Combining acoustic and visual detections in habitat models of Dall's porpoise

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Abstract

Habitat-based distribution modelling is an established method for predicting species distributions and is necessary for many conservation and management applications. Cetacean habitat models have primarily been developed using data from visual surveys. However, numerous techniques exist for detecting animal presence and each capture a portion of the true population. Combining detection data gathered from multiple survey methods, such as visual and acoustic surveys, may lead to a more robust picture of a species distribution and ecology. We compare habitat models for Dall's porpoise built with visual versus acoustic survey data from a line-transect survey in the California Current and develop a combined model, utilizing both acoustic detections and visual sightings. Combining acoustic and visual detections increases sample size and allows for detections under a greater range of oceanographic conditions. Consequently, the combined model shows a modest expansion of predicted distribution of Dall's porpoise compared to either single-source model. However, this study reveals that acoustic and visual methods appear to be more complementary, rather than directly additive. Models built with acoustic data display differences from those built with visual data. Different predictor variables were selected across models and the acoustic model predicts a distribution shifted slightly south of the visual distribution. Results from the current study show promise for incorporating acoustics into habitat models but also identify discrepancies in population sampling between these two methods that should inform future population assessments and modelling efforts.

1. Introduction

A foundational step in the management or conservation of any species is to understand spatial and temporal changes in distribution patterns. Habitat-based distribution modelling is an established method for examining the biotic and abiotic variables that best characterize the observed distribution of a species (Redfern *et al.*, 2006; Franklin, 2010; Bailey *et al.*, 2009; Becker *et al.*, 2012a; Pardo *et al.*, 2015). However, for highly mobile marine predators, model performance and ecological understanding are often constrained by sparse distribution data. Numerous techniques have been developed for detecting animal presence, each capturing a portion of the true population of cetaceans in an area. However, the majority of habitat models have been built with one source or type of distribution data (e.g. visual or acoustic or telemetry data). While combining detection data gathered from multiple survey methods may lead to a more robust picture of a species distribution and ecology, the significant challenges involved in merging data types have hindered the development of combination models.

Visual and acoustic detection methods are two of the most common methods used for studying and assessing marine mammal populations. Consequently, there is great interest in using these data to better predict cetacean distribution and habitat use. Habitat models built with visual sightings data are now commonplace and have proven to be an effective management and conservation tool (Redfern *et al.*, 2006; Becker *et al.*, 2012a; Redfern *et al.*, 2013; Canadas *et al.*, 2018). Models built with acoustic data have been developed more recently (Booth *et al.*, 2013; Yack *et al.* 2013). Passive acoustic techniques have the potential to sample more consistently and supplement limited ship time (Mellinger *et al.,* 2007; van Parijs *et al,* 2009; Klinck *et al.,* 2012). Additionally, for highly mobile or cryptic species passive acoustic monitoring (PAM) may be more likely to detect animal presence than visual observation (Mellinger *et al*., 2007; Marques *et al*., 2009; Marques *et al.,*2013; Rogers *et al*., 2013). Both visual and acoustic techniques have strengths and weaknesses that vary by species and application. In many respects, these two techniques are complementary: visual surveys capture animals at the surface but are affected by sighting conditions and the percentage of time an individual spends at the surface while acoustic surveys capture animals under water but rely on animals vocalizing within range of the acoustic device. Consequently, combining acoustic and visual detections in habitat models is expected to improve ecological understanding and distribution predictions. Yet, there are numerous challenges in joining visual and acoustic data in habitat models. First, the number of taxa that can be identified to species using acoustics is limited (Marques *et al*., 2013). Second, many of the species that can be identified using acoustics have vast differences in their visual and acoustic detection ranges, which can complicate the interpretation, matching, and geographic assignment of detections. Finally, and perhaps most significantly, innate differences between acoustic and visual methods result in different acoustic and visual survey effort. Even for acoustic and visual surveys conducted simultaneously from the same platform this poses a significant challenge in merging these two techniques.

Since all visual and acoustic surveys will have discrepancies in survey effort, any attempt to combine or directly compare these data must aim to understand and reduce these discrepancies. To date, attempts to integrate visual and acoustic detection data have primarily compared visual-based habitat models to acoustic detection rates and trends in the surrounding area (Brookes *et al.,* 2013; Thompson *et al*., 2015; Rayment *et al.* 2017).

While these efforts represent important advances in comparing and contrasting the distribution patterns captured by the two detection techniques, there are several methodological issues with such an approach. These comparisons have used different data sets collected from different platforms and across different temporal and spatial scales. For example, passive acoustic presence/absence data from moored devices (e.g. CPODs and MARUs) have been compared to visual-based habitat models created from aerial or ship-based visual surveys (Brookes *et al*., 2013; Soldevilla *et al.*, 2014). Since acoustic and visual detections may reflect different behaviors and habitat use patterns of cetaceans, models built with different data types collected from different times and places contain additional experimental variables. These variables can skew model results with the multi-platform experimental design providing little opportunity to determine if the results are due to diverse behavioral patterns captured by the detection methodologies or spatial and temporal variability in conditions experienced by the animals. It is therefore pertinent to control for time and place in order to directly compare and combine visual and acoustic models. In this study, we develop and compare visual, acoustic, and combined habitat models built with visual and acoustic data collected simultaneously from a ship-based survey in the California Current Ecosystem (CCE). To our knowledge, this is the first study to build an acoustic habitat model from ship-board towed array data in the Pacific and the first to build a combined habitat model using visual and acoustic data for any cetacean species.

Dall's porpoise, *Phocoenoides dalli*, was selected as a case study for model building and comparison. Dall's porpoise are found in cool temperate pelagic waters of the North Pacific between 32°N and ~63°N (Jefferson, 1988). This species was selected, in part, because previous habitat models of Dall's porpoise built with only visual data have shown consistent habitat relationships and provided validated interannual, seasonal, and near real-time forecasts of distribution and density in the CCE with which to compare initial acoustic modelling efforts (Forney 2000; Barlow *et al*., 2009; Becker *et al.,* 2010, 2012a, 2012b; Becker *et al.,* 2014, 2016). Additionally, Dall's porpoise regularly react to ships which can bias abundance estimates (Bouchet *et al*., 1983). This reactive movement leads to artificially raised observed densities, especially in rougher sea states where sighting distance is restricted and observers are less likely to spot animals before they react to the vessel (Bouchet *et al* 1983; Dawson *et al*., 2008). Consequently, some past visual-based estimates of abundance have been restricted to Beaufort sea states two or less (Barlow, 1995; Barlow & Forney, 2007). Acoustics thus offered a promising approach. The selection of Dall's porpoise was also motivated by their acoustic behavior. Dall's porpoise produce narrow-band high-frequency (NBHF) echolocation clicks, readily discernible from most species in our study region in the CCE (Basset *et al.,* 2009). Additionally, the acoustic and visual detection ranges for Dall's porpoise are both within the range of a single segment length used in our model construction (5km), allowing both detection types to be reliably assigned to the same geographic segment of the transect. Specifically, the effective strip width (ESW), or typical distance at which Dall's porpoise are seen, is 1.5km (Barlow *et al*., 2011) and estimates of their acoustic detection range are on the order of a few hundred meters (along the main axis of the click) (Kyhn *et* al., 2013). Finally, the selection of Dall's porpoise as a case study was motivated by survey design considerations. Many cetacean assessment surveys employ a "closing mode" protocol during which a ship conducting a line transect survey diverges from the trackline to estimate group size visually thereby ceasing acoustic survey effort until the ship resumes its planned trackline. This approach was not used for Dall's porpoise for the present study, which helped minimize discrepancies in standardized trackline effort between visual and acoustic survey methods.

