Modeling the occurrence of endangered killer whales near a U.S. Navy Training Range in Washington State using satellite-tag locations to improve acoustic detection data

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14. ABSTRACT
1. We integrated opportunistic visual sightings, and the output from an updated state-space movement model fit to the locations from several satellite-tagged Southern Resident killer whales to fill in the detection gaps in the acoustic detections of this population in the coastal waters of the U.S. over a 4-year period when satellite tags were not deployed.
2. The predictions from our updated state-space movement model indicate that in the winters of 2013 and 2015, tagged SRKWs spent the highest density of time located off the Columbia River and near Westport. Other areas with relatively high occurrence were off the northern coasts of Washington and California.
3. Acoustic data were obtained from 6-13 recorders deployed off the coasts of Washington, Oregon, and California from 2011-2016 resulting in 11,718 monitoring days. Over a third of the monitoring days (4,314) were from sites within NWTRC W237.
4. Southern resident killer whales were acoustically detected 246 times between 2011 and 2016. The highest number of detections in a year (71, 2014) also coincided with the greatest monitoring effort. SRKW were detected at 13 of the 21 sites recorders were deployed. The furthest offshore they were detected was at the Cape Flattery Offshore site, 62km west of the northern Washington coast. No detections occurred at either of the sites located off the continental shelf.

5. Nine of the 21 monitoring sites were located in NWTRC W237. SRKWs were detected at four of the nine sites. 67 detections occurred over 4,314 days that sites within W237 were monitored between 2011-2016 for an average detection rate of 0.43 per month. The highest rate of detection in W237 occurred at LaPush (1.27 detections/month),
6. The acoustic detection probability was updated with data from two additional winter cruises (2015, 2016). Both were relative consistent with 2013 for an overall estimate of SRKWs vocalizing on average only 44% of time in the winter.
7. Updated annual predictive maps of the acoustic recorder detections indicate a pattern of distribution similar to years that whales were satellite tagged. While the winter monthly occurrence patterns appear to be similar to the annual patterns, there are some months that exhibit greater variation.
8. The increased number of recorders, particularly in locations identified as high occurrence sites, did not result in reducing the duration of days between detections (3.4 days in 2014, 4.6 days in 2015 compared to 2.7days in 2011).
9. A simulation analysis for an optimal recorder deployment scheme indicated that a whale could be detected 95% of the time, even if only vocalizing 50% of the time, with recorders spaced at 20km. A total of 28 recorders were estimated to be necessary to achieve this level of detection off the Washington coast.

APPENDIX ABSTRACT: Ocean fisheries often target and catch aggregations comprised of multiple populations or groups of a given species. Chinook salmon originating from rivers throughout the west coast of North America support mixed-stock ocean fisheries and other ecosystem components, notably as prey for marine mammals. We construct the first coastwide state space model for fall Chinook salmon tagged fish released from California to British Columbia between 1977 and 1990 to estimate of seasonal ocean distribution along the west coast of North America. We incorporate recoveries from multiple ocean fisheries and allow for regional variation in fisheries vulnerability and maturation. We show that Chinook salmon ocean distribution depends strongly on region of origin and varies seasonally while survival showed regionally varying temporal patterns. Simulations incorporating juvenile production data provide proportional stock composition in different ocean regions and the first coastwide projections of Chinook salmon aggregate abundance. Our model provides an extendable framework that can be applied to understand drivers of Chinook salmon biology (e.g. climate effects on ocean distribution) and management effects (e.g. consequences of juvenile production changes).

15. SUBJECT TERMS
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Executive Summary

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2. The predictions from our updated state-space movement model indicate that in the winters of 2013 and 2015, tagged SRKWs spent the highest density of time located off the Columbia River and near Westport. Other areas with relatively high occurrence were off the northern coasts of Washington and California.

3. Acoustic data were obtained from 6-13 recorders deployed off the coasts of Washington, Oregon, and California from 2011-2016 resulting in 11,718 monitoring days. Over a third of the monitoring days (4,314) were from sites within NWTRC W237.

