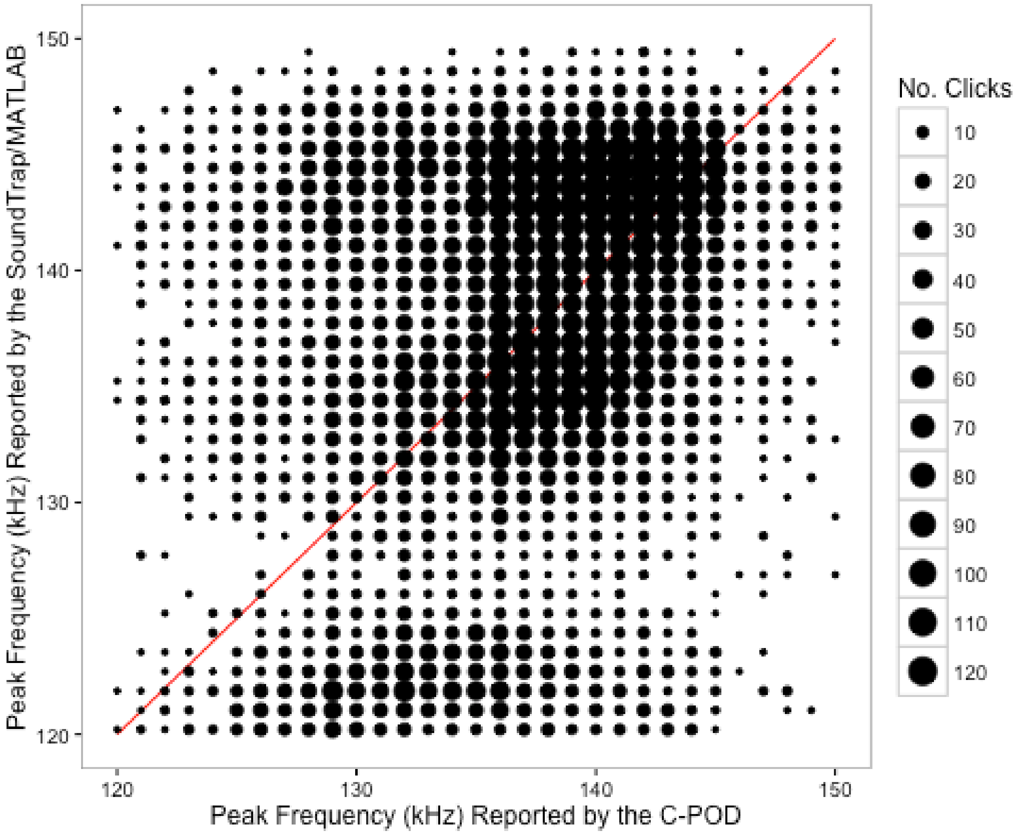

Figure 9: Comparison of measured peak frequencies of matched harbor porpoise echolocation clicks recorded by the C-POD (*x*-axis) and the SoundTrap/MATLAB routine (*y*-axis) over a 24-h period. The size of the point indicates the number of matched clicks, and the red line indicates perfect agreement between the measurements.

amplitudes, so that higher amplitude components of the signal are more influential to the measurement of peak frequency than lower amplitude components. The zero-crossings approach ignores the amplitude variation in the signal and only analyzes the most energetic part of the signal. Because the zero-crossings approach does not capture the frequency-time information of the original signal, it produces less accurate estimates of the peak frequency of the signal (Parsons et al. 2000). For very narrow-band clicks, zero-crossings and spectral methods should produce similar estimates of peak frequency, but as clicks become more broadband the zero-crossings approach to calculating peak frequency becomes more of an approximation.

In our data set, the difference in mean peak frequency recorded by the C-POD versus the SoundTrap/MATLAB of all echolocation clicks was 3.2 kHz. This is a small difference, but similar in magnitude to the difference in peak frequency between Dall's porpoise and harbor porpoise echolocation clicks (3 kHz; Tab. 1; Kyhn et al. 2013). Additionally, it does not appear that the C-POD is reporting consistently lower peak frequencies than the SoundTrap/MATLAB. If this were the case, we would expect to see the same distribution in the histograms of peak frequency shown in Fig. 6, but with the histogram of peak frequencies recorded by the C-POD shifted to have a lower mean. Furthermore, as shown in Fig. 9, there is low correlation (R^2 = 0.27) between the peak frequencies of individually matched echolocation clicks, although this may be partly due to the difficulty in simultaneously detecting echolocation clicks on both instruments or to inaccurate synchronization between instruments.

Summary and Conclusions

Harbor porpoise echolocation clicks were simultaneously recorded on a hydrophone (SoundTrap 202HF) and a passive acoustic monitoring device (C-POD) in Monterey Bay, California, USA over a 3-day period. SoundTrap data were processed using a custom-written MATLAB click detection and measurement routine while C-POD data were processed using the KERNO classifier within the proprietary software CPOD.exe. The time series of echolocation activity reported by the co-deployed instruments were highly correlated ($R^2 = 0.95$), although the absolute number of echolocation clicks detected by the SoundTrap/MATLAB was 13% greater than that detected by the C-POD/KERNO classifier. The average peak frequency of echolocation clicks reported by the C-POD was 3.2 kHz lower than that reported by the SoundTrap/MATLAB. However, this difference was not consistent at the level of individually matched echolocation clicks; correlation in peak frequencies of individually matched clicks was poor ($R^2 = 0.27$). The C-POD uses a more computationally efficient method to detect echolocation clicks and to calculate peak frequencies, but this efficiency comes at the expense of detailed information about the echolocation signals, making it difficult to accurately measure species-identifying features of echolocation clicks. Based on these findings, we do not think it will be feasible to monitor harbor porpoise using C-PODs in areas with multiple NBHF species; however, we recommend further data collection and analysis to support or refute this preliminary conclusion.

Future Directions

Regional variation has been observed in echolocation signals of NBHF species (Tab. 1). The extent and magnitude of this variation is not well-resolved. A collaborative effort to collect and analyze recordings from different NBHF species and regions using a variety of instruments, particularly when multiple instruments can be deployed simultaneously, would be useful to researchers hoping to use PAM for long-term monitoring of NBHF species. In the present study, we focused on peak frequency as a possible metric for distinguishing harbor porpoise from Dall's porpoise echolocation clicks; however, other metrics (e.g., bandwidth, duration, and ICI; see Kyhn et al. 2013) might prove more useful in distinguishing NBHF echolocation clicks produced by different species. Further, two new technologies may replace C-PODs as the default instrument for PAM of harbor porpoise. The F-POD (Chelonia Ltd., UK) is an extension of the C-POD which records full waveform data when echolocation clicks are detected. This instrument is currently under development and might be a good option in areas where it is necessary to distinguish multiple species with similar echolocation signals. Additionally, firmware for click detection-triggered recording has been developed for the SoundTrap (Ocean Instruments New Zealand), which would extend the deployment duration and could make it possible to use this instrument for long-term PAM.

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Chapter 4

Using paired visual and passive acoustic surveys to estimate passive acoustic detection parameters for harbor porpoise abundance estimates

Using paired visual and passive acoustic surveys to estimate passive acoustic detection parameters for harbor porpoise abundance estimates

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Passive acoustic monitoring is a promising approach for monitoring long-term trends in harbor porpoise (*Phocoena phocoena*) abundance. Before passive acoustic monitoring can be implemented to estimate harbor porpoise abundance, information about the detectability of harbor porpoise is needed to convert recorded numbers of echolocation clicks to harbor porpoise densities. In the present study, paired data from a grid of nine passive acoustic click detectors (C-PODs, Chelonia Ltd., United Kingdom) and three days of simultaneous aerial line-transect visual surveys were collected over a 370 km^2 study area. The focus of the study was estimating the effective detection area of the passive acoustic sensors, which was defined as the product of the sound production rate of individual animals and the area within which those sounds are detected by the passive acoustic sensors. Visually estimated porpoise densities were used as informative priors in a Bayesian model to solve for the effective detection area for individual harbor porpoises. This model-based approach resulted in a posterior distribution of the effective detection area of individual harbor porpoises consistent with previously published values. This technique is a viable alternative for estimating the effective detection area of passive acoustic sensors when other experimental approaches are not feasible.

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I. INTRODUCTION

Fixed passive acoustic technologies are promising tools for long-term assessment of cetacean populations (Mellinger *et al.*, 2007). However, to use passive acoustic sensors to estimate cetacean density and abundance, the probability of detecting individuals must be known or estimated (Marques *et al.*, 2009). There are two components of this detectability: (1) the rate at which animals produce sounds and (2) the probability of detecting sounds produced at varying distances from the passive acoustic sensor (the detection function). In wild animal populations, the sound production rates of individuals and the detection functions of passive acoustic sensors are difficult to measure experimentally. Rather than directly measuring these quantities, we used simultaneous visual surveys and a deployment of passive acoustic sensors to create a paired dataset that allowed us to estimate the product of the sound production rate and the area monitored by the passive acoustic sensors, which we refer to as the effective detection area (EDA). This paper uses a harbor porpoise population in California as a case study to present a new approach for determining a conversion factor between sounds detected and animal density that can be used for long-term passive acoustic monitoring (PAM) of animal abundance.

Along the central and northern California coast, harbor porpoise (*Phocoena phocoena*) occur in four distinct populations (Calambokidis and Barlow, 1991; Chivers *et al.*, 2002). Harbor porpoises in this region are distributed in areas with bottom depths less than 100 m, with greatest densities where bottom depths are 10–40 m (Barlow, 1988; Carretta *et al.*, 2001; Forney *et al.*, 2001). Due to their nearshore distribution, harbor porpoise are exposed to a diverse array of lethal and sublethal anthropogenic impacts including pollution, noise, and fishery interactions (Barlow and Forney, 1994). In some areas, cumulative anthropogenic impacts have led to the decline or disappearance of harbor porpoise populations (Calambokidis *et al.*, 1984). For example, harbor porpoises disappeared from the San Francisco Bay and the Puget Sound in the mid-20th century, possibly due to high concentrations of toxic chemicals (Calambokidis *et al.*, 1985; Raum-Suryan and Harvey, 1998) and have only recently repopulated these areas (Keener *et al.*, 2011; Anderson, 2014).

In central California, harbor porpoises were caught incidentally in set gillnets targeting halibut from the 1960s to the 1990s, with particularly high take in the 1980s (Barlow and Forney, 1994; Jefferson *et al.*, 1994). Due to this

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[a)] Electronic mail: eiren.jacobson@gmail.com incidental take, the central California population may have been reduced by as much as 70% of their pre-bycatch abundance (Barlow and Hanan, 1995). Currently, all California populations are believed to be either stable or recovering from past gillnet take (Forney *et al.*, 2014). The abundance of the Monterey Bay harbor porpoise population was most recently estimated to be 3715 [Coefficient of Variation (CV) = 0.51; Forney *et al.*, 2014]. Fishery mortality is currently considered to be insignificant for this stock, and there are no known habitat issues (Carretta *et al.*, 2015); however, over the past decade there has been some mortality due to bottlenose dolphin (*Tursiops truncatus*) attacks on harbor porpoise in this region (Cotter *et al.*, 2011; Wilkin *et al.*, 2012; Jacobson *et al.*, 2014).

Harbor porpoise populations in California have been monitored using aerial surveys since the late 1980s; however, these surveys are expensive, restricted by weather, and have a limited ability to detect trends in harbor porpoise abundance (Forney *et al.*, 1991). Fixed PAM, which has been used successfully elsewhere (e.g., Gallus *et al.*, 2012) might be more effective for monitoring harbor porpoise populations in this region.

Harbor porpoise produce highly directional echolocation clicks with peak frequencies around 130 kHz (Au *et al.*, 1999) that are used for navigation, foraging, and communication (Akamatsu *et al.*, 2007; Clausen *et al.*, 2010; Linnenschmidt *et al.*, 2012; Wisniewska *et al.*, 2016). These clicks attenuate rapidly in seawater, resulting in an active acoustic space of several hundred meters (DeRuiter *et al.*, 2010). Because harbor porpoise echolocation clicks are well described and do not travel long distances, they can be used as a proxy for animal density around a passive acoustic sensor.