The aims of this study are to directly compare visual and acoustic habitat models of Dall's porpoise in the California Current Ecosystem and to trial a methodology for the combination of visual and acoustic survey data in a single model. In doing so, we explore the contribution of each of these data types in capturing the species distribution. These aims are driven by the hypothesis that more distribution data produces models with more predictive power. The following specific objectives guide this study: 1) build a habitat model with visual detections for Dall's porpoise in the CCE using the same methodology that has been established by previous studies using visual detections; 2) build a habitat model with acoustic detections for Dall's porpoise in the CCE using the same methodology employed for the visual model in this study; 3) compare the models built with acoustic and visual detections; 4) build a single habitat model combining visual and acoustic detections; 5) compare the combined model to the two single-stream models. In developing the methodology for combining visual and acoustic data in habitat models, we identify key research that is needed to improve this approach.

2. Methods

2.1 Field Methods

Acoustic and visual data were collected as part of the ORCAWALE (Oregon, California, Washington Line-transect and Ecosystem) survey conducted on the NOAA R/V *McArthur* II from July 28- November 30, 2008. The survey area encompassed waters off the US west coast out to 555km (300nmi) from shore. The line-transect survey followed a regular grid pattern (Fig. 1a) at a speed of 18.5km/hr (10 knots). Dedicated marine mammal observers collected cetacean sighting data from the ship's flying bridge (observation height = 15.24 m) along all transects. Observers rotated between 3 stations with the left and right observers using 25 x 150 mounted binoculars and the central observer searching with the naked eye or (occasionally) hand-held binoculars. For all marine mammal sightings, the time, position, distance and bearing from ship, species identification, group composition and group size were recorded.

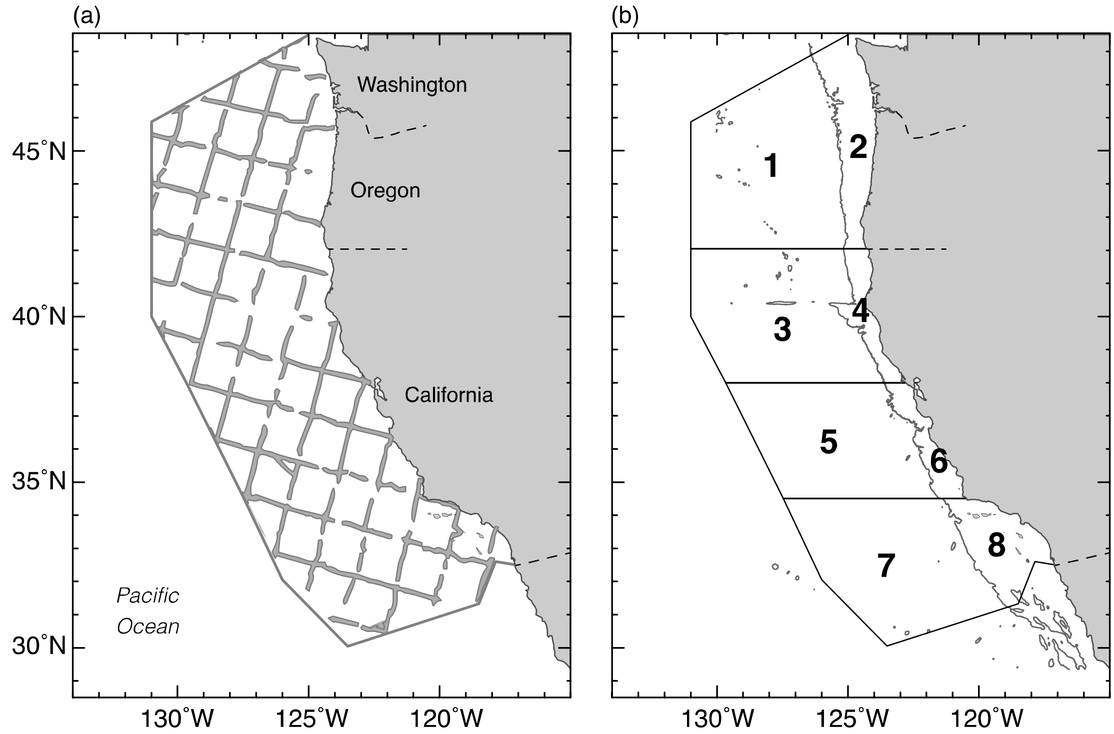


Fig. 1: (a) Completed transects for the 2008 ORCAWALE survey between July 28th and November 30th, 2008. (b): Geographic regions used for evaluation of spatial patterns of encounter rates detailed in Table 2. The grey north-south line through the study area represents the 2000m isobath (Reproduced from Barlow, 2010 and Becker et al. 2012a).

A five-element hydrophone array was towed approximately 300m from the stern of the ship at a depth of 4-8m during daylight hours to detect echolocation clicks (Barlow *et al.*, 2010). Three high-frequency hydrophones were encased in an oil-filled array (Reson TC4013 hydrophones with a frequency response of 1.5 to 150 kHz ±3 dB with a sensitivity of -170 dB re 1V/μPa after 40 dB pre-amplification). Hydrophones 1 and 2 were spaced 30cm apart and hydrophone 3 was 200cm from hydrophone 2. Rainbow Click software (International Fund for Animal Welfare, IFAW) (Gillespie & Leaper, 1996) was used to record any high-frequency detections. Logger 2000 software (IFAW) was used with Rainbow Click to record GPS locations and plot detected clicks of possible porpoise on a real-time spectrographic display that was monitored continuously. The array was monitored aurally and visually for cetacean vocalizations from a real-time spectrographic display for a total of 762 hours during 11,465 km of survey trackline. Data from the high-frequency hydrophones were digitized at a sampling rate of 480 kHz using a National Instruments USB-6251 soundcard and were recorded to hard disk for later post-processing. To detect and classify Dall's porpoise detections used in model building, all of the data files from the cruise were reviewed manually. In post-processing visual review of click detections, five criteria were assessed in Rainbow Click including (1) wave form, (2) power spectrum and peak frequency, (3) time-frequency structure as viewed through a Wigner-Ville transformation plot, (4) number of clicks, and (5) ability to localize clicks based on the convergence of bearing angles. A Wigner plot is a quadratic time-frequency representation (QTFR) used to analyze the time-frequency structure of broadband cetacean clicks (Preis & Georgopoulos, 1999). Detections with 5 or more clicks, clear track patterns (i.e. some clicks were not along the beam), a clean wave form, a peak frequency between 129 and 137kHz and a Wigner plot with a strong single energy peak were classified as "definite" (Fig. S1). Detections meeting these criteria but with only three or four clicks in a series were labeled as "probable". If the detection had only two clicks in a series, but all other characteristics were shared with the "probable" assessment, then it was categorized as "possible".