4. Southern resident killer whales were acoustically detected 246 times between 2011 and 2016. The highest number of detections in a year (71, 2014) also coincided with the greatest monitoring effort. SRKW were detected at 13 of the 21 sites recorders were deployed. The furthest offshore they were detected was at the Cape Flattery Offshore site, 62km west of the northern Washington coast. No detections occurred at either of the sites located off the continental shelf.

5. Nine of the 21 monitoring sites were located in NWTRC W237. SRKWs were detected at four of the nine sites. 67 detections occurred over 4,314 days that sites within W237 were monitored between 2011-2016 for an average detection rate of 0.43 per month. The highest rate of detection in W237 occurred at LaPush (1.27 detections/month),

6. The acoustic detection probability was updated with data from two additional winter cruises (2015, 2016). Both were relative consistent with 2013 for an overall estimate of SRKWs vocalizing on average only 44% of time in the winter.

7. Updated annual predictive maps of the acoustic recorder detections indicate a pattern of distribution similar to years that whales were satellite tagged. While the winter monthly occurrence patterns appear to be similar to the annual patterns, there are some months that exhibit greater variation.

8. The increased number of recorders, particularly in locations identified as high occurrence sites, did not result in reducing the duration of days between detections (3.4 days in 2014, 4.6 days in 2015 compared to 2.7days in 2011).

9. A simulation analysis for an optimal recorder deployment scheme indicated that a whale could be detected 95% of the time, even if only vocalizing 50% of the time, with recorders spaced at 20km. A total of 28 recorders were estimated to be necessary to achieve this level of detection off the Washington coast.

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List of Acronyms

EAR - Ecological Acoustic Recorder

ESA - Endangered Species Act

MCMC - Markov Chain Monte Carlo

MCP - Minimum Convex Polygon

MOA – Military Operations Area

NWTRC – Northwest Training Range Complex

PODs – Pacific Orcinus Distribution survey

SRKW - Southern resident killer whale

Introduction

Over the last decade, acoustic monitoring surveys have become increasingly widespread as a powerful ecological tool to quantify habitat use by terrestrial and aquatic wildlife – recent examples include applications to birds (Dawson and Efford 2009), bats (Patriquin et al. 2003), marine mammals (Moore et al. 2006), fish (Rountree et al. 2006), and frogs (MacKenzie et al. 2002). In addition to monitoring species presence or densities, acoustic monitoring also contributes to soundscape ecology, providing estimates of anthropogenic acoustic disturbances to animal populations (Pijanowski 2011, Erbe et al. 2012).

Acoustic monitoring may be done with active or passive technology, where the latter represents silent monitoring devices (such as microphones or hydrophones). Recent technological advances in hardware has enabled large numbers of passive acoustic arrays to be deployed in terrestrial and aquatic environments (Mellinger et al. 2007, Efford et al. 2009, Blumstein et al. 2011). These vast arrays have the ability to better understand fine scale movements and density, and recorders that overlap in space may be used to make more precise estimates of an animal's location.

Depending on the species being detected, these acoustic sensors also allow researchers to better understand distribution at the individual level. While these large acoustic arrays represent ideal scenarios, more often the number and placement of acoustic devices may be limited by research budgets or constrained by interference with commercial or military operations. In these data-limited cases, acoustic monitoring data is still a reliable tool, and the utility of these data may be improved by integrating these data with additional data sources.