One passive acoustic sensor that has been widely used to study harbor porpoise is the C-POD (Tregenza (2012), Chelonia Ltd., United Kingdom, www.chelonia.co.uk). C-PODs are relatively inexpensive, easy to operate, and can be deployed for 3–6 months at a time. C-PODs detect individual echolocation clicks and store digital summary information about each click. No waveform data are collected. In post-processing, clicks can be classified as likely to have been produced by a harbor porpoise using characteristics including the peak frequency and duration of clicks along with the inter-click interval.

Metrics of harbor porpoise occurrence derived from passive acoustic data have been shown to correlate positively with density estimates derived from visual observations (e.g., Kyhn *et al.*, 2012; Williamson *et al.*, 2016). C-PODs and their predecessors, the POD and T-POD, have been used to document harbor porpoise habitat use (e.g., Carlstrom, 2005; Verfuß *et al.*, 2007), to monitor the impacts of anthropogenic activities (e.g., Carstensen *et al.*, 2006; Brandt *et al.*, 2011; Dähne *et al.*, 2013a; Thompson *et al.*, 2013; Brandt *et al.*, 2014) and to assess population abundance and trend (Gallus *et al.*, 2012; Jaramillo-Legorreta *et al.*, 2016).

To convert echolocation clicks detected by C-PODs to animal densities, a detection function is needed to describe the probability of detection as a function of distance from the C-POD (Buckland *et al.*, 2001; Marques *et al.*, 2013). Traditionally, it is assumed that animals at zero distance from the sensor are detected with certainty (Buckland *et al.*, 2001); however, because harbor porpoises produce highly directional echolocation clicks, and because they do not click continuously, the probability of detection at zero distance is less than one. Therefore, the click rate of individual porpoises is needed to scale the detection function appropriately. From these two pieces of information we can estimate the EDA of the C-POD.

Kyhn *et al.* (2012) used paired visual and PAM sessions in a mark-recapture framework to estimate the detection functions of individual T-PODs in an area with relatively low harbor porpoise densities where individual porpoises could be visually tracked. Using these paired data, they estimated the effective detection radii of individual T-PODs to be between 22 and 104 m. C-PODs have been found to be less variable in sensitivity than T-PODs (Dähne *et al.*, 2013b) and thus we would expect the range of detection radii for individual C-PODs to be narrower, though this has not yet been shown experimentally. One recent experiment tracked harbor porpoises in three dimensions as they moved through a closely spaced array of sensors; however, this approach to estimating the detection function was foiled in part by the extremely high directionality of harbor porpoise echolocation, resulting in very few simultaneous detections on multiple sensors required for estimation of a detection function using this approach (Koblitz, 2015).

To estimate the echolocation click rate of individual porpoises, researchers in Denmark affixed acoustic sensors to wild harbor porpoises and found that harbor porpoise echolocate almost continuously (Akamatsu *et al.*, 2007; Linnenschmidt *et al.*, 2012; Wisniewska *et al.*, 2016). However, individual variation in reported echolocation activity was sometimes large, and the small sample size inherent to tagging studies (<10 animals in total) makes it difficult to extrapolate results to an entire population or species.

In the present study, we did not attempt to estimate the detection function and the echolocation click rate independently; instead, we treated the EDA as an unknown quantity that allows conversion from passive acoustic data to animal density. By using an established visual method to estimate harbor porpoise density in our study area at the same time that passive acoustic sensors were deployed, we were able to solve for the unknown EDA. This allowed us to estimate harbor porpoise density in our study area using passive acoustic data at times when visual surveys were not conducted.

II. MATERIALS AND METHODS

This section describes how passive acoustic and visual survey data were collected, provides an overview of data processing and analytical techniques, and explains how the two datasets were combined in a Bayesian model framework to estimate the EDA of the passive acoustic instruments. Finally, we show how the estimated EDA can be applied to long-term passive acoustic datasets to estimate harbor porpoise abundance.

A. Data collection

1. Passive acoustic methods

In 2013, we installed a grid of PAM devices (C-PODs) in northern Monterey Bay (Fig. 1). We deployed 11 C-PODs at the end of August 2013 and retrieved 10 C-PODs during the first week of January 2014. For this experiment, we chose Monterey Bay as our study site because the local population of harbor porpoises is relatively well studied and believed to be stable (Carretta *et al.*, 2015). The bathymetry of northern Monterey Bay results in a rapid spatial gradient of harbor porpoise densities, with relatively high densities in the nearshore areas and relatively low densities near the deep Monterey Canyon. The study area included waters from 10 to 100 m depth, north of 36.8° N and east of 122.10° W, with a total area of 370 km^2. Our study area represents approximately 15% of the Monterey Bay harbor porpoise stock range (Forney *et al.*, 2014), but has a disproportionally high density of harbor porpoises relative to the rest of the region occupied by this population. The study design was a systematic, randomly positioned offset grid of 11 C-PODs spaced 0.035° latitude and 0.07° longitude apart and oriented to follow the shape of the coastline. As a result of this design, the lateral distance between instruments was 3.4 km, the medial distance was 2.1 km, and the diagonal distance was 2.7 km.

2. Aerial survey methods

Three replicate fine-scale aerial surveys were flown over the northern Monterey Bay study area during the C-POD grid deployment on October 15, 17, and 31, 2013 (Fig. 1). The exact dates of the aerial surveys were determined by suitable weather conditions. These simultaneous surveys were designed to estimate the density and abundance of harbor porpoise in the 370 km^2 study area. Aerial surveys covered a randomly placed, systematic set of 20 east–west transect lines spaced 0.0083° (960 m) apart that were designed independently from the grid of C-POD moorings. The coverage of the line transects was restricted in part by logistical constraints; this level of coverage was realizable in a single attempt given limited calm weather windows and an approximate 4-h flight time due to fuel capacity. Surveys were conducted from a Partenavia P-68 high-wing twin-engine aircraft using standard aerial line-transect survey methods (Forney *et al.*, 1991). In summary, two observers searched from bubble windows on either side of the aircraft while a third observer searched from a belly window in the rear of the aircraft. A data recorder transcribed verbal sighting information for cetaceans and turtles (including declination angle, species, and number of animals) and environmental (visibility conditions) information from the observers into a custom-written software program on a laptop computer (Toshiba T-1000, Japan) that was directly connected to a handheld Global Positioning System (Garmin 12XL, USA).

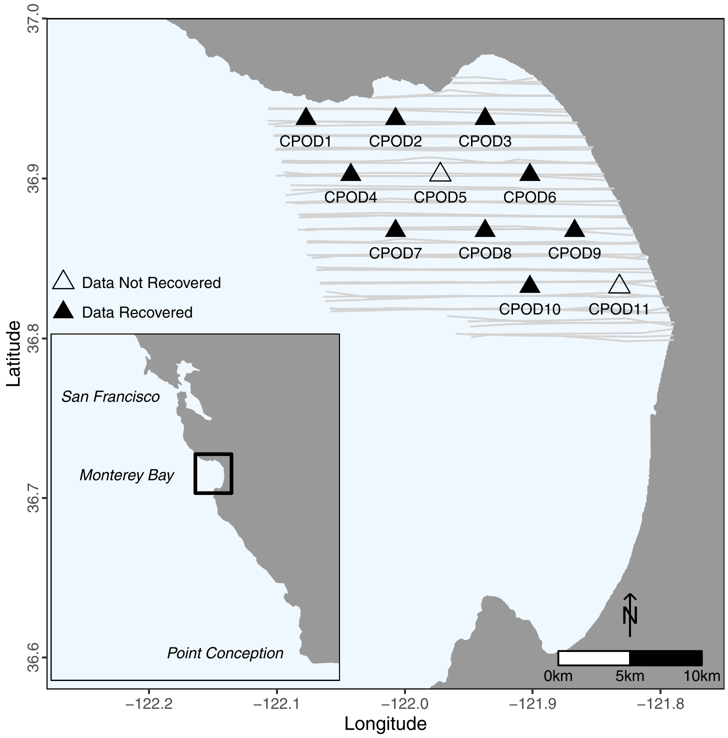

FIG. 1. (Color online) Completed replicates of aerial survey line transects (gray lines) and C-POD deployment locations (triangles) in Monterey Bay, California. C-PODs from which data were successfully recovered in 2013 are indicated by filled triangles, while open triangles indicate C-PODs that did not return data.

B. Analytical methods

1. C-POD data processing

Once the C-PODs were recovered, data were processed using the KERNO algorithm in the program CPOD.exe (v. 2.044; Tregenza, 2012) to detect click trains. All narrowband, high-frequency (NBHF) click trains were classified as belonging to harbor porpoise, and we chose to include only high-quality click trains (as defined by the KERNO algorithm) in our analysis in order to minimize false positives in the dataset. High-quality NBHF click trains detected on the three days of acoustic effort considered in the present study were visually validated. No false positives were detected in the dataset. While Dall's porpoise (*Phocoenoides dalli*) also occur along the U.S. West Coast and produce very similar NBHF echolocation signals, we are confident that our dataset includes only harbor porpoise echolocation click trains because Dall's porpoise are typically found in water hundreds to thousands of m deep (Forney, 2000) and because no Dall's porpoise were sighted in our study area during the aerial surveys conducted as part of this study or in any other aerial surveys conducted in 2011 or 2013. Data were exported from CPOD.exe and all further analyses were performed in R (v. 3.2.2; R Core Team, 2016).

We considered a variety of passive acoustic metrics, including counts of echolocation clicks (e.g., Bailey *et al.*, 2010; Marques *et al.*, 2009) and of echolocation click-positive intervals (e.g., Brandt *et al.*, 2011; Williamson *et al.*, 2016), over periods of seconds, minutes, hours, and days. We found that counts of individual echolocation clicks tended to be overdispersed, and because the click production rates of individual porpoises are so variable (Akamatsu *et al.*, 2007; Linnenschmidt *et al.*, 2012; Wisniewska *et al.*, 2016) we did not feel confident that the number of echolocation clicks per time would scale linearly with the number of animals present. Because our goal was to estimate the number of individuals, not groups, we could not use metrics like detection positive minutes or hours where more than one individual would likely be detected, which would result in biased estimates of density and abundance. We chose to use the proportion of porpoise positive seconds (PPS) as our passive acoustic metric because this metric is less likely to become saturated when multiple animals are present and because it reduces the impact of animal orientation on detectability by effectively averaging over 1-s periods. Our methods assume that only one porpoise can be detected within any 1-s period, which is likely given the narrow beam width of harbor porpoises and the resulting rapid changes in detectability with animal movement and orientation (Koblitz *et al.*, 2012). To determine the time period over which PPS should be calculated, we calculated PPS for 3-, 6-, and 12-h intervals and correlated these values with the corresponding density estimates from the aerial surveys (see Sec. II B 3 for details). While PPS calculated over a 3-h period had the highest correlation with the aerial survey dataset, a large proportion of the acoustic data points (17/27) were zeros. The second highest correlation was with 12-h periods and produced fewer (6/27) zeros in the acoustic dataset. This metric also makes biological sense since diel changes in echolocation behavior have been reported for this species (Carlstrom, 2005). Therefore, we calculated the PPS recorded by each C-POD during daylight hours (between civil dawn and dusk, approximately 7 a.m. to 7 p.m. PST) on each of the days on which aerial surveys were flown.

2. Estimating harbor porpoise densities using distance sampling

Aerial survey line transect effort was divided first into segments with continuous effort in constant sighting conditions (Beaufort sea state) and then divided again into 1-km effort subsegments. Following Becker *et al.* (2010), when it was not possible to divide effort segments exactly into 1-km subsegments, if the remainder of the effort segment was less than 500 m it was added randomly to one of the subsegments, while if the remainder was greater than 500 m a new subsegment was created and positioned randomly into the effort segment. Due to the low probability of observing harbor porpoise in high sea states, only data from the aerial survey effort obtained in Beaufort sea states 0–3 were included. We used the package Distance (v. 0.9.4; Miller, 2015) to fit a detection function to the aerial survey data using a half-normal key function with cosine adjustments. We considered models with and without Beaufort sea state as a covariate and used Akaike's Information Criterion (AIC) to select the best model.