At-sea oceanographic data collection included sea-surface temperature (SST), salinity (SSS), mixed layer depth (MLD; here defined as the depth at which temperature is 0.5°C less than the surface temperature), chlorophyll concentration (CHL), and Beaufort sea state. SST and SSS were collected continuously at 0.5- to 2-minute intervals using a thermosalinograph sensor mounted at a depth of 3 meters and averaged over 5km intervals. MLD was measured by expendable bathythermographs (XBTs) deployed five times a day and conductivity-temperature-depth (CTD) casts conducted every evening. Surface chlorophyll concentration (CHL, mg m^{-3}) was measured 3-5 times per day using CTD surface water samples and bucket water samples (Barlow *et al.*, 2010). CHL values were log transformed prior to analyses. MLD and CHL measurements were interpolated to create continuous spatial grids of the oceanographic data with ordinary kriging using the ArcGIS Geostatistical Analyst tool (Version 10.1, ESRI, Inc.). In addition to these habitat variables collected in the field, data on sea-floor depth and distance from shore were obtained from ETOPO2, a 2-minute global relief data set (U.S. Department of Commerce 2006) and extracted using ArcGIS Spatial Analyst. The full suite of potential predictor variables included SST, SSS, CHL (log transformed), Beaufort sea state, MLD, depth, and distance from shore.

2.2 Habitat modelling

The overall modelling approach is schematically outlined in Figure 2. In preparation for model building, both the acoustic and visual survey data were divided into approximately 5km segments of continuous effort following Becker *et al.* (2010) to create two distinct effort databases. The visual database was later used as the foundation to construct the combined database (see below) (Fig.2). The acoustic database includes 2,361 segments while the visual database includes 2,556 effort segments. The "on-effort" segments vary between these two methods for multiple reasons. For example, sea state conditions above Beaufort 5 typically necessitated visual observers to go off-effort. Consequently, the visual database includes segments in Beaufort conditions 0-5 while the acoustic database includes segments in conditions 0-6. Additionally, acoustic equipment status and personnel coverage sometimes necessitated that acoustics was 'off-effort'. Finally, when the visual team was in closing mode and diverged from the trackline, acoustics was 'off-effort'. The interpolated (MLD, CHL, depth, distance from shore) or averaged (SST, SSS, Beaufort) habitat variables were then associated with segment midpoints in each database using ArcGIS. Student's t-tests were used to compare oceanographic conditions during acoustic and visual detections. Porpoise encounters, either visual sightings or acoustic detections, were assigned to the segment on which they were detected. Porpoise sighting data were truncated at 3km range (e.g. excluded from analyses if they were farther from the trackline than an established truncation distance) for consistency with species specific effective strip width estimates used in previous modelling efforts (Barlow *et al.*, 2011). Since we are currently unable to determine the number of individual Dall's porpoises vocalizing in an acoustic detection event, we used these two data sets to create models of encounter rate (number of sightings/detections per segment) rather than density. All on-effort transect segments, regardless of whether or not they contained sightings or detections, were included in the databases for model building, as described in previous publications detailing encounter rate modelling (Barlow *et al.,* 2009).

In order to build the combined database, two major methodological concerns required consideration. The first was the spatial and temporal discrepancy in effort between the acoustic and visual surveys. While the shared platform and concurrent surveys largely aligned these methods, the slight differences in active status of each detection team created some differences in 'on-effort' segments. This was addressed by only using segments for which both visual and acoustic teams were 'on-effort' in our combined database (Fig. 2). Although this reduced the number of distinct detections that could be used in model building, this approach was a conservative starting point to address the challenge of merging two approaches with inherently different effort. By including only the segments surveyed by both methods, all spatial and temporal variability in habitat conditions are controlled for, thus enabling direct comparison of the detection methods. The second concern was the possibility of double counting a single Dall's porpoise detection as one visual detection and one distinct acoustic detection. To address this, definite acoustic detections that occurred while the visual team was on-effort were cross-referenced with the visual segment database. The location of each definite acoustic detection was determined and since the effective strip width for Dall's porpoise is 1.5km, any visual detection that was within 1.5km of the acoustic detection was regarded as the same detection (Barlow *et al.,* 2011). If there was no visual sighting within the ESW distance, the acoustic detection was determined to be distinct and therefore an additional detection event. Consequently, the combined database included all visual sightings (some of which had also been detected acoustically) as well as definite acoustic detections that had not been visually observed yet occurred while the visual team was on-effort.