As a case study of integrating multiple types of data into the analysis of passive acoustic detections, we focus on a small population of fish-eating killer whales distributed off the coast of the western USA, known as the Southern Resident Killer Whale (SRKW) population. Because of its declining trend, this population was listed under the US Endangered Species Act in 2005, and has declined further since then (76 whales at the end of 2017). To identify winter habitat and distribution of these whales in order better assess potential risk factors, passive acoustic recorders have been deployed off the U.S. west coast since 2006, and data has been collected in most years since. A first challenge in assessing distribution from acoustic data alone is that the number of recorders deployed annually has typically been small (< 6). Second, the number of vocalizations recorded per year is small – in the 120 days between January 1 and May 1 for instance, SRKW have been detected on 16.5 days (see Hanson et al. 2013). Part of the reason for the limited number of detections is that the recorders have an unknown, but limited (~5km) detection range. In addition, although resident type killer whales generally vocalize frequently, they do not vocalize all the time. Although the population size of SRKW is known exactly, an additional challenge is that vocalizations from individual killer whales are not recognizable. This latter point prohibits the use of spatial capture-recapture or methods to estimate density (Buckland 2004, Efford et al. 2009). However, in many cases identification to each of the three pods (J, K, L) can be made acoustically for this population due to the stereotypic calls unique to each pod although in some cases each pod may split into subgroups, complicating assessment of pod movements. Detections may be limited due to ambient noise, both environmental and anthropogenic. Finally, another potential factor limiting detections is recorder placement which needs to mitigate for multiple uses of some areas relative to known whale use. This limitation, can be indirect, e.g., high anthropogenic noise associated with shipping lanes, or direct, e.g., recorder mooring loss due to interactions with commercial fishing.

Although the number of SRKW acoustic detections are limited, these data may be analyzed alongside other data sources to inform the distribution and habitat use of this population. Two other datasets that exist for SRKW are opportunistic visual sightings of individuals and a limited number of satellite tagged whales. Each individual SRKW is recognizable by photo-ID, and this knowledge of individual sighting histories has been used in previous studies to estimate demographic rates (Olesiuk et al. 1990, Ward et al. 2009, Ward et al. 2011). During the deployment of acoustic recorders since 2006, several satellite-tags have been deployed on SRKW. Although a few of these tags detached after 2-3 days, the most successful of these over the winters of 2013-2016 transmitted for 1-3 months.

The objective of our analysis is to illustrate the utility of passive acoustic detections, even when sample sizes are small and individuals are not distinguishable. Given the availability of other data sources, such as locations from satellite tags, we construct a state-space model of detections, equivalent to Bayesian occupancy models (Royle et al. 2005, Kery and Schaub 2012). Finally, we illustrate how the combination of movement information (visual and satellite tag) and acoustic detections can be used to construct maps of habitat use when fine scale satellite locations aren't available. For species at risk, such as the SRKW used in our case study, this integrated approach has the opportunity to (1) inform precise management actions (such as designation of Critical Habitat) and (2) aid in the deployment of acoustic devices in future surveys.

Methods

Data

Satellite-linked tags deployed on SRKW

We opportunistically deployed satellite-linked tags (Wildlife Computers Spot 5) on SRKW in Puget Sound or in the coastal waters of Washington and Oregon between 2012 and 2016 (Table 1). These tags transmitted via the Argos system, providing multiple locations per day. Due to variability in the error associated with each location, these were filtered with Douglas filter (available at: http://alaska.usgs.gov/science/biology/spatial/douglas.html) based on maximum potential velocity and turning angle.

Because these location data were available in near real-time, we were also able to spend 8 days following tagged whale K25 (as well as the other 60 associated whales) in 2013, J27 (and other members of J pod) for 3 days in 2015, L84 (and other members of L pod) for 12 days in 2015, and L95 (and other L pod whales) in 2016 for 3 days. We were also able to visually track J pod periodically for 5 days in 2016. During the course of all these visual follows we also monitored a towed array deployed off a 70m research vessel to record vocalizations by the whales. These data were used to estimate the rate of sound production by the whales (presence/absence of clicks, whistles, and calls) for each 10 min interval when visual confirmation of the whales within 2 km was available.

Autonomous Passive acoustic recorders

The second dataset consists of recordings by autonomous passive acoustic recorders deployed off the coast of California, Oregon, and Washington. The Northwest Fisheries Science Center has been deploying passive acoustic recorders in most years since the fall 2006. In the early years of the study the recorders were deployed on the continental shelf at sites where the whales had been previously observed or their prey was thought aggregate and more recently deployed at sites that tagged whales were known to frequent as well as deep water sites of adjacent to areas of known use. These recorders are programmed to record at a sample rate of 25 kHz for 30 seconds every 10 minutes (additional details in (Hanson et al. 2013)). In years prior to the initiation of this study (winters of 2007-09, 2011), data was recovered from 2 to 6 acoustic recorders, resulting in 1 to 38 detections per recorder each of these years, Hanson et al. (2013). Between 2011 and 2014 additional detections were obtained at 6 to 9 of the previously used sites and in years 2014 and 2015 the number of recorders was expanded to include up to 17 (Figure 1) sites. The additional locations were selected based on 1) high use areas identified in the duration of occurrence model for SRKW K25 (Hanson et al. 2017), 2) additional sites within the U.S. Navy's NWTRC W237 that included areas that the tagged SRKWs occurred infrequently in winter (mid-shelf) or not all (base of the continental slope), in order to determine if SRKWs used these areas in other seasons when satellite-linked tags were not deployed.