For each subsegment of aerial survey effort, the point density of the harbor porpoise at the midpoint of that subsegment was calculated as

$$\mathrm{d} = \frac{\text{no. harbor porpoise}}{\text{segment length} \times \mathrm{ESW}_{\mathrm{BF}}}, \tag{1}$$

where $\mathrm{ESW}_{\mathrm{BF}}$ is the Beaufort-specific effective strip width. This calculation does not include a correction for the probability of seeing animals directly on the trackline, $g(0)$. In traditional line-transect methods, it is assumed that $g(0) = 1$; however, since cetaceans spend time below the sea surface where they are not detectable by visual observers, $g(0)$ for cetaceans can be considerably less than 1 (Buckland *et al.*, 2001). Our dataset did not allow us to estimate $g(0)$, but a previous study by Laake *et al.* (1997) derived an estimate of $g(0)$ for harbor porpoise in a different region from the same aircraft using the same survey methods under similar survey conditions. Rather than applying this estimate of $g(0)$ directly, we chose to include it as a parameter to be estimated in our Bayesian model in Sec. II B 3 based on prior information (point estimate and associated uncertainty) from Laake *et al.* (1997).

3. Estimating harbor porpoise densities at C-POD locations

To estimate the density of harbor porpoises at the locations of C-POD moorings on each day of aerial surveys, we needed to interpolate the aerial survey observations across the study area. Previously, splines have been used to interpolate discrete observations smoothly to estimate average spatial density (e.g., Forney *et al.*, 2012). Splines create the smoothest possible interpolation and can be useful for visualizing average cetacean densities over long time scales (e.g., seasons, decades; see Becker *et al.*, 2012). In our application, we wished to estimate the spatial density of harbor porpoises separately for each day of aerial survey effort. Splines do not consider the data covariance, which is low over short time scales due to patchy harbor porpoise distributions. To preserve the observed patchiness in the spatial distribution of harbor porpoises, we used a least-squares approach known as objective mapping or Gauss-Markov smoothing (Gandin, 1965; Bretherton *et al.*, 1976; Thomson and Emery, 2014) to estimate the spatial density of harbor porpoises across the study area on each day of aerial survey effort. This technique uses the covariance of the harbor porpoise density data over space to determine the length scales of interpolation and seeks to minimize the interpolation error variance (McIntosh, 1990). Using this objective interpolation technique, we estimated the density of harbor porpoises with associated error at the location of each C-POD on each of the days on which aerial surveys were conducted. It would be preferable to estimate the density of a harbor porpoise within the EDA of each C-POD; however, the EDA of the C-PODs is not known.

4. Bayesian estimation of unknown acoustic detection parameters

Following Marques *et al*. (2009), the proportions of PPS recorded are related to the aerial survey density estimates at each C-POD on each day by the equation

$$\frac{\hat{D}_{m,d}}{\hat{g}(0)} = \frac{n_{m,d}}{T_{m,d}\hat{vp}}, \tag{2}$$

where $\hat{D}_{m,d}$ is the estimated harbor porpoise density (km^{-2}) from the objective interpolation of aerial survey density estimates as estimated for each C-POD location m on each day d. $\hat{g}(0)$ is an informed prior (taken from Laake *et al.*, 1997) on the probability of detecting animals directly on the trackline. $n_{m,d}$ are the number of PPS recorded by each mooring m on each day d, and $T_{m,d}$ is the time (in seconds) monitored between dawn and dusk. $\hat{vp}$ is an uninformed prior on the product of $\hat{v}$, the EDA of the C-POD, and $\hat{p}$, the probability of echolocating within a 1-s period for individual harbor porpoises.

For modeling purposes, we rearranged the equation to solve for $n_{m,d}$,

$$n_{m,d} = \frac{\hat{D}_{m,d}}{\hat{g}(0)} \times T_{m,d} \times \hat{vp}. \tag{3}$$

The passive acoustic data, $n_{m,d}$, were modeled using an overdispersed negative binomial distribution. The parameters of interest to us are $\hat{v}$ and $\hat{p}$. Based on previous research (DeRuiter *et al.*, 2010), we consider $\hat{v}$ to fall between 0 and 0.0314 km^2 (corresponding to radii of 0 to 100 m). Since $\hat{p}$ is a probability, it must fall between 0 and 1.

Due to the high level of uncertainty in the density estimates $\hat{D}_{m,d}$ calculated from the objective analysis of aerial survey data, these estimates were included with their errors and were also estimated by the Bayesian model. $\hat{D}_{m,d}$ were highly informed priors; each $\hat{D}_{m,d}$ was drawn from a lognormal distribution according to the density estimate and associated uncertainty for each C-POD location on each day.

The probability of seeing a harbor porpoise directly on the trackline, $\hat{g}(0)$, has been estimated by Laake *et al.* (1997). In our model $\hat{g}(0)$ was added as a multiplier with a prior distribution based on the estimate from Laake *et al.* [$\mu = 0.292$, standard error (SE) $= 0.107$] converted to a beta distribution.

We implemented this model using the package R2jags (v. 0.5–7; Su and Yajima, 2015). Our model run included 250 000 Markov Chain Monte Carlo samples on four parallel chains, with a burn-in period of 50 000 samples and tenfold thinning.

5. Density estimation using passive acoustic data

To evaluate whether our estimate of $\hat{vp}$ was consistent with previous studies, we explored the parameter space of $\hat{v}$ and $\hat{p}$ consistent with the model estimate. Further, we constructed daily and monthly passive acoustic estimates of harbor porpoise abundance in our study area according to Eq. (2) and compared them to the visual estimates of abundance from our aerial survey dataset. Analytical lognormal 95% confidence intervals were calculated for both the passive acoustic and visual estimates of abundance using the delta method (Seber, 1982; Marques *et al.*, 2009) to incorporate error in the estimates of $\hat{g}(0)$ and $\hat{vp}$. To illustrate how PAM could be used to monitor trends in abundance when knowledge of absolute abundance is not required, we also calculated passive acoustic estimates of abundance assuming that $\hat{g}(0)$ and $\hat{vp}$ were fixed at their median values, so that only variability in the passive acoustic data contributed to the uncertainty of the abundance estimates.

III. RESULTS

A. Data collection

1. Passive acoustic data collected

We deployed a grid of 11 C-PODs in north Monterey Bay at the end of August 2013 and retrieved 10 C-PODs during the first week of January 2014. One mooring became accidentally entangled in fishing gear and was retrieved and returned to us in mid-December 2013. Of our 11 C-PODs, nine instruments returned data (Fig. 1). During daylight hours on the dates when aerial surveys were flown, the nine C-PODs detected a total of 640 high-quality echolocation click trains for a total of 15 717 echolocation clicks. Individual instruments detected between 0 and 97 click trains per day, or between 0 and 2341 echolocation clicks. The resulting number of PPS during daylight hours ranged from 0 to 114 s (Table I), with proportions of PPS per time between 0 and 0.0027 (Fig. 2). In general, instruments

TABLE I. Predicted porpoise densities [PPSQKM (km^{-2}) with associated CVs] at each C-POD location (reported in X and Y m from the centroid of the study area) and observed porpoise positive seconds (PPS) on each year-day (YDay) of monitoring (T = seconds monitored) corresponding to an aerial overflight.

Mooring	X	Y	YDay	PPSQKM	CV	PPS	T
CPOD1	−11499	6273	288	0.05	50.02	0	43 680
CPOD1	−11499	6273	290	0.43	9.19	0	43 380
CPOD1	−11499	6273	304	0.1	34.17	0	41 640
CPOD2	−5278	6273	288	0.16	13.77	3	43 680
CPOD2	−5278	6273	290	3.36	1.16	5	43 380
CPOD2	−5278	6273	304	0.88	3.78	112	41 640
CPOD3	944	6273	288	2.05	1.1	5	43 680
CPOD3	944	6273	290	0.6	6.49	27	43 380
CPOD3	944	6273	304	0.33	10.08	58	41 640
CPOD4	−8392	2381	288	0.04	61.77	29	43 680
CPOD4	−8392	2381	290	0.09	40.88	4	43 380
CPOD4	−8392	2381	304	0.62	5.37	0	41 640
CPOD5	−2168	2381	288	0.52	4.35	NA	0
CPOD5	−2168	2381	290	0.18	21.4	NA	0
CPOD5	−2168	2381	304	0.06	50.76	NA	0
CPOD6	4056	2381	288	4.24	0.53	114	43 680
CPOD6	4056	2381	290	8.74	0.45	99	43 380
CPOD6	4056	2381	304	5.99	0.55	53	41 640
CPOD7	−5283	−1511	88	0.4	5.61	9	43 680
CPOD7	−5283	−1511	290	0.77	4.93	18	43 380
CPOD7	−5283	−1511	304	0.42	7.97	0	41 640
CPOD8	945	−1511	288	1.43	1.59	66	43 680
CPOD8	945	−1511	290	1.64	2.37	32	43 380
CPOD8	945	−1511	304	0.24	13.93	33	41 640
CPOD9	7172	−1511	288	0.91	2.51	28	43 680
CPOD9	7172	−1511	290	15.25	0.25	55	43 380
CPOD9	7172	−1511	304	0.83	4.03	19	41 640
CPOD10	4060	−5403	288	0.02	119	9	43 680
CPOD10	4060	−5403	290	0.09	42.24	1	43 380
CPOD10	4060	−5403	304	0.09	39.28	0	41 640
CPOD11	10290	−5403	288	0.03	88.95	NA	0
CPOD11	10290	−5403	290	0.2	18.56	NA	0
CPOD11	10290	−5403	304	1.34	2.51	NA	0

moored in shallow water recorded higher levels of echolocation activity than those moored in deeper water.

2. Aerial survey data collected

We flew the planned aerial survey tracklines once each on October 15, 17, and 31, 2013, resulting in three replicate aerial surveys in our 370 km^2 study area (Fig. 3). During these three days of aerial surveys, we completed 1228 km of effort in good conditions and observed a total of 245 groups of harbor porpoises. Seventy-two groups were observed on October 15, 104 groups were observed on October 17, and 69 groups were observed on October 31. The mean size of harbor porpoise groups was two individuals. On each of the three survey days, 35%–38% of the study area was effectively searched, based on the estimated ESW of the aerial survey (see below).

B. Analytical results

1. Estimates of harbor porpoise density

We combined the data from our three replicate aerial surveys to estimate the abundance of harbor porpoises in our study area. Our estimate, corrected for $g(0)$ using the estimate from Laake *et al.* (1997) for purposes of comparison, was $N = 1446$ (CV = 0.18) resulting in an average density of 3.9 km^{-2} within the northern Monterey Bay study area. This harbor porpoise abundance estimate is consistent with an independent estimate using the same aerial survey methods of $N = 3715$ harbor porpoises in the entire Monterey Bay population (Forney *et al.*, 2014). Using AIC, we determined that fitting separate detection functions for Beaufort sea states 0–1 and 2–3 (AIC = 2707) was preferable to both a model that ignored Beaufort sea state (AIC = 2711) and a model which fit separate detection functions for each Beaufort sea state (AIC = 2709). The effective strip half-width values for our aerial surveys were 180 m for Beaufort sea states 0–1 and 134 m for Beaufort sea states 2–3. Point densities calculated at individual subsegments ranged from 0 to 42 km^{-2} prior to correction for $\hat{g}(0)$ (see Fig. 3).

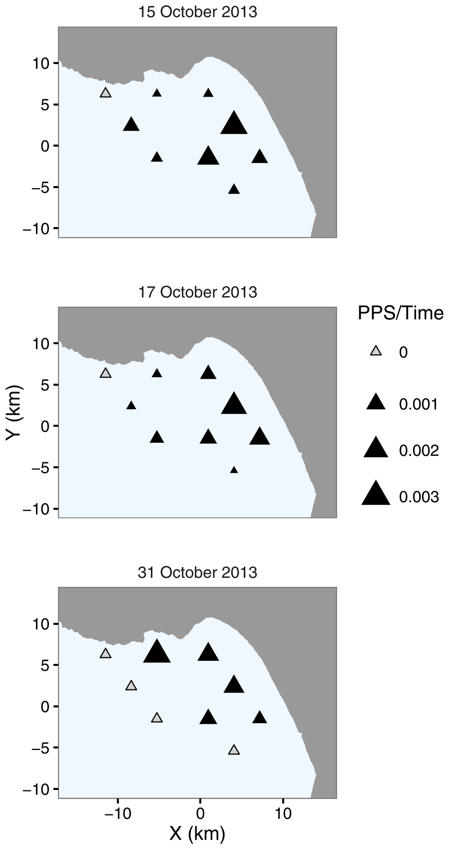

FIG. 2. (Color online) Proportion of seconds between dawn and dusk (approximately 7 a.m. to 7 p.m. PST) during which harbor porpoise were detected acoustically (PPS) by each of nine C-PODs (triangles) on each of the three days when aerial surveys were flown over the study area. Gray triangles indicate instruments that did not detect any high-quality harbor porpoise echolocation clicks, while black triangles are scaled with the non-zero PPS calculated from the C-POD data.