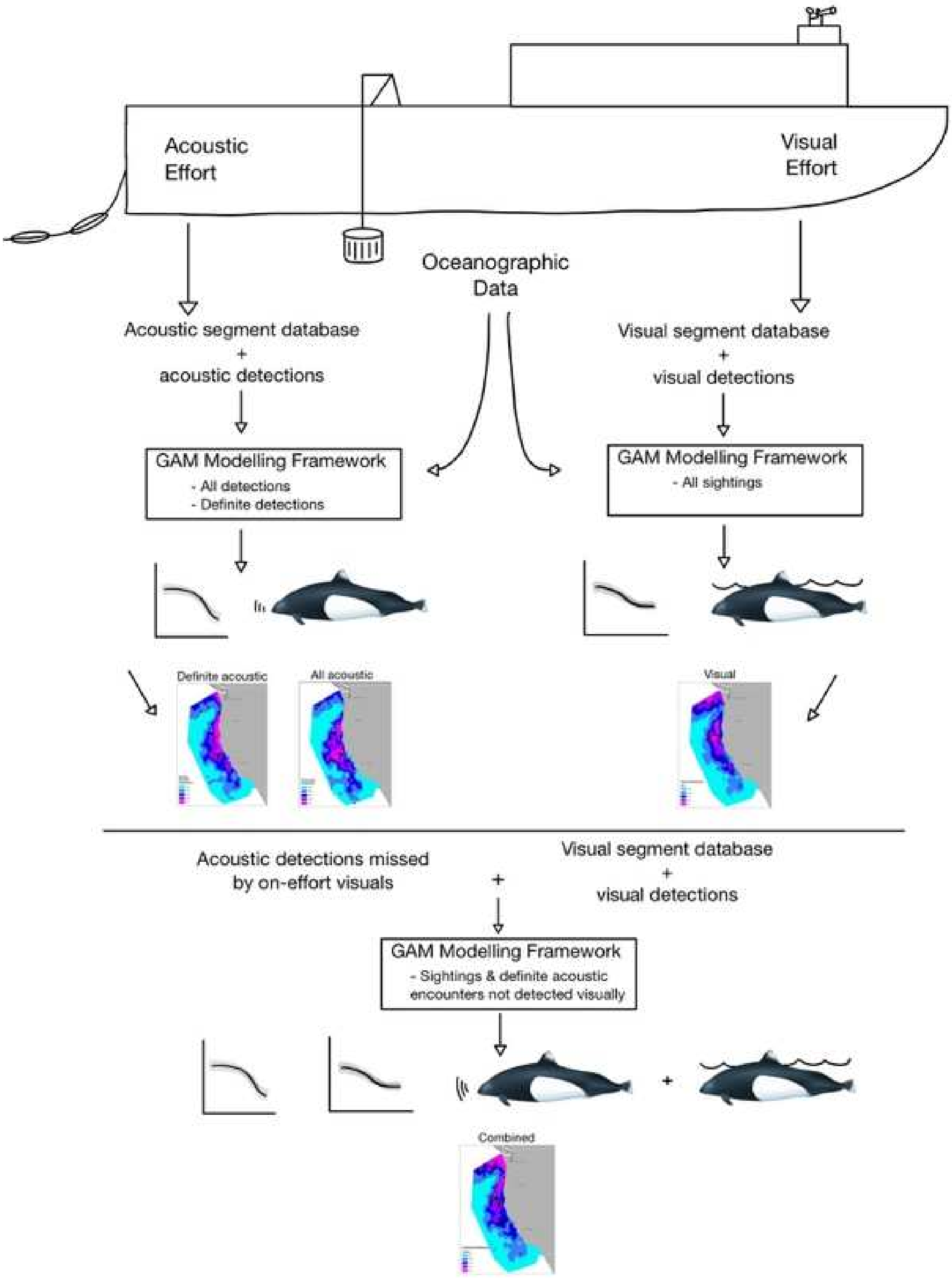


Figure 2: Schematic outlining the overall modelling approach executed in this study. Two different acoustic models were built (one with all of the on-effort acoustic detections and one with the 'definite' on-effort acoustic detections). One visual model was built with all of the on-effort sightings. A combined model was built with all of the on-effort sightings as well as the 'definite' on-effort acoustic detections that had not been visually observed.

The three databases were used to construct four models. The visual database was used to build one model, two models were built with the acoustic database (one with definite acoustic detections and one with all acoustic detections to examine the impact of less certain detections on model predictions), and one model was built with the combined database (i.e. sightings and 'definite' on-effort acoustic detections that had not been visually observed). Given the high number of potential predictor variables and small number of sightings/detections, we first conducted an exploratory analysis to identify the most significant predictor variables. Correlation coefficients between all predictor variables were calculated and those with R^2 values > 0.65 were eliminated from further analyses (Table S1). This cut-off value was selected as it is the correlation value between distance from shore and depth, which is known to be highly correlated in the CCE. This process resulted in a revised set of potential predictors that included SST, SSS, depth, and Beaufort sea state and eliminated chlorophyll, distance from shore, and MLD.

Modelling methods largely follow those of Becker *et al.* (2016) with some exceptions due to the nature of our questions and the small sample size of detections contained in our single year dataset. In brief, generalized additive models (GAM) (Hedley *et al*., 1999; Ferguson *et al*., 2006) were developed in R (v. 3.2.2, R Development Core Team, 2015) using the mgcv package (v. 1.8-7) (Wood, 2008; Wood, 2011) to relate the number of acoustic and visual encounters of Dall's porpoise per segment (the response variable) to the oceanographic variables. Beaufort sea state was included as a predictor in all models to explore the potential variable effects of sea state on detection probabilities between visual and acoustic techniques.

The natural logarithm of segment length was used as an offset to account for differing segment lengths. Degrees of freedom were limited to k=4 due to the small sample sizes of Dall's porpoise detections. Since encounter rates are sparse count data with large numbers of zeros, models were built using a log-link function, and quasi-Poisson, negative binomial and Tweedie error distributions were compared. The latter was selected based on its suitability for zero-inflated count data (Miller *et al.,* 2013) and on inspection of diagnostic plots of model residuals and quantiles. Restricted maximum likelihood (REML) was used to optimize the parameter estimates (Wood, 2011). Model selection was performed with automatic term selection (Marra & Wood, 2011), informed by the approximate p-values of each predictor (Wood, 2011). Variables found to be non-significant (α=0.05) were excluded and models re-fit until all variables were significant. Functional forms of the modeled relationships as well as the p-values of each significant predictor variable were used to determine order of variable importance.

The best model for each data set (visual, definite acoustic, all acoustic, and combined visual and acoustic) was then used to predict segment-specific encounter rates. These predicted encounter rates were interpolated to the entire CCE study area by Empirical Bayesian kriging using the ArcGIS Geostatistical Analyst tool to create predicted distributions at 5km^2 resolution (from a 10km x 10km regular grid with Power semivariogram, overlap factor =1). The final distribution maps for the models thus provide predicted encounter rates across the CCE for the summer/fall of 2008. Sightings and acoustic detections were overlaid on these prediction grids to allow for comparison of the model predictions and observations (Barlow *et al.,* 2009; Becker *et al.,* 2010, 2012a; 2012b; 2016; Forney *et al.*, 2012).

3. Results

During the 2008 survey, there were 79 on-effort sightings of Dall's porpoise. Post-processing of acoustic data resulted in 44 on-effort detections with 28 definite, 10 probable and 6 possible detections. Ten of the 28 definite Dall's porpoise acoustic detections were also recorded as visual detections. The combined visual and acoustic database was composed of the 79 sightings and the 18 definite acoustic detections that were not sighted. Both visual and acoustic detections of Dall's porpoise were more common nearshore and north of 38°N.