Cetacean vocalizations on the recovered hard drives from the acoustic recorders were manually scored (see Hanson et al. 2013 for method), and categorized by species. Killer whales were classified to ecotype to the extent possible and SRKW were also classified to pod to the extent possible although 2 of the 3 pods are often not differentiable (K and L pod). Because these latter groups spend more time on the outer coast and were the focus of the satellite tagging, we focused on the combined vocalizations of these groups (assuming they traveled together). Monthly detection rates were estimated by dividing the number detections into the total number of days monitored which had been divided by 30.

To complement the acoustic recorder data in years without satellite-tagged individuals, we compiled a database of visual sightings of SRKWs (see Hanson et al. 2015). The number of visual sightings was smaller than acoustic detections, ranging from 6 to 11 days with detections during the January – April months (See supplemental material).

Satellite-tag deployments overlapped in the winters of 2012-2016 (Table 1) with acoustic recorder deployments (Table 2). Because our modeling framework is focused on integrating the satellite-tagged locations with acoustic and visual detections, we limited our analysis to the overlap in space and time across these different datasets. Specifically, we used sightings and detections in the months of January – April, and only included groups of whales that associate with the tagged whale (K and L pods, which often associate together).

Analyzing tracking data

We fit a Bayesian state-space movement model to the location data from the two longest duration tag deployments, K25 (96 days) and L84 (93 days), following the approach of (Jonsen et al. 2005). State-space movement models have been applied to a wide range of tracking data from terrestrial and aquatic species (Jonsen et al. 2003). One of the advantages of these methods is that they improve the precision of estimated locations (and resulting estimates of rates of travel) because they partition the total variance in the observed track into process variance (changes in speeds and turning angles) and observation variance (representing the measurement uncertainty associated with the Argos location quality of each individual location).

Like previous state-space analyses of animal movement (Jonsen et al. 2005), we conducted Bayesian estimation using the JAGS language and the R2jags package in R (Plummer 2003, R Core Development Team 2015, Su and Yajima 2015). We generated 10000 Markov Chain Monte Carlo (MCMC) samples across 4 parallel chains.

Estimating detection probability

To estimate the detection probability of killer whales from acoustic recorders, we used the overlapping satellite tagging data and five acoustic recorders. We constructed a detection model based on the occupancy modeling framework with latent states (Royle et al. 2005, Kery and Schaub 2012).

In this model,

$$y_{t,s} \sim \text{Bernoulli}(z_{t,s} p)$$

$$z_{t,s} \sim \text{Bernoulli}(<p_{t,s})$$

where $y_{t,s}$ represents the detection (0, 1) at time *t* and location *s*, conditional on the occurrence $z_{t,s}$ and detection probability p. The parameter $<p_{t,s}$ represents the probability of occupancy. The matrices y and z were dimensioned by the number of 10 minute intervals in our satellite tagging model (n = 13722 10-minute intervals) and number of recorders (n = 5). For known detections, we initialized the value of $z_{t,s} = 1$, but treated all other values of *z* as latent states. Various approaches exist to model $<p_{t,s}$ (Royle and Dorazio 2008), and in this analysis we derived estimates of $<p_{t,s}$ from the state space model output (Figure 2). Specifically, we assumed the detection radius of each recorder to be fixed at 8km, and used the estimated posterior distribution of locations at time *t* across all 10000 MCMC iterations to calculate the probability of being in the 8km radius of each recorder. Mathematically, this means that $<p_{t,s}$ $\frac{\sum_{i=1}^{n_{MCMC}} I_i}{n_{MCMC}}$, where the indicator function I_i $\left\{ \begin{matrix} 1 \text{ if the location} < 8\text{km} \\ 0 \text{ otherwise} \end{matrix} \right\}$.