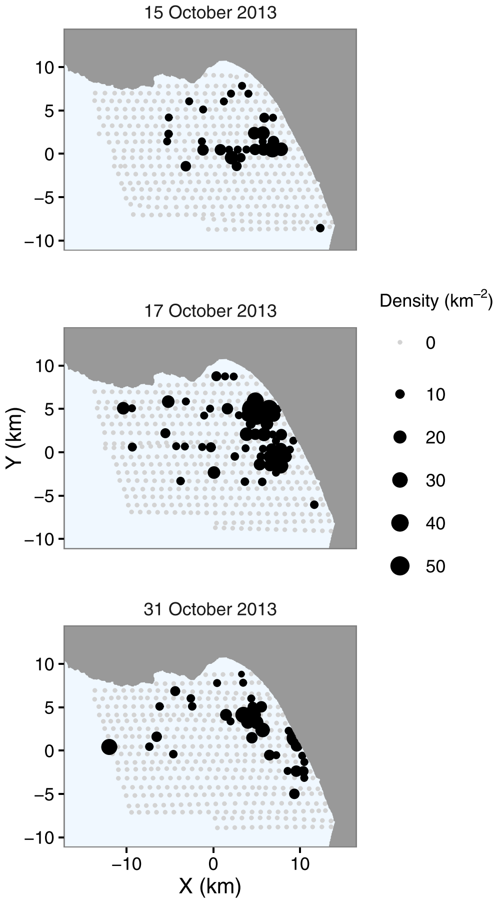

FIG. 3. (Color online) Calculated harbor porpoise point density [uncorrected for $\hat{g}(0)$] at the midpoint of each 1 km aerial survey effort subsegment. Gray circles indicate effort segments where the calculated density was zero, while black circles are scaled with non-zero densities.

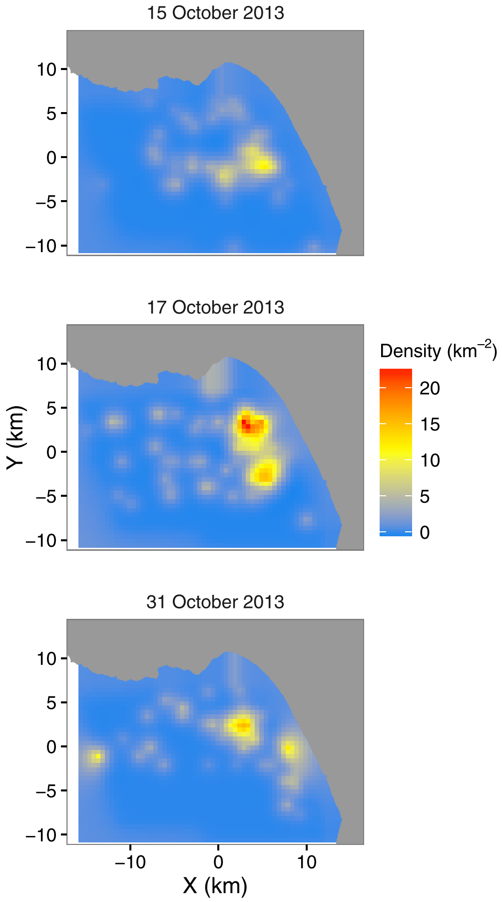

FIG. 4. (Color online) Objective interpolation of harbor porpoise density (km^{-2}) constructed using aerial survey density estimates from three days of aerial surveys in northern Monterey Bay. Note that the reported densities are uncorrected for $\hat{g}(0)$.

2. Maps of interpolated harbor porpoise density

We used objective interpolation to estimate the spatial density of a harbor porpoise across our study area. This allowed us to estimate the density of a harbor porpoise at the point locations of each of the C-PODs on each day that aerial surveys were flown.

The interpolated values of harbor porpoise density ranged from 0 to 66 km^{-2} (Fig. 4). The interpolated densities at individual C-POD locations ranged from 0.06 to 16 km^{-2} (Table I). As is typical with aerial survey data, we observed high levels of uncertainty associated with our density estimates (Table I). The distance between each C-POD and the closest aerial survey effort subsegment ranged from 100 to 500 m. The first zero crossing of the autocorrelation of harbor porpoise density observed on aerial survey effort subsegments was between 6 and 8 km. Since the distance between C-PODs and the nearest aerial survey subsegment fell well within the autocorrelation range of the aerial survey data, we felt confident using objective interpolation to interpolate aerial survey data across our study area. Harbor porpoise density estimates at individual C-PODs were positively correlated with PPS recorded during daylight hours on the days on which aerial surveys were flown ($R^2 = 0.46$; Fig. 5).

3. Bayesian estimation of unknown acoustic detection parameters

We constructed a Bayesian model to combine our visual and acoustic data with previously published information. This was an effective way to incorporate documented uncertainty in our dataset and in previous studies into our analysis.

The posterior distribution of $\hat{g}(0)$ estimated by our model was very similar to the prior distribution and had a

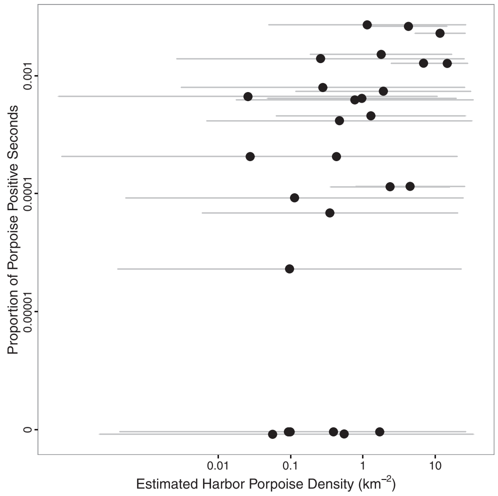

FIG. 5. Harbor porpoise densities at each C-POD location on each day ($N = 27$) as estimated by objective interpolation of aerial survey density estimates with associated 95% confidence intervals (*x* axis) and the proportion of PPS recorded by each C-POD between dawn and dusk on the three days of the simultaneous aerial surveys (*y* axis). Note that the reported porpoise densities are uncorrected for $\hat{g}(0)$.

mean of 0.33, a median of 0.32, and a standard deviation of 0.11 (Fig. 6). Since we did not provide any new information regarding $\hat{g}(0)$ to the model, this result is not unexpected. The posterior distribution of the EDA, $\hat{v}\hat{p}$, had a mean of 0.001 km^2, a median of 7×10^{-4} km^2, and a standard deviation of 0.001 km^2. This result was very different from the mean and standard deviation of the prior distribution given to the model (Fig. 6).

Since we estimated the product of the detection area ($\hat{v}$) and the probability of clicking within a 1-s period ($\hat{p}$), we are unable to resolve the true values of either parameter. However, we plotted the parameter space consistent with our estimate of $\hat{v}\hat{p}$ in terms of $\hat{v}$ and $\hat{p}$ (Fig. 7). If the true value of $\hat{v}$ were very small, we would expect $\hat{p}$ to be large. Conversely, if the true value of $\hat{v}$ were very large, we would expect the true value of $\hat{p}$ to be small. For example, if we knew the true detection radius $\hat{v}$ to be 50 m, we could estimate the probability of clicking within each 1-s period $\hat{p}$ to be, on average, 0.08.

The prior and posterior distributions of individual density estimates associated with each C-POD on each day of aerial surveys are shown in Fig. 8. Estimates that did not overlap the one-to-one line indicate that the posterior density estimate was considerably different from the estimate provided as a prior.

IV. DISCUSSION

Our objective was to use paired visual and passive acoustic surveys to estimate the EDA of C-PODs for the harbor porpoise in Monterey Bay, CA. Using a Bayesian modeling framework, we combined visual and passive acoustic survey data with previously published information to estimate the unknown EDA. With this estimate of the EDA, we were able to estimate harbor porpoise abundance in our study area using passive acoustic data collected over a 3-month period. The approach outlined here can be applied

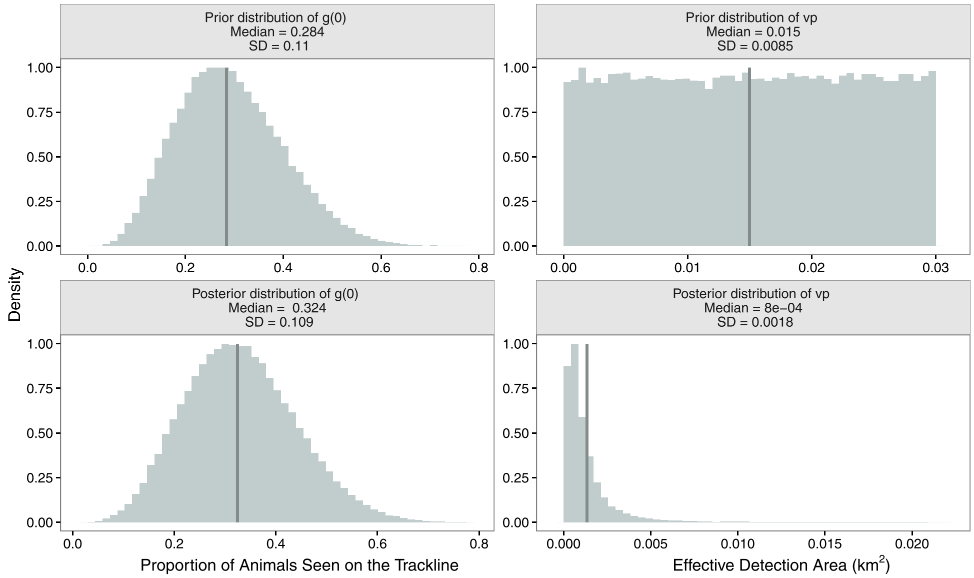

FIG. 6. (Color online) Prior (upper panels) and posterior (lower panels) distributions of $\hat{g}(0)$ (upper panels) and $\hat{v}\hat{p}$ (lower panels) with associated medians (gray lines). Note that the scale of the *x* axis is not constant across plots.

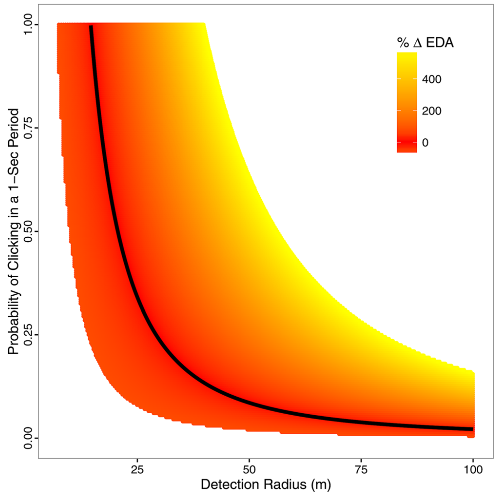

FIG. 7. (Color online) Parameter space of the detection radius (v) and the probability of clicking within a 1-s period (p) consistent with the model estimate of the EDA ($\widehat{vp}$). The black line indicates the median estimate and all possible combinations of v and p that fall within the 95% credibility interval of the model estimate of the EDA are shown. The color scale indicates the percent change in EDA relative to the estimate, with darker colors indicating values closest to the median.

to other species and regions where researchers wish to transition from aerial surveys to passive acoustic methods for monitoring trends in cetacean abundance.

We used objective interpolation to estimate the spatial density of the harbor porpoise across our study area from line-transect aerial surveys. Aerial survey data are inherently highly variable, due to both process (e.g., patchy harbor porpoise distribution) and observation (intermittent visual availability, observer perception) errors. Multiple aerial surveys conducted on a single day would likely reduce the uncertainty associated with point estimates of harbor porpoise density at individual C-POD locations; however, this would be an expensive and logistically difficult undertaking. Due to the variability in aerial survey data, it is difficult to interpolate these data with a high degree of certainty. Our adaptation of objective interpolation for this task used the underlying statistics of the data to determine the length scales of interpolation, allowing us to interpolate across the study area while recognizing the uncertainty associated with doing so. This approach also avoided oversmoothing the aerial survey data and preserved the patchy harbor porpoise distributions observed during aerial surveys.