The oceanographic conditions differed between sightings (n=79) and acoustic detections (n=44). The median Beaufort sea state throughout the cruise was 4 and both sightings and acoustic detections were made frequently in this sea state. However, the mean Beaufort sea state varied significantly between visual and acoustic detections (T = -5.2, df = 97.5, $P < 0.0001$). Numerous sightings were made in calm sea states (Beaufort 1-3; avg. 2.9 ± 1.2) while acoustic detections were more frequent in sea states 4 and 5 (avg. 4.0 ± 0.8) (Fig. 3). Additionally, acoustic detections were made in significantly more saline (T = -3.3, df = 77.7, $P < 0.001$) and less stratified waters (T = -4.1, df = 46.7, $P < 0.0001$) (Table 1). There were also regional differences between acoustic and visual detections (Table 2). Eighty percent of sightings occurred in the northern half of the study area (Regions 1-4) while acoustic detections were more geographically spread with 38% of detections made in the southern half of the CCE (Regions 5-8). Most of the encounters that were acoustically detected but not visually observed were in offshore northern waters (Regions 1-3).

Table 1: Mean and standard deviations of oceanographic conditions by detection type. Significant differences in oceanographic conditions between visual and acoustic detections are highlighted in bold (*P<0.01*).

Habitat Variable	Visual Detections (n=79)	Acoustic Detections (n=44)
Beaufort	**2.9 (±1.2)**	**4.0 (±0.87)**
Sea Surface Temperature °C	14.7 (±1.2)	15.0 (±1.4)
Sea Surface Salinity ‰	**32.6 (±0.51)**	**32.9 (±0.47)**
Mixed Layer Depth (m)	**21.2 (±6.18)**	**29.6 (±11.6)**
Depth (m)	2856.7 (±887.99)	3153.7 (±1116.518)

Table 2: Percentage of detections made in each region of the study area. Numbers shown are percentages of total acoustic (44), visual (79) and acoustic detections missed by visual sightings (18). Numbers next to Region titles correspond to Figure 1(b).

Region	Acoustic	Visual	Missed Sightings
WA/OR offshore (1)	18	30	28
WA/OR inshore (2)	5	4	11
NorCal offshore (3)	36	43	39
NorCal inshore (4)	2	3	11
CenCal offshore (5)	27	13	6
CenCal inshore (6)	2	8	0
SoCal offshore (7)	9	0	6
SoCal inshore (8)	0	0	0

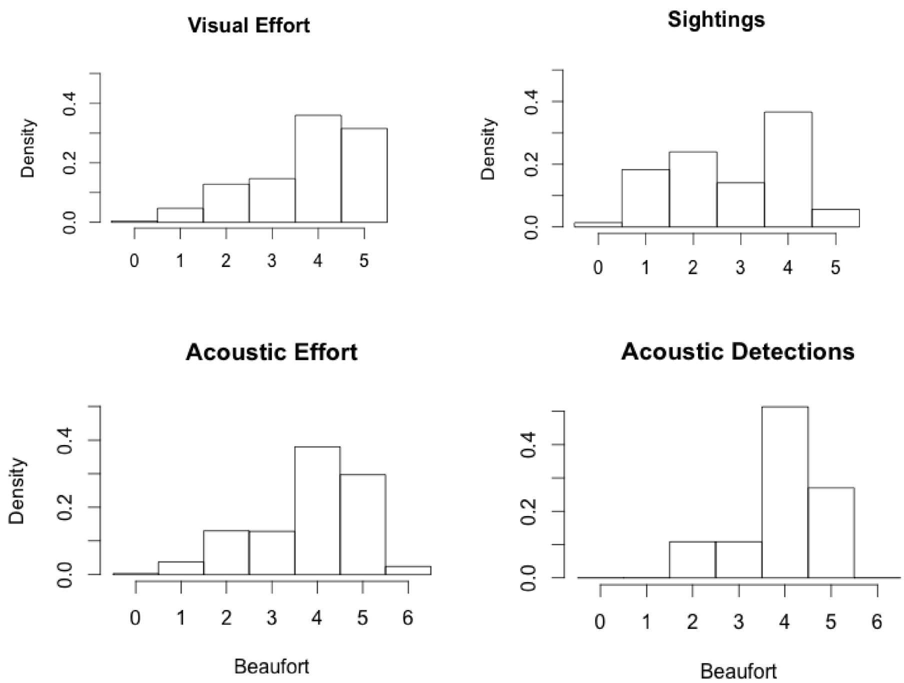


Figure 3: Histograms of survey effort and Dall's porpoise detections at Beaufort sea states 0-5 for visual methods and 0-6 for acoustic survey methods. Density on the y-axis is the number of segments (for the effort plots) or detections (for the sightings and acoustic detections plots) in each sea state divided by the total number of segments or detections for that detection type.

3.1 Selected Habitat Predictor Variables: Visual Models

The best-fit model for Dall's porpoise visual encounter rates included SST, Beaufort, SSS, and depth (Fig. 4a). Sightings declined steeply in waters warmer than 16°C and showed a gradual decline with increasing salinity. Sightings were most common in depths of approximately 2000-3500m and declined in rougher sea states.

3.2 Selected Habitat Predictor Variables: Acoustic Models

Two sets of models were built with acoustic data, one using the definite acoustic detections (Fig. 4b) and one using all acoustic detections (Fig. 4c). The best definite detections model included only SST. Acoustic detections, similar to sightings, declined in waters with SSTs above 16°C. The best-fit model for all acoustic detections of Dall's porpoise included SST and depth (Fig. 4c). The functional form of the relationship between Dall's porpoise acoustic detections and SST in the "all" detections model displayed a slightly more linear decline with increasing temperature, compared to the visual model. The "all" acoustic detections model displayed a slight decline in detections from deep to shallow waters in contrast to the visual models which showed a decline in detections in deep waters (>4000m) and a peak in detections between 2500 and 3000m.

3.3 Selected Habitat Predictor Variables: Combined Visual & Acoustic Models

The best-fit model for Dall's porpoise combined encounters (visual and definite acoustic encounters not detected visually) included SST, Beaufort, SSS, and depth (Fig. 4d). These were the same variables as those included in the best visual-only model, which is expected given the high proportion of visual sightings in this model. The functional forms of the relationships between Dall's porpoise encounters and these predictor variables were also similar to those displayed in the visual-only model.