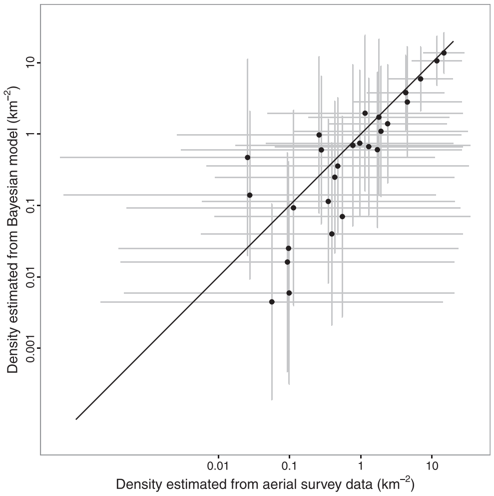

FIG. 8. Mean harbor porpoise density (km^{-2}) at the location of each C-POD on each day ($N = 27$) as estimated by the objective interpolation of aerial survey data (x axis) and as estimated by the Bayesian model (y axis) with associated 95% confidence and credibility intervals for the two approaches. The one-to-one line (black line) indicates perfect agreement.

Daily and monthly estimates of abundance generated using visual and passive acoustic data had similar means; however, uncertainty was much greater in the passive acoustic estimates than in the visual estimates of abundance (Fig. 9, first and second panels). Uncertainty in the passive acoustic abundance estimate is large because of variability in both the passive acoustic records and in the aerial survey data; since the passive acoustic abundance estimate relies on the EDA estimated using aerial survey data it effectively incorporates all uncertainty in both survey methods. However, the mean abundance estimates were relatively stable over time, giving us confidence that this method works albeit with large uncertainties.

Ideally, the EDA should be estimated separately for each instrument and each set of environmental conditions (Kyhn *et al.*, 2012). Harbor porpoise click propagation can change with factors including temperature, depth, salinity, and substrate type (DeRuiter *et al.*, 2010) resulting in different EDAs. Similarly, harbor porpoise foraging and echolocation behavior can vary with time of day, season, and location (Carlstrom, 2005). With our limited dataset, we were not able to estimate EDAs specific to each C-POD. If enough paired surveys (e.g., $N = 10$) were conducted, a hierarchical framework could be used to estimate an EDA specific to each C-POD. It is possible that some of the variance in the posterior density distributions is due to this unaccounted for source of variation in detectability, since, for example, sensors in shallow water may have different EDAs from sensors in deep water.

If we assumed that detectability were constant over time (i.e., no seasonal changes in echolocation click rates or detectability), our estimated EDA could be used to estimate harbor porpoise abundance in our study area at times when visual surveys were not conducted (Fig. 9, second and third panels). If we wished to estimate trends in abundance rather than absolute abundance, we could ignore the uncertainty in the estimated EDA, though changes in the EDA over time and space would still be an issue. When the uncertainty in the EDA was not included (Fig. 9, fourth panel) the uncertainty in the passive acoustic abundance estimates was considerably lower and more in line with that of the visual abundance estimates. In our study, aerial surveys were

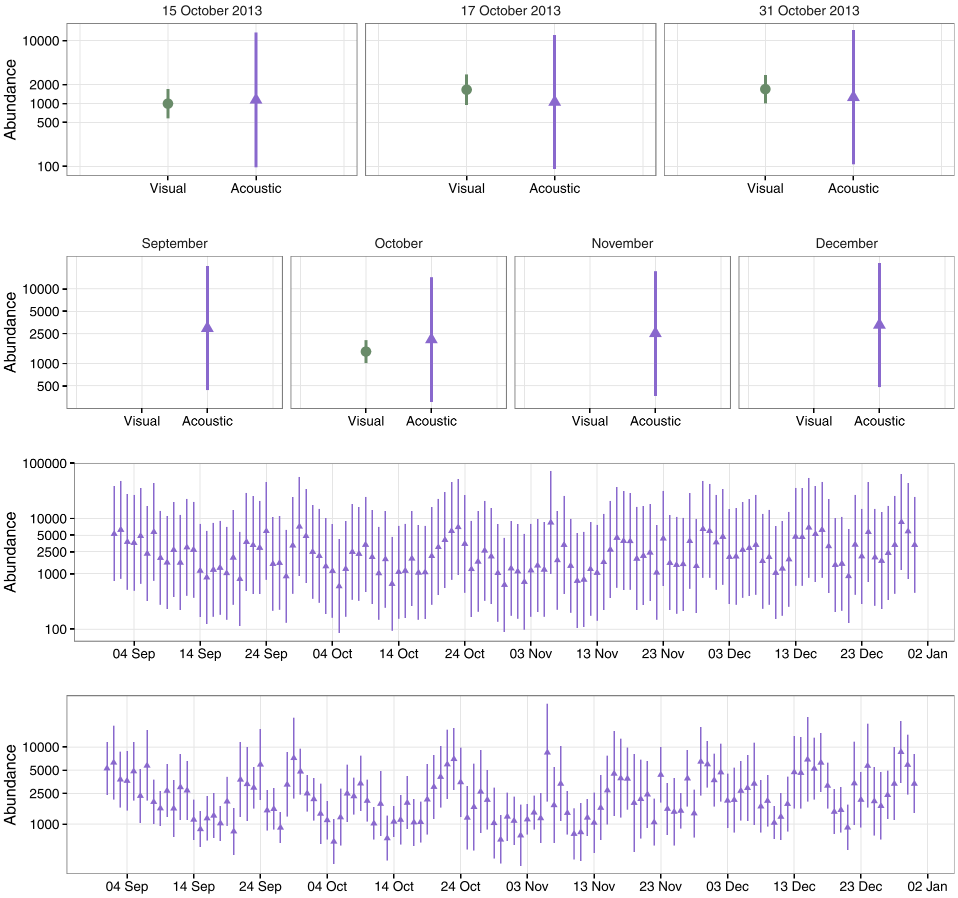

FIG. 9. (Color online) Visual (green circles) and passive acoustic (purple triangles) estimates of harbor porpoise abundance in the Monterey Bay study area with 95% confidence intervals calculated for each of the three days of effort used in this study (first panel), each month for which passive acoustic data were available (second panel), and for each day on which passive acoustic data were available with error in the estimates of $\hat{vp}$ and $\hat{g}(0)$ included (third panel) and without error in the estimates of $\hat{vp}$ and $\hat{g}(0)$ included (fourth panel).

conducted on days with relatively low recorded echolocation activity (Fig. 9, fourth panel), indicating that the visual estimate may be an underestimate of the average abundance of harbor porpoise in this area.

V. CONCLUSIONS

Paired visual and passive acoustic surveys can be used to estimate the detectability of cetaceans. Our study demonstrates that using this technique, it is possible to generate passive acoustic estimates of harbor porpoise abundance that are consistent with aerial survey estimates of abundance. This approach is most feasible in areas with high cetacean densities and may not work in regions where very few animals are observed during visual surveys and reliable interpolation of visual survey data are not possible. For paired survey parameter estimation to be used effectively, more visual surveys are needed to increase the sample size of the paired dataset and decrease the uncertainty in the estimated EDA. With enough simultaneous aerial surveys, it might be possible to estimate EDAs specific to individual passive acoustic sensors. This would allow parameters to be estimated for instruments in different water depths and with different substrate types, facilitating the extrapolation of estimated parameters to regions where paired surveys have not been conducted.

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Chapter 4, in full, is a reprint of material as it appears in the Journal of the Acoustical Society of America: Jacobson, E. K., K. A. Forney, and J. Barlow, 2017, volume 141, pages 219-230. The dissertation author was the primary investigator and author of this paper.

Chapter 5

PAMPower: Investigating the statistical power of passive acoustic monitoring networks to detect trends in cetacean abundance

Abstract

Passive acoustic surveys for long-term monitoring of cetacean populations are now feasible; however, there is no framework for optimizing such surveys to maximize their precision and the resulting statistical power to detect trends in abundance. In this study, we used simulations to explore alternative fixed passive acoustic survey designs for detecting trends in the abundance of harbor porpoise in Monterey Bay, CA. Using aerial survey and passive acoustic data collected in Monterey Bay, we simulated datasets for hypothetical passive acoustic monitoring network designs and changes in harbor porpoise abundance. We considered the number and geographic placement of sensors and scenarios of overall population decline as well as range contraction to a core habitat area. When the population declined uniformly over its geographic range, the placement of sensors did not impact power to detect a trend in abundance. However, scenarios in which animals contracted to core, high-quality habitat resulted in lower power to detect trends in abundance. Our simulation study demonstrated that the effectiveness of PAM varies greatly depending on both survey design (number and placement of sensors) and manifestation of the change in the population (extent and spatial pattern of increase or decrease). When planning passive acoustic surveys, it will be important to consider different possible population responses so that power can be accurately assessed and an appropriate number and placement of sensors employed. While this simulation study was specific to the Monterey Bay population of harbor porpoise and employed a specific type of passive acoustic sensor, our results are generalizable to other regions, species, and types of passive acoustic surveys.

5.1 Introduction

Knowledge of population abundance and trend is crucial for effective management and conservation. Animal abundance is monitored to identify species of concern, to evaluate the success of conservation actions, and to calculate allowable removal or incidental harm of individuals. Because it is rarely possible to count all of the individuals within a population, statistical methods for estimating population size have been developed. For marine mammals, these methods have traditionally relied on visual observations of the species of interest. For cryptic or visually inaccessible taxa, like many cetaceans, visual surveys often produce imprecise estimates of animal abundance. However, these hard-to-see species produce sounds that are comparatively easy to detect and therefore can be used as proxies for the animals themselves (Zimmer, 2009). Recent advances in recording technology, detection and classification algorithms, and statistical methods have led to the development and rapid growth of passive acoustic monitoring (PAM) and, in particular, passive acoustic density and abundance estimation of cetaceans (Marques et al., 2013). For many cetacean species, there is enormous potential to use passive acoustic methods to increase the precision of abundance estimates, thereby improving our ability to monitor and detect changes in populations over time.

Here, we focus on cetaceans, which are particularly difficult to monitor using visual methods because they spend much of their time below the surface of the water, where they are not observable. High natural variability in cetacean distributions combined with the high sampling variance associated with typical visual surveys (e.g., due to low effort, inclement conditions, missed groups, and group size estimation error) lead to low precision in visual abundance estimates and, therefore, low statistical power to detect changes in abundance. In the U.S., given the current frequency and extent of cetacean surveys, 50% declines over a 15-year period would be undetectable in 90% of beaked whale populations and 78% of dolphin and porpoise populations (Taylor et al., 2007). Without the ability to detect changes in the abundance of these populations, it is difficult to implement effective management actions.

PAM is an excellent alternative to visual surveys for odontocete cetaceans which frequently produce echolocation clicks, whistles, and other vocalizations that can be detected at distances that are similar to or greater than visual detection distances. Fixed PAM networks in particular are a relatively inexpensive monitoring technology and can be deployed for months at a time. Compared to visual surveys, the long deployments of PAM sensors provide data with lower variance, which increases the precision of the resulting abundance estimates and therefore statistical power to detect trends. PAM networks have been used to estimate the abundance of Blainville's beaked whales (*Mesoplodon densirostris;* Marques et al., 2009) and sperm whales (*Physeter macrocephalus;* Ward et al., 2012) in the Bahamas, Baltic Sea harbor porpoise (*Phocoena phocoena;* Benke et al., 2014) and North Pacific right whale (*Eubalaena japonica;* Marques et al., 2011), and to document the decline of the critically endangered vaquita (*Phocoena sinus;* Jaramillo-Legorreta et al., 2017) in the Gulf of California.

Long-term monitoring of cetacean populations is now feasible through advances in affordable underwater instrumentation, improvements in cetacean vocalization detection algorithms, and development of statistical methods for estimating animal abundance using passive acoustic data (Zimmer, 2009). However, there is no framework for optimizing PAM surveys to maximize precision. To date, most studies attempting to estimate cetacean abundance using passive acoustic data have either used existing acoustic datasets (e.g., Harris et al., 2013) or relied on general design principles from the visual survey literature to guide data collection (e.g., Jaramillo-Legorreta et al., 2017). There is a growing need in science, management, and industry for quantitative design criteria to optimize the implementation of passive acoustic monitoring networks for cetaceans.

We use the Monterey Bay population of harbor porpoise as a case study to evaluate the statistical power of potential passive acoustic network designs to detect trends in abundance. This population occupies a nearshore area of approximately 2,500 km^2 and consists of approximately 3,700 individuals (Forney et al., 2014). This population is distinct from other harbor porpoise populations along the U.S. West Coast (Calambokidis and Barlow, 1991; Chivers et al., 2002). While fishery mortality is currently insignificant for this population (Carretta et al., 2015) the population is likely still recovering from bycatch in set gillnet fisheries for halibut that operated in the late-20th century (Jefferson et al., 1994; Forney et al., 2014) and earlier gillnet fisheries for white seabass (Barlow and Hanan, 1995). There have also been some deaths over the past decade due to bottlenose dolphin *(Tursiops truncatus)* attacks on harbor porpoise in this region (Cotter et al., 2012; Wilkin et al., 2012; Jacobson et al., 2014). The Monterey Bay population of harbor porpoise has been studied using line-transect aerial surveys since the late 1980s (Forney et al., 1991). Additionally, since 2000, line-transect aerial surveys targeting leatherback sea turtles have been conducted in the region using the same survey methodology, thereby also collecting data on cetaceans including harbor porpoises.

In the present study, we use aerial survey data collected in Monterey Bay to estimate the mean density of harbor porpoise across the region. Then, we relate these underlying mean porpoise densities to passive acoustic detection rates observed over a three-year period. Using this paired dataset, we simulate hypothetical changes in harbor porpoise abundance and corresponding changes in passive acoustic detection rates. Through these simulations we explore alternative fixed passive acoustic survey design for detecting trends in the abundance of the Monterey Bay population of harbor porpoise.

5.2 Methods

Aerial survey data collection and analysis

Aerial surveys have been conducted in the Monterey Bay region using a consistent survey methodology since the late 1980s (Forney et al., 1991). In the present study, we use aerial survey data collected during surveys for harbor porpoise and leatherback sea turtles between 2000 and 2013 (Fig. 5.2, left panel; Table 5.2). All surveys were conducted from a Partenavia P-68 high-wing two-engine aircraft. During aerial surveys, two observers searched from bubble windows on either side of the aircraft while a third observer searched from a belly window in the rear of the aircraft. A data recorder transcribed verbal sighting information for cetaceans and turtles (including declination angle, species, and number of animals) and environmental (visibility conditions) information from the observers into a custom-written software program on a laptop computer that was directly connected to a hand-held Global Positioning System.

Aerial survey line-transect data were read from tab-delimited files into R (v. 3.2.2, R Core Team, 2016) for processing. All data were converted from geographic coordinates (latitude and longitude) into a custom two-dimensional projection (X and Y km from the centroid of the study area) using the spherical law of cosines to ensure uniformity of calculated distances (Miller et al., 2013). Aerial survey line transect effort was divided first into segments with continuous effort in constant sighting conditions (Beaufort sea state) and then divided again into 1-km effort subsegments. Following Becker et al. (2010) and Jacobson et al. (2017), when it was not possible to divide effort segments exactly into 1-km subsegments, if the remainder of the effort segment was less than 500m it was added randomly to one of the subsegments, while if the remainder was greater than 500m a new subsegment was created and positioned randomly into the effort segment. Due to the low probability of observing harbor porpoise in high sea states, only data from the aerial survey effort obtained in Beaufort sea states 0–3 are included.

We used the R package Distance (v. 0.9.4; Miller, 2016) to fit a detection function to the aerial survey data using a halfnormal key function with cosine adjustments. We considered models with and without Beaufort sea state as a covariate and used Akaike's Information Criterion (AIC) to select the best model. Following Jacobson et al. (2017), we calculated the point density of harbor porpoise at the midpoint of each subsegment of aerial survey effort. This calculation does not include a correction for the probability of missing animals directly on the trackline (i.e., $g(0) < 1$).

To generate an average, decadal-scale harbor porpoise density surface in our study region, we used a generalized additive model (GAM; Hastie and Tibshirani, 1986) implemented in the package mgcv (v. 1.8-12; Wood, 2017) with a log link to model harbor porpoise density at the midpoint of each effort subsegment as a function of a two-dimensional thin-plate regression spline (Wood, 2003) on projected coordinates X and Y from the centroid of the study area. We used a Tweedie distribution to account for overdispersion in the response variable. The smoothing spline was optimized using the outer Newton method and penalized for overparameterization with restricted maximum likelihood (REML).

Passive acoustic data collection and analysis

In 2013, 2014, and 2015 we installed a grid of PAM sensors (C-PODs; Chelonia Ltd., United Kingdom, www.chelonia.co.uk) in northern Monterey Bay (Fig. 5.2, right panel). C-PODs detect harbor porpoise echolocation clicks and store summary information about detected clicks. Instruments were deployed between late July and late August and retrieved between early December and early February each year. In all years, instruments were consistently deployed for the months of September, October, and November, with exact deployment and retrieval dates dependent on suitable weather conditions and availability of a research vessel and required personnel. These seasonal deployments were designed to be consistent with historical aerial survey effort in the region, most of which has occurred in August, September, and October. The passive acoustic study area included waters from 10 to 100 m depth, north of 36.8° N and east of 122.1° W, with a total area of 370 km^2. The study design was a systematic, randomly positioned offset grid of 11 C-PODs spaced 0.035° latitude and 0.07° longitude apart and oriented to follow the shape of the coastline (see Fig. 5.2, right panel). Further details of passive acoustic instrument deployments can be found in Jacobson et al. (2015) and Jacobson et al. (2017).

C-POD data were processed using the KERNO algorithm in the program CPOD.exe (v. 2.044; Tregenza, 2012) to detect click trains. All narrowband, high-frequency (NBHF) click trains were classified as belonging to harbor porpoise. Dall's porpoise *(Phocoenoides dalli)* are also found along the U.S. West Coast and produce similar NBHF echolocation signals; however, Dall's porpoise are typically found in deep water (100s to 1000s of m deep; Forney, 2000) and no Dall's porpoise were seen in our study area during aerial surveys conducted in 2011 or 2013. We chose to include only high-quality click trains (as defined by the KERNO algorithm) in our analysis in order to minimize false positives in the dataset. Data were exported from CPOD.exe and all further analyses are performed in R (v. 3.2.2; R Core Team, 2016).

Following Jacobson et al. (2017), we chose to use the number of porpoise positive seconds (PPS) as our passive acoustic metric. This metric is less likely to become saturated when multiple animals are present and it reduces the impact of animal orientation on detectability by effectively averaging over 1-s periods. This metric assumes that only one porpoise can be detected within any 1-s period. For each instrument and year, PPS was calculated as the total number of porpoise positive seconds between September 1st and December 1st of each year (a 91 day period).

Relating passive acoustic and aerial survey data

To simulate changes in passive acoustic detection rates resulting from changes in harbor porpoise abundance, we first need to describe the relationship between the density of harbor porpoise (as estimated using aerial survey data) and observed passive acoustic detection rates. We used a generalized linear model (GLM; Eq. 5.1) to relate the log-transformed passive acoustic detection rate (PPS) at each instrument n and year y to the log-transformed average underlying harbor porpoise density at the location of each instrument ($\hat{D}_n$) as estimated by the spatial smooth of aerial survey observations. The intercept α_0 and covariate β_1 describe the relationship between the density of harbor porpoise and the passive acoustic detection rate.

$$log(PPS_{n,y}) \sim \alpha_0 + \beta_1 log(\hat{D}_n) + \beta_2 Y_y + \varepsilon \tag{5.1}$$

We include a covariate (β_2) for year (Y_y) to account for potential differences in the actual passive acoustic detection rates between years (e.g., due to continuing population recovery from past impacts). By explicitly describing between-year variance in the model formulation, we are able to more precisely estimate the relationship between the density of harbor porpoise and the passive acoustic detection rate. This allows us to simulate only the hypothetical changes in density that we wanted to investigate. The error term ε describes unexplained variance in the relationship between harbor porpoise density and passive acoustic detection rate.

Simulation methods

We use the estimated harbor porpoise density surface from aerial surveys and the observed relationship between passive acoustic detection rates and harbor porpoise density (as described by Eq. 5.1) to create simulated datasets for hypothetical passive acoustic monitoring networks over 10-yr periods. Our simulation explores three possible survey designs and two possible behavioral responses to population change, resulting in six hypothetical scenarios. We simulate changes in abundance from -50% to +50% over 10-yr periods and designs with 5 to 100 passive acoustic sensors. All combinations of survey design, response to disturbance, change in abundance, and number of passive acoustic sensors (see Table 5.1) are repeated 1,000 times. Power is defined as the proportion of the 1,000 simulations in which a statistically significant change in the population ($\alpha = 0.05$) is detected with the correct sign (i.e, positive or negative).

Three possible strategies for sensor placement are investigated. In the *random* sampling scenario, sensors are placed randomly throughout the study area in water 0 to 150 m deep (Fig. 5.1, left panel). Harbor porpoise densities are highest near shore, so we also generate a *stratified* sampling strategy where sensors are allocated to shallow (0-40 m deep) and deep (40-150 m deep) strata in proportion to harbor porpoise density in the two strata (Fig. 5.1, right panel). Finally, we develop a sampling strategy proportional to the mean density of harbor porpoise in our study area, which we refer to as a *scaled* sampling design. For this third design, we rescale the density values calculated using the aerial survey data to be between 0 and 1; i.e., locations with highest densities are assigned a value of 1, but the distribution of densities is not altered. Then, we iteratively select points at random and conduct a binomial trial where the probability of success was equal to the rescaled harbor porpoise density at that point. If the trial is successful, that point is included as a location for sensor deployment; we repeat this process until we achieve the desired number of sensors. This method results in a distribution of sensors that mirrors the distribution of

Table 5.1: Description of variables used in the simulation.

Variable	**Description**	**Values**
Design	Controls simulated placement of sensors	Random, Stratified, or Scaled
Response	Controls how animals respond to change	Uniform or Range Contraction
Change	Change in the population over a 10-yr period	-50% to +50%
No. Sensors	Number of sensors deployed each year	5 to 100

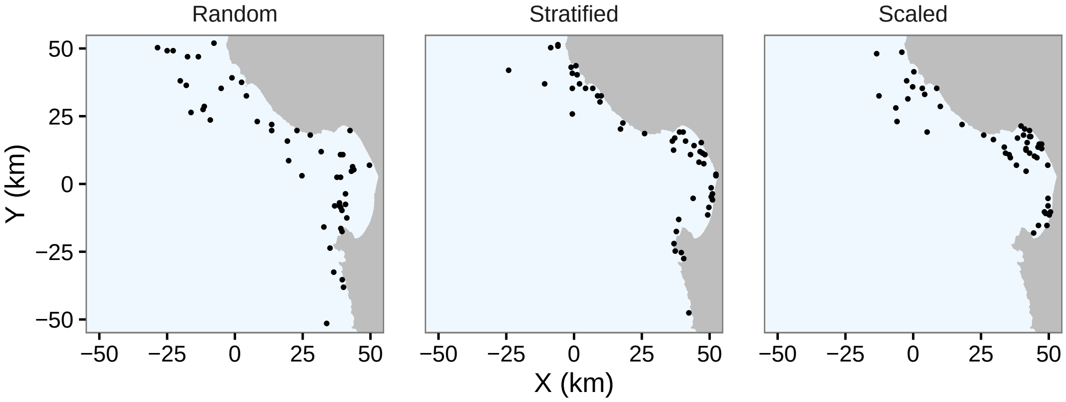

Figure 5.1: Example simulated placement of 75 sensors in the Monterey Bay study area using random (left panel), stratified (center panel), and scaled (right panel) sampling design strategies in water 0-150 m deep.

harbor porpoise, with more sensors in high-density areas and fewer sensors in low-density areas. For each of the three possible survey designs, we simulate designs with 5-100 sensors. For computational efficiency, spacing between sensors is not considered in any of our three sampling designs.

We simulate two possible scenarios of harbor porpoise population response to disturbance. In the base scenario, the population is assumed to change uniformly over the study area. In the range contraction scenario, we hypothesize that animals may contract their distribution to the highest-quality habitat as the population declines (Lomolino and Channell, 1995). To implement this, we again use the underlying mean density of harbor porpoise as calculated from the aerial survey data to inform a habitat quality score for each point in the study area. We assume that harbor porpoise density is positively and linearly related to habitat quality. We use this relationship to scale the simulated impact, so that high-density, high-quality habitat areas experienced less severe decline than low-density, low-quality habitat areas.