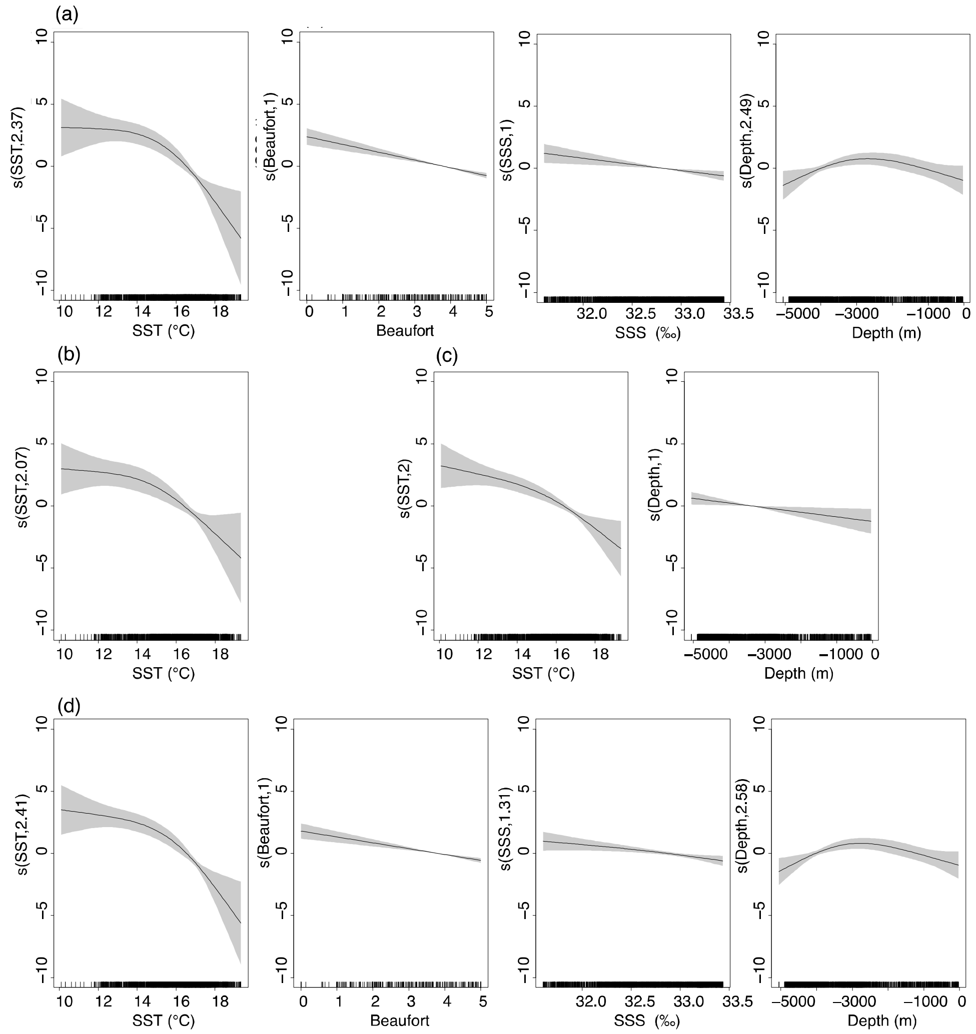
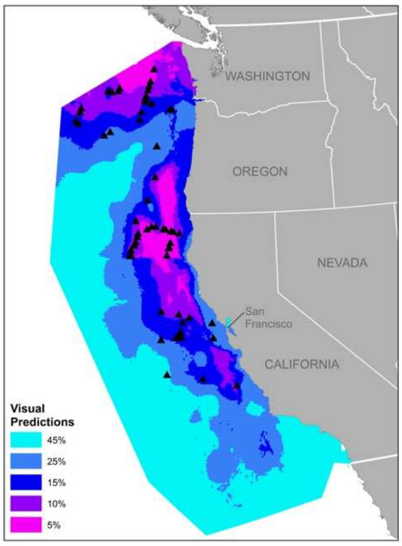


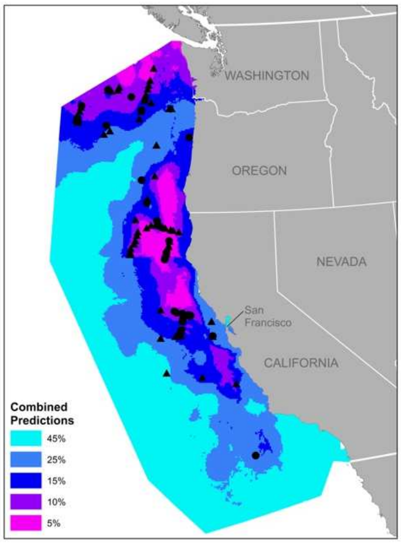
Figure 4: Scaled encounter rate model functions for Dall's porpoise for a) visual model; b) acoustic model built with definite detections; c) acoustic model built with all detections; d) combined model built with both visual and acoustic detections. Degrees of freedom are in parentheses on y-axis. The y-axes represent the term's function (linear or spline). Zero on y-axes indicate no effect of the predictor variable on Dall's porpoise encounter rate. Y-axes have been scaled to show relative effects of predictor variables on encounter rate. Data points for each variable are shown as tick marks along x-axis. Shaded area reflects 95% confidence interval.

3.4 Predicted Distributions

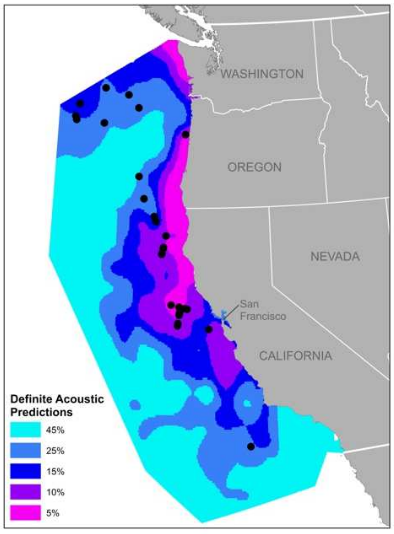
Inspection of the encounter rate maps show that visual and acoustic models resulted in different predicted distributions of Dall's porpoise (Fig. 5). The visual model predicted high encounter rates off Washington and Oregon, extending into northern California waters (Fig. 5a). In contrast to the visual predictions, highest encounter predictions from the acoustic models are concentrated further south. The model built with all acoustic detections (Fig. 5d) predicted density hotspots in the waters just north of San Francisco while the definite acoustic detections model predicted a more coastal distribution from central California to the northern extent of the study area (Fig. 5c). The area of high encounters off Washington predicted by both the visual and definite acoustic detections models was missed by the all acoustic detections model. The combined model predicted distribution (Fig. 5b) was similar to that of the visual model but with additional distribution hotspots predicted off central California.

(a) **(b)**





(c) **(d)**



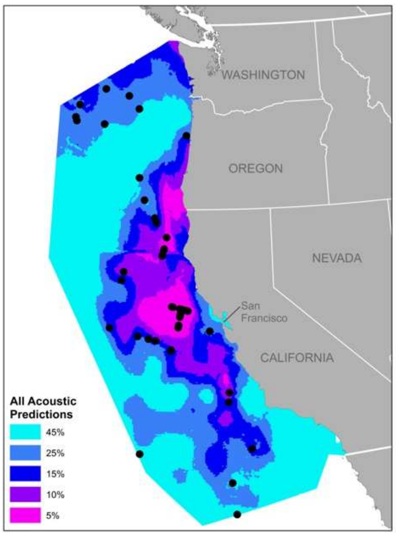


Fig 5: Modeled predicted encounter rates for Dall's porpoise in the CCE in the summer/fall of 2008. Shading indicates the relative likelihood of encounters, shown in percentiles (e.g. pink corresponds to the top 5% or 95th percentile of predicted encounter rates). Models predict (a) number of encounters using visual sightings, (b) number of encounters using a combination of visual and definite acoustic detections, (c) number of encounters using definite acoustic detections, (d) number of encounters using all acoustic detections. Black triangles in panel (a) and (b) are sighting locations and black circles in panels (c) and (d) are acoustic detections.

4. Discussion

The aims of this study are to directly compare visual and acoustic habitat models of Dall's porpoise and trial a methodology for the combination of visual and acoustic detections in a single model. These aims are driven by the hypothesis that more distribution data produces models with more predictive power and therefore developing such a methodology could enhance understanding for numerous species for which passive acoustic data has been or will be collected. In the previous sections we have developed a methodology for a combined habitat model for Dall's porpoise, with the resulting model displaying a modest expansion of the predicted distribution compared to either of the single-stream models. Yet the process of developing the combined model revealed that acoustic and visual methodologies, while complementary, may not be simply additive. The current study highlights discrepancies in population sampling between visual and acoustic methods that can help identify the strengths and limitations of future population assessments and modelling efforts.

4.1 Differences between acoustic and visual models & predicted distributions

The acoustic and visual sets of models developed in this study produce different predicted distributions for Dall's porpoise in the CCE. One of the most important predictor variables in the visual model is Beaufort sea state yet it is absent from the acoustic-only models. This is consistent with previous studies detailing the challenges in surveying Dall's porpoise visually (Barlow, 1995, Barlow *et al.* 2001; Barlow & Forney, 2007; Dawson *et al.*, 2008). Sea surface temperature is a primary predictor variable included in the visual model and in both the acoustic models. This also agrees with past habitat models of Dall's porpoise in the CCE which have consistently predicted Dall's porpoise in cool waters. The visual model and the acoustic built with all acoustic detections included depth but the acoustic model built with definite acoustic detections did not. This is likely due to the smaller number of definite acoustic detections and their more limited depth range. The visual model also included SSS which was not included in either of the acoustic models. Examination of the oceanographic conditions present during detections show there were significant differences in SSS and MLD between acoustic detections and visual sightings (Table 1).

The discrepancies that exist between the models built with visual and acoustic data are likely due to three primary factors: the inherent differences in their detection capabilities, the sample size of detections utilized in each model, and the species behavior captured by each detection method.

The differences in detection capabilities between the two methods stem from multiple sources. First, as was mentioned in the methods, the ESW for Dall's porpoise varies between acoustics and visuals. The difference between these two methods for Dall's porpoise (~1.5km for visuals and 0.5km for acoustics) is smaller than for many species but this inherent discrepancy in ESW results in slightly different surveyed areas. Second, since visual observations are restricted to surfacing animals, sightings are affected by Beaufort sea state (Barlow *et al.*, 2001; Barlow & Forney, 2007). Most of the 2008 cruise was characterized by a Beaufort sea state of 4-5 (Fig. 3) yet the mean sea state during visual sightings was less than 3 (Table 1). As to be expected, Beaufort had less of an impact on acoustics. The distribution of acoustic detections relative to Beaufort sea state is more similar to the distribution of the cruise conditions, with the majority of detections made in sea states of Beaufort 4 and 5 (Fig. 3). The mean sea state during encounters which were acoustically detected but not visually observed was 4.25. Additionally, the 2008 ORCAWALE cruise was conducted from north to south, beginning off Washington in the late summer and surveying off southern California in the late fall. This cruise plan was designed to capture as calm weather as possible in the northern latitudes. However, in doing so, the southern regions of the study area were surveyed during the fall months. This latitudinal and seasonal gradient likely introduced a regional difference in detection likelihood for visual effort but not for acoustic effort. As a result, the predicted distributions from the acoustic and combined models are elevated over the visual model in the southern half of the study area.

Acoustic models are based on a limited sample size compared to the visual model. However, part of the interest in developing the acoustic models is to compare them to models built with more extensive datasets to evaluate the potential of data-limited models (whether such data limitation results from infrequent species encounters, restricted acoustic detection distance, limited temporal coverage, or a combination of factors). Given the interest in passive acoustic detections for cryptic and poorly understood species, sample size constraints are likely to be a recurring challenge in acoustic-based approaches. Indeed, calculations of explained deviance for models in the present study suggests that a smaller sample size reduces the predictive performance of acoustic-based models (Table S2). However, comparisons of the predicted distribution from this study to multi-year and methodologically similar models of Dall's porpoise distribution developed from previous studies (Becker *et al.,* 2016), show that the current models predict a similar overall distribution pattern (Fig. S2). For example, examination of the overlap between detections and predictions shows that the model built with definite acoustic detections (Fig. 5c) has some areas of high predicted density devoid of detections. Yet these coastal areas of predicted density match those observed in the multi-year model, suggesting that despite small sample size, the definite acoustic model still captures the species-habitat relationships. For some species that are understudied and difficult to survey visually, the insight provided by the definite acoustic model presented here may substantially increase understanding of species distribution patterns.

The final primary factor driving the discrepancies between the visual and acoustic models and predicted distributions is the behavior captured by the two detection methods. Though little is known about Dall's porpoise acoustic behavior or regularity of vocalizations, echolocation clicks are typically produced for locating prey (Kyhn *et al.* 2013). If acoustic detections are mostly from foraging animals, many of these individuals may be diving at the time of detection, which would cause them to be missed by the visual observers. In the present study, Dall's porpoise were acoustically detected in waters with greater MLDs compared to the waters in which they were sighted. Dall's porpoise are known to feed on mesopelagic fish and cephalopods (Okamoto *et al.,* 2010). If Dall's porpoise feed at or below the mixed layer they would be less likely to be visually sighted at the surface. Conversely, though they are believed to be frequent echolocators, there were many visual sightings that were not acoustically detected during this cruise. This could have resulted from visual detections outside the range of acoustics (e.g. past ~500m from the array). Alternatively, if Dall's porpoise are not acoustically active during periods of travel or other non-foraging behavior, acoustic methods would only sample certain behavioral states. Behavior may also result in perceived regional or habitat differences between acoustic and visual models. Williamson *et al.* (2017) found that visual and acoustic surveys indicated different primary habitat areas for harbor porpoise in the Moray Firth. Acoustic methods revealed harbor porpoise occupied muddy bottom habitats at night while visual surveys found they occupied sandy bottom habitats during the day. Additionally, it has been hypothesized that Dall's porpoise may feed primarily at night and therefore if the species is more vocally active at night, acoustic surveys during daylight hours may significantly underestimate species presence (Amano *et al.*, 1998). Behavioral context for vocalizations is therefore valuable for interpretations of distributions determined through acoustic detections and for the development of models using a combination of acoustic and visual detection data.