The simulated rate of change is divided into incremental change rates r_y over $y = 10$

yr such that the product of the r_y is equal to the total desired change R. Because a population is unlikely to change in identical stepwise increments each year, we choose to add variability to the rate of change over time. We draw $y-2$ values of r_y from a normal distribution with mean = $(1+R)^{(1/(y-1))}$ and standard deviation (SD) = 0.05. The choice of SD is arbitrary. The final r_y value is calculated so that $R = \prod_{i=1}^{y-1} r_y$. Finally, the values of r_y are randomly reordered. We simulate rates of change from -50% (i.e., the population decreased by half) to +50% (i.e., the population increased by half).

For each simulation run, a single intercept term a is drawn from a normal distribution with a mean and standard error (SE) from the GLM model estimate of α_0. For each of n simulated sensors, a spatial location is drawn randomly according to the survey design and a simulated underlying density d_n is drawn from a normal distribution with mean and SE of the estimated $\hat{D}$ at that location. Coefficients for the effect of density on detection rate at the location of each sensor $b_{1,n}$ are drawn from a normal distribution with mean and SE from the model estimate of β_1. As described above, a cumulative rate of change $\prod_{i=1}^{y-1} r_y$ is applied in each time step. Because there is unexplained variance in the modeled relationship between harbor porpoise density and passive acoustic detection rate (see Eq. 5.1), we add an error term $E_{n,y}$ drawn from a normal distribution with a mean of 0 and a SD equal to the residual SD of the GLM.

$$pps_{n,y} = e^{(a_0+b_{1,n}log(d_n)+E_{n,y})} \times \prod_{i=1}^{y-1} r_y \tag{5.2}$$

Once data $pps_{n,y}$ are generated for n moorings and y years, each simulated dataset is evaluated using a mixed effects model (Eq. 5.3) with $log(pps_{n,y})$ modeled as a function of year (fixed effect) and sensor (random effect). This model differs from the GLM in Eq. 5.1 in that the underlying mean density is assumed to be unknown, so a random effect is used to account for sensor-specific differences in detection rates. For each simulated dataset, if the year term in this mixed effects model is significant ($\alpha < 0.05$) and the sign of the covariate

λ matches the sign of the simulated change in the population, that particular iteration is marked as a success.

$$log(pps_{n,y}) \sim \lambda y + \gamma_n + \varepsilon \tag{5.3}$$

This process is repeated for each of the 1,000 simulated datasets and statistical power is calculated as the proportion of those 1,000 datasets in which a change (in the correct direction, positive or negative) was statistically significant ($\alpha < 0.05$). We repeat the simulation methods for each possible combination of survey design, response to change, number of sensors, and change in the population.

5.3 Results

Aerial survey data collected

Between 2000 and 2013, 31,722 km of aerial survey effort in good weather conditions (Beaufort sea states 0-3) was conducted in the Monterey Bay region (Fig. 5.2, left panel),

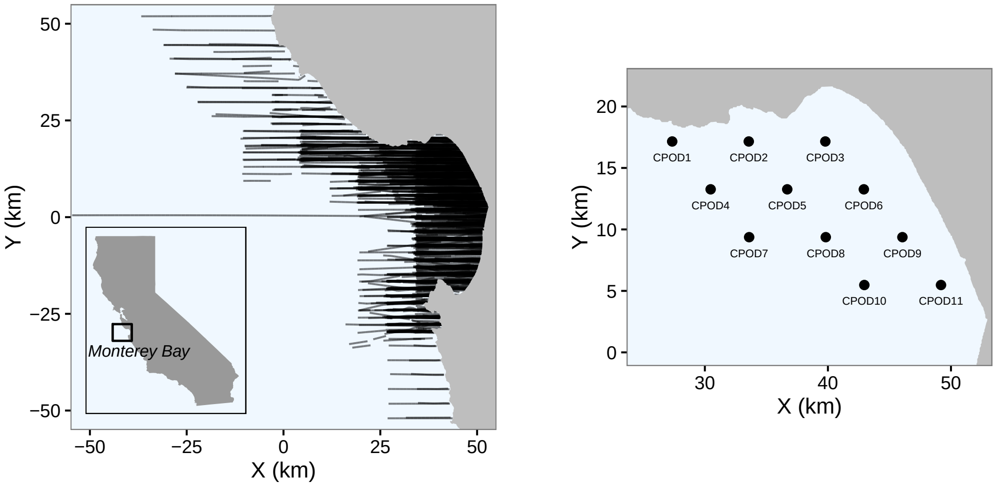

Figure 5.2: Map of completed aerial survey tracklines (left panel, black lines) and passive acoustic instrument deployments (right panel, black circles) in Monterey Bay, CA.

Table 5.2: Aerial survey effort (km) and number of harbor porpoise sightings (groups) per year between 2000 and 2013.

Year	**Survey Effort (km)**	**Porpoise Sightings**
2000	342	11
2001	2,972	200
2002	4,017	252
2003	3,837	300
2004	6,840	528
2005	2,124	202
2006	1,178	76
2007	1,271	91
2008	137	9
2009	1,500	176
2010	951	161
2011	2,566	202
2012	1,014	94
2013	2,973	383
Total	31,722	2,715

resulting in 2,715 sightings of harbor porpoise groups (Table 5.2). More sightings occurred in shallow (0-40 m) water depths than in deep (40-150 m) depths (Fig. 5.4, lower panel). 17% of effort and less than 2% of sightings occurred in water 150-1000 m deep. The quantity of aerial survey effort varied among years (Table 5.2) and months (Fig. 5.3), with most effort occurring in August, September, and October. Most aerial survey effort occurred within the Monterey Bay itself (Fig. 5.2, left panel). The GAM explained 24.7% of deviance in the aerial survey data, which is comparable to other cetacean-habitat models (e.g., Gilles et al., 2016). The bivariate smooth term on X and Y km from the centroid of the study region was significant ($p < 0.001$). The GAM predicted highest densities of harbor porpoise in the northern part of Monterey Bay with moderate densities predicted in nearshore southern Monterey Bay (Fig. 5.5).

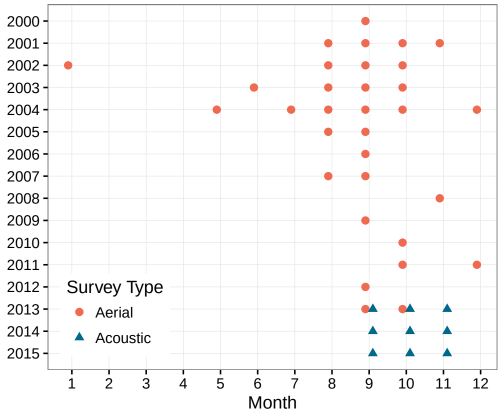

Figure 5.3: Visual representation of aerial survey and passive acoustic data collection in the Monterey Bay region in different months (*x*-axis) between 2000 and 2015 (*y*-axis). Circles indicate month/year combinations during which aerial surveys were conducted, while triangles indicated month/year combinations during which passive acoustic data were collected.

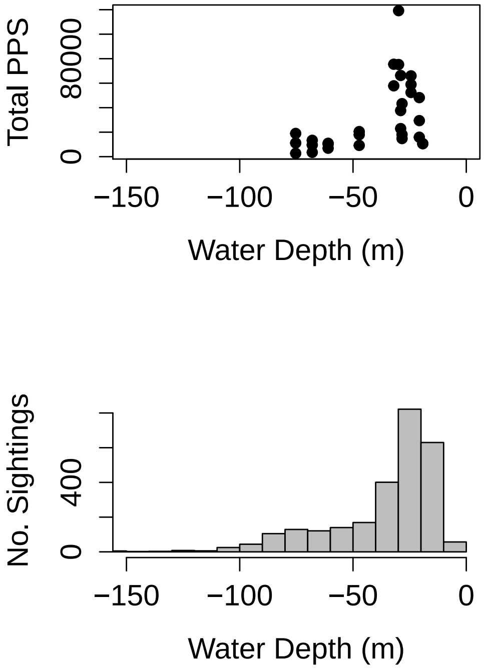

Figure 5.4: Water depth (0-150 m, *x*-axis) in Monterey Bay vs. total PPS observed by C-PODs (top panel) and number of visual harbor porpoise sightings (bottom panel).

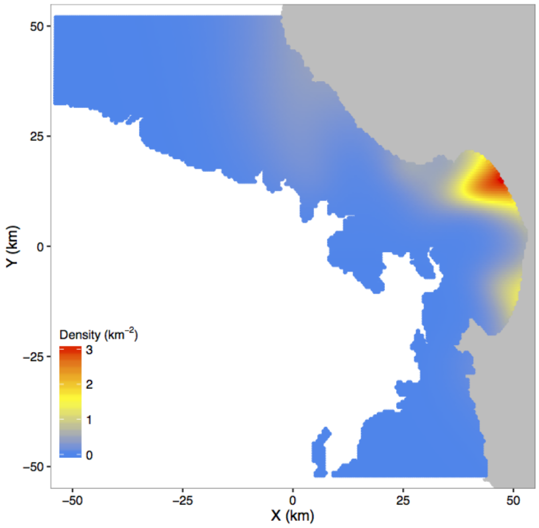

Figure 5.5: Harbor porpoise density (km^{-2}) in water 0-1000 m deep estimated using a two-dimensional spline on harbor porpoise density calculated using aerial survey observations. Note that densities are not corrected for $\hat{g}(0)$.

Passive acoustic data collected

We deployed 11 C-PODs in north Monterey Bay in the late summer or early fall of 2013, 2014, and 2015. Instruments were retrieved between early December and early February each year, so that instruments were deployed for approximately four months per year. Data were recovered from nine instruments in the 2013 season, 10 instruments in the 2014 season, and 11 instruments in the 2015 season, for a total data loss rate of 9% over the three-year study. Passive acoustic detection rates varied by two orders of magnitude among instruments, with recorded values as low as 30 PPS per day and as high as 1,320 PPS per day, and total PPS over the course of the season as low as 2,707 and as high as 119,209 (Table 5.3). Nearshore instruments (C-POD 3, C-POD 6, and C-POD 9) recorded higher detection rates than offshore instruments (C-POD 4, C-POD 5, C-POD 7, C-POD 8, C-POD 10; Table 5.3; Fig. 5.2; Fig. 5.4).

Table 5.3: Passive acoustic detection rates (total PPS over 91 days) recorded on each of 11 C-PODs (rows) during three years of data collection (columns). NA values indicate that the instrument was lost or that no data were recovered from the instrument.

Instrument	**PPS**		
	2013	2014	2015
C-POD 1	18,057	14,771	43,280
C-POD 2	10,601	NA	10,610
C-POD 3	15,879	48,206	29,426
C-POD 4	20,481	9,201	17,919
C-POD 5	NA	75,473	57,840
C-POD 6	65,991	58,923	52,403
C-POD 7	9,585	3,528	13,331
C-POD 8	6,872	10,923	10,228
C-POD 9	22,925	66,293	37,639
C-POD 10	2,707	11,143	18,959
C-POD 11	NA	119,209	75,229

Relationship between passive acoustic and aerial survey data

Underlying mean density surface as calculated using aerial survey observations is a significant predictor of harbor porpoise click detection rate ($p < 0.001$; Fig. 5.6). A GLM with a year term included performs better (AIC = 71) than a GLM with only harbor porpoise density as a predictor (AIC = 74). The pseudo-R^2 of this model was 0.44. The year term is also significant ($p < 0.05$) with a positive covariate indicating a possible increase in the population or movement of animals into the study area over the three-year passive acoustic monitoring period.

Simulation results

With random placement of sensors and geographically uniform changes in the population, a -50% change in the population over a 10-yr period can be detected 80% of the time with as few as 10 sensors (Fig. 5.7). With 100 sensors, a -20% change in the population is detectable 80% of the time, and a -30% change is detectable 100% of the time. When considering increases and decreases of the same magnitude (e.g., a +25% vs. -25% change),

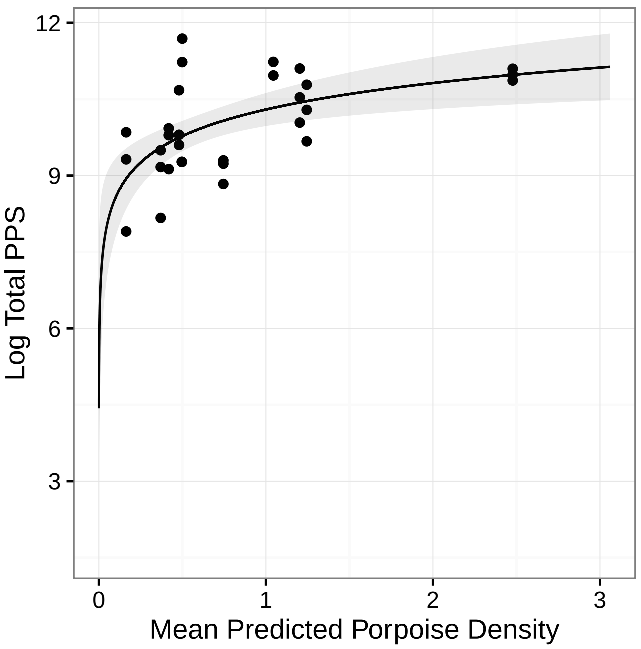

Figure 5.6: Black dots indicate estimated mean harbor porpoise density at the location of each C-POD (km^{-2}; x-axis) and mean observed acoustic detection rate in each year (PPS; y-axis). The black line is the modeled relationship between mean density and mean acoustic detection rate (pooled across all years) and the gray shading indicates the 95% confidence interval of the model fit.

statistical power is greater for decreases than for increases. This asymmetry is due to the relative effect size of the change.

When the simulated population declines uniformly over its geographic range, the placement of sensors (random, stratified, or scaled) does not impact power to detect a trend in abundance. However, scenarios where animals contract to core, high-quality habitat result in lower power to detect trends in abundance. For example, when 75 sensors are used and the population declines by 25% over the 10-yr period (Table 5.4), random placement of sensors results in the lowest power when animals respond with range contraction (power = 0.72); using a stratified design improves power (power = 0.79), and a survey design with sensors placed in proportion to the underlying harbor porpoise density (scaled design) results in the highest power to detect trends in abundance under the range contraction scenario (power =

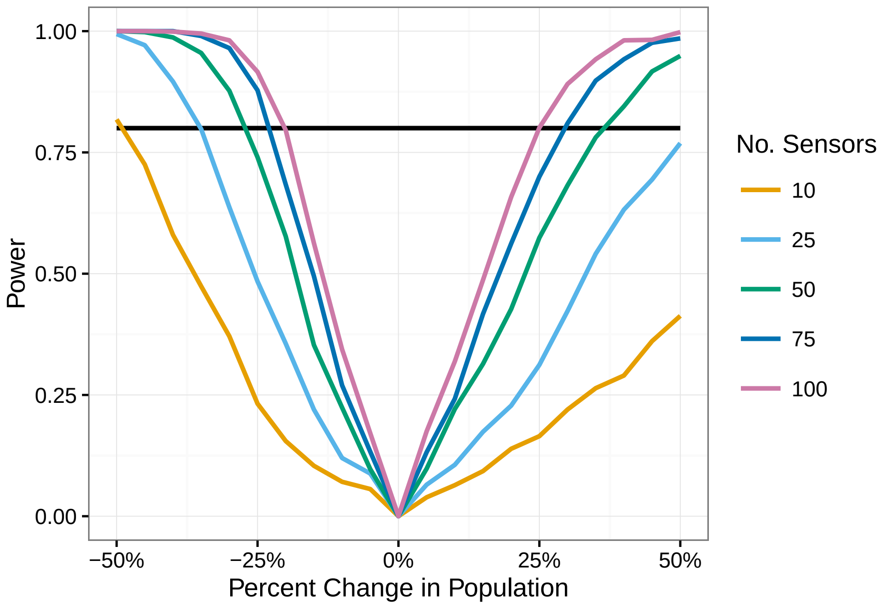

Figure 5.7: Statistical power (y-axis) to detect simulated changes in the Monterey Bay population of harbor porpoise over a 10-yr period (x-axis) using 10-100 sensors (colored lines) placed randomly in water 0-150 m deep. The black line indicates conventionally accepted power of 0.8, which represents an 80% probability of detecting a change in the population when a change does occur.

0.83).

Table 5.4: Power to detect a -25% decline over a 10-yr period with 75 passive acoustic sensors using three different sampling designs (random, stratified, and scaled) under two different decline scenarios (uniform decline across the entire range and range contraction to preferred habitat).

Design	**Power**	
	Uniform	Range Contraction
Random	0.87	0.72
Stratified	0.87	0.79
Scaled	0.87	0.83

When few (<25) sensors are used in a simulation wherein the population decreases by 25% and animals contract to core habitat, design impacts power very little (Fig. 5.8). However, with many (> 75) sensors, the stratified and scaled designs perform much better (power > 0.8 with 75+ sensors) than the random design, which achieves power = 0.75 with 100 sensors. Similarly, when the simulated change in the population is relatively small (<

15%; Fig. 5.9) and 75 sensors are used, the three designs produced similarly low power (< 0.5). When the simulated change in the population is greater than 15%, the scaled and stratified designs clearly outperform the random design; however, with catastrophic changes in the population (>50%) it appears that with 75 sensors all designs would have power approaching 1.

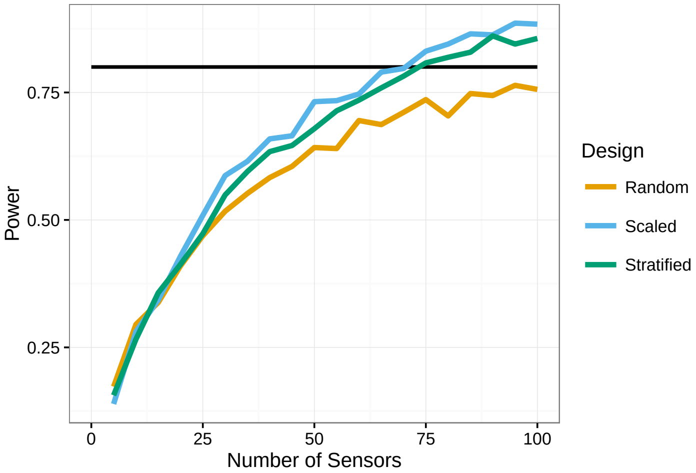

Figure 5.8: Statistical power (y-axis) when the population decreases by 25% and animals contract to core habitat with varying number of sensors (x-axis) and placement of sensors (Design, colored lines). The black line indicates conventionally acceptable power of 0.8.

5.4 Discussion

Our simulation study demonstrates that the effectiveness of PAM varies greatly depending on both survey design (number and placement of sensors) and manifestation of the change in the population (extent and spatial pattern of increase or decrease). When planning passive acoustic surveys, it is important to consider different possible population responses so that power can be accurately assessed and an appropriate number and design of sensors employed. While this simulation study was specific to the Monterey Bay population of harbor porpoise and employed a specific type of passive acoustic sensor, our results are generalizable to other regions, species, and types of passive acoustic surveys.

We expect to achieve higher statistical power with stratified or scaled survey designs than with a random design. However, in our study, when changes in the population are assumed to occur uniformly over its range, the design of the passive acoustic survey does not affect power (Table 1.4). This could be because in Monterey Bay, within water 0-150 m deep, mean harbor porpoise density is never estimated to be zero. Therefore, simulated

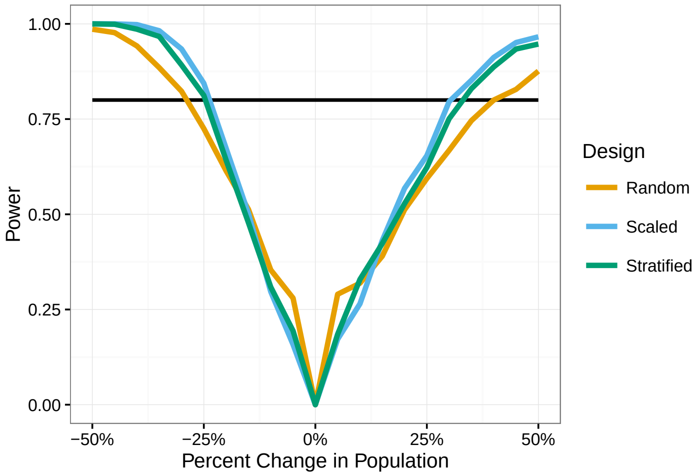

Figure 5.9: Statistical power (*y*-axis) to detect changes in the harbor porpoise population varying from -50% to +50% (*x*-axis) using 75 sensors when the simulated population contracts its range to core habitat with three different designs (colored lines). The black line indicates conventionally acceptable power of 0.8.

passive acoustic detection rates are rarely zero, and changes in the population are more easily detected. When animal density is very low, or when range extent is unknown, we expect to see many more sensors with zero detections in the lowest density areas, and therefore could achieve higher statistical power using stratified or scaled designs rather than random placement of sensors. Another possible explanation is that our simulation method does not accurately reproduce variance in the data, and therefore we are overestimating statistical power or failing to recognize differences in statistical power between survey designs. Similarly, we expect that with a limited number of sensors, sensor placement will have a greater impact on power than when many sensors are used; however, our results indicate that sensor placement is less important with few sensors than with many (Fig. 5.8). This may be because with few ($<$25) sensors, the differences between survey designs are less noticeable; all survey designs appear random with few sensors. However, this result may also be due to insufficient between-site variance in our simulated data. Our simulations do not consider distance between sensors as a criteria for sensor placement. In practice, a uniform grid with a random starting point would minimize the correlation between sensors and effectively increase sample size.

To achieve statistical power $>$ 0.8 to detect a 25% decline in the Monterey Bay harbor porpoise population would require at least 75 passive acoustic sensors to be deployed annually during September, October, and November over the 10-yr period (Table 5.4; Fig. 5.7). Based on reported precision of aerial surveys (Forney et al., 2014), to detect the same change in the population using aerial surveys would require approximately 20 replicate surveys per year. To put that in perspective, current aerial survey effort is at the level of one replicate every four years. In addition to cost, weather in the region would likely not allow for 20 replicates per year during suitable weather conditions. Considerably more resources would be required to implement this level of monitoring for the Monterey Bay harbor porpoise population using either passive acoustic or visual survey methods, which may not be warranted given the current lack of threats to the population. In cases where impacts from anthropogenic activities are expected, PAM and aerial surveys are both capable of achieving acceptable power to detect trends in abundance; however, PAM may be preferable due to safety concerns about aerial surveys.

The Monterey Bay population of harbor porpoise is unusually well studied; we would not typically expect to have such detailed spatial information on the distribution and density of a cetacean population. The scaled design of passive acoustic surveys for cetaceans is not likely to be widely practicable. However, based on our results, the stratified design performed similarly to the scaled design and required less information about distribution and density to implement (Fig. 5.8, 5.9). Our simulation of range contraction to core habitat also relied on detailed information on distribution and abundance of harbor porpoise in the study area; however, literature suggests that this pattern of range collapse as a population declines is persistent across mammalian species (Lomolino and Channell, 1995) and therefore could potentially be simulated in a more generic sense when detailed information about a population of interest is not available. In fact, the R package DSsim (Marshall, 2016), which simulates distance sampling surveys, allows for the user to create density ”hotspots” in the study area; this method could be used in simulations of passive acoustic surveys where the spatial distribution of animals is less well-known.

Our methods evaluated simulated data using traditional null hypothesis significance testing (NHST) and associated decision rules (Gerrodette, 1987). This framework minimizes the probability of incorrectly detecting a change when the population is stable at the expense of increasing the probability of failing to recognize a true change, and the appropriateness of this framework for conservation and management has been questioned (Taylor and Gerrodette, 2017). In future, a Bayesian approach may be more appropriate for quantifying trends in animal populations over time. Several recent studies have used a Bayesian approach to trend analysis for cetacean populations (Moore and Barlow, 2013, 2014). Bayesian trend analysis provides the range and likelihood of trend parameters consistent with the data, which are more practical and intuitive results than the rejection of the null hypothesis in NHST methods (Wade, 2000). For example, this approach can determine the probability that a population is declining. Additionally, a Bayesian approach can be used to compare and optimize the statistical power of different survey designs, where power is defined as the probability of achieving the goal of the study (Kruschke, 2013).

Several ancillary pieces of information are required to estimate absolute animal abundance from passive acoustic data, including the rate at which the species of interest vocalizes and the distances at which those vocalizations can be detected by a passive acoustic sensor (Marques et al., 2013). The certainty with which these parameters are known affects the precision of the resulting abundance estimate, and therefore the power of PAM to detect trends in abundance. Future simulations could explore how expected power can be gained by reducing uncertainty in the relationship between animal density and passive acoustic detection rates.

Finally, the scenarios of population change explored in this study were extremely generic. In the future, it would be worthwhile to work with managers to investigate more plausible scenarios of population impacts, and to consider different possible goals and practical decision criteria relevant to management needs.

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