4.2 Combined model & predicted distribution

The most significant challenge in combining (and comparing) detection data types in habitat models is the difference in survey effort between data collection methods. To combine acoustic and visual methods, effort must be standardized. In the combined model in this study, this was accomplished by collecting visual and acoustic data simultaneously from the same platform and by including detections made while both teams were on-effort. The visual team was off-effort in Beaufort sea states above 5 while acoustic effort continued in higher sea states. Therefore, potential acoustic detections made in sea states higher than 5 were not included in the model. In the current study, this methodological step did not impact our final combined database as there were no acoustic detections in Beaufort sea state 6. However, this may not be the case for all species. The exclusion of detections made in rough seas and acoustic detections that were identified as duplications of the visual sightings may substantially discount the advantage of acoustic techniques and render acoustic modelling efforts incomplete. Since the difference between acoustic and visual detection parameters will vary across species and platforms, the approaches used in this study may not be relevant for all combined models. Future research will require species- and platform-specific considerations. Thus, developing additional approaches to reconcile differences in effort across detection methods requires further research attention.

The current study is an initial attempt at merging these disparate methods and the first step in a larger effort by the US NOAA Fisheries Science Centers to refine the use of passive acoustic data in cetacean population assessments. Starting with simultaneously collected data from a single shipboard survey, enables a more direct comparison between acoustic, visual, and combined models than previously published multi-platform studies. This initial trial of a combined model increases the sample size of detections by ~23% over the visual-only model and allows for detections under a greater range of conditions and habitats (Table 1, Fig. 4). The same predictor variables were included in the combined and visual models but the addition of acoustic detections in the combined model reduces the importance of Beaufort in the model (inferred from predictor variable p-values between the two models). The resulting predicted distribution includes regions previously absent from the visual prediction map. However, given the discrepancies between visual and acoustic models discussed above, we posit that these two methods are not directly additive. The two techniques likely capture multiple behavioral states of a target species, both at the surface and at depth (e.g. traveling and feeding) and while this may add more data points to a population assessment, they may not all be governed by the same ecological processes. The behavioral and ecological differences underlying acoustic and visual detection methods will require both species- and platform-specific consideration in future studies combining these techniques.

4.3 Future Directions

Both the comparison and combination of visual and acoustic methods offer insights that can direct additional research and improve future studies incorporating acoustic data into habitat distribution models.

First, the differences in distribution predicted by the model built with all acoustic detections and the model built with definite acoustic detections highlight the importance of accurate acoustic detections. While unlikely, some of the possible and probable Dall's detections may have been high-frequency noises resulting from ship operations, turbulence or array position, or a misclassified alternative species. There are three other species in the study area that produce similarly high-frequency sounds and must be considered as possible candidates for misclassification. Harbor porpoise are found in the California Current (Barlow, 1995) and produce very similar echo-location clicks (Kastelein *et al.,* 2002; Kyhn *et al.,* 2013). However, their distribution is largely limited to shelf waters less than 60m in depth (Carretta *et al.*, 2001) where towed hydrophone data were not collected during this survey. While there is the potential for geographic overlap, it is likely low due to the current survey design. Additionally, Kyhn *et al.* (2013) found that harbor porpoise just north of our study area, in British Columbia, are distinguishable from Dall's porpoise in their peak frequency, with Dall's porpoise clicks falling below 139 kHz while harbor porpoise clicks were shifted slightly higher, centered at 141 kHz.

Pygmy and dwarf sperm whales (*Kogia breviceps* and *K. sima*) are also found in the study area and produce echolocation clicks with frequencies higher than 100 kHz (Madsen *et al.,* 2005). Current research indicates that signals from *Kogia* spp. may be distinguishable from Dall's porpoise (Merkens *et al.,* 2015), however there are little published data on the species. The observations that do exist from both published studies and very recent field work in the California Current and Hawaiian Islands report peak frequencies ranging from 125-129 kHz, lower than Dall's porpoise vocalizations (Marten, 2000; Merkens *pers. comm.* 2016; Barlow *pers. comm.,* 2016). In addition to differences in vocalizations, the abundance of Kogia in the region is estimated to be an order of magnitude lower than Dall's porpoise, rendering the potential for misassignment 10% or less of classified Dall's detections. The potential for confounding species or noises should be considered in modelling approaches developed with acoustic data. Just as visual models only utilize sightings that are confirmed to species, acoustic models should only utilize the most rigorous detections of the target species. Further research on acoustic detection and classification at the species-specific level, is needed to improve future acoustic and combination models and expand the diversity of species that can be included in such models.

One of the most significant limitations of acoustic-based models is group size uncertainty and therefore the ability to estimate density. However, the field of density estimation based on passive acoustic data is expanding rapidly and for some species and platforms, density models built with acoustic detections may be possible (e.g. beaked whales and fixed-location sensors) (Marques *et al*., 2009; Kusel *et* al., 2011; Marques *et* al., 2013; Department of the Navy, 2015). Density estimation also requires reliable and species-specific truncation distance to determine the effective area surveyed. For example, the high frequency of Dall's porpoise calls and resulting high attenuation reduce the acoustic detection distance of this species and ultimately limit the number of detections that may be available for modelling. While this can pose sample size constraints, it allows for accurate linking of a detection and the proximate habitat characteristics. Species with long-range vocalizations (e.g. sperm whales and blue whales) may present challenges in accurately modelling species-habitat relationships given the broad spatial scale across which these species could be detected. Further research is needed on species-specific detection distance and vocalization rates, similar to the body of work that has established trackline detection probabilities and effective strip width for cetacean species during visual line-transect surveys (Barlow, *et al.,* 2001; Barlow *et al.*, 2011).

5. Conclusion

We selected a well-studied species to develop habitat models built with acoustic data and a combination of visual and acoustic data. The process of building multiple models from a single shipboard survey allowed for a more direct inspection of the consistency of these two methods in capturing Dall's porpoise distribution. The combined model of Dall's porpoise shows promise for future efforts combining visual and acoustic data into cetacean habitat models. However, for this species, the two methodologies appear to be more complementary rather than directly additive. The current study highlights discrepancies in population sampling between acoustic and visual survey methods that should inform future population assessments and modelling efforts using these techniques.

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