In the occupancy model described above, the only estimated parameter of interest is the detection probability *p*, which is assumed to be constant over time and space. Variation in the ambient noise near each recorder may lead to differential detection probabilities for example. We initially constructed a model with an uninformative (uniform) prior on *p*. As a sensitivity analysis, we wanted to examine how more informative priors might be used to improve the precision of the estimated detection probability, as well as how estimates from passive acoustic recorders compared to estimates from other acoustic monitoring studies. We used data from two external active monitoring surveys to develop informative priors.

In the first dataset, we used acoustic detections from three winter research cruises conducted aboard a 70m vessel equipped with a towed hydrophone array. Data were collected on 8-days in March 2013, 15 days in February and March 2015, and 8 days in March 2016 (NWFSC unpubl. data). These detections were collected while SRKWs were being visually followed at a distance of under 2km and resulted in 110, 152, and 80 one minute time intervals being collected, each spaced at least 10-minutes apart, in 2013, 2015, and 2016 respectively. For our second prior, we used similar acoustic data collected from summer research surveys (Holt et al. 2009), where 145 10 minute intervals (spaced 20-minutes apart) were collected and vocalizations were present in 128 of them. Each of these priors has associated strengths and weaknesses – for example, the Holt et al. (2009) study includes a larger sample size, but is from a different spatial area and season (inland waters in summer). Both priors was implemented using beta distributions, so that $rr_1 \sim \text{Beta}(29, 36)$ and $rr_2 \sim \text{Beta}(129, 18)$.

Projecting spatial distributions

For winters of 2007-2011 when SRKWs were not tagged, we sought to combine the results from all of the above data sources to make better predictions of coastal habitat use. Because some of the opportunistic visual sightings are from citizen scientists, the date, time, and location associated with these sightings may have a high degree of uncertainty, so these data occur at a much coarser scale (daily) compared to the fine scale satellite tracking data.

To estimate a coarse daily estimate of movement from the state-space model, we first used our posterior estimates at 10-minute intervals to generate 2-dimensional kernel densities of movement, with covariance matrix Σ. Second, we summarized each of the visual and acoustic detections in these earlier years on a daily time-step, and fit a random walk model to these locations data, with the covariance matrix Σ. Mathematically, this can be described as,

$$X_{t+1,1:2} \quad X_{t,1:2} + O_t, \text{ where } O_t \sim MVN(0, \Sigma)$$

Because this model may also include residual error (observation error), we linked the observed locations $Y_{t+1,1:2}$ to the estimated locations with an observation model,

$$Y_{t+1,1:2} \quad X_{t,1:2} + w_t, \text{ with } w_t \sim MVN(0, R)$$

where R was designated as a diagonal matrix (with the diagonal set to 2, corresponding to the detection radius of the recorders).

We used output from this model to make predictions about the spatial distribution of animals in years and months without satellite tagged animals, as well as to evaluate how the frequency of acoustic detections affects the uncertainty in these estimates.

Optimal recorder deployment

Using the estimated movement parameters from satellite tagged killer whales we conducted a simulation study to evaluate the effectiveness of alternative sampling designs with respect to acoustic recorder presence. Specifically, we were interested in evaluating how densities of recorders affected the probability of detecting whales on daily time steps.

Each simulation involved 1-day time steps over a 30-day window. At each 10-minute interval (corresponding to the recording rate in the present study) we identified the number of killer whale locations within 5 km of acoustic recorders, and simulated detection as a Binomial process. We assumed the detection probability (or probability of whales vocalizing) and being detected was 50%. Whale movement was simulated using output from Bayesian state space movement models from tagged whales (K25, L84, J27, L87). If whales avoided detection, that particular realization of the simulation was stopped, and the procedure was repeated. For the grid density in each scenario, we performed 1000 simulations, and the probability of detecting whales continuously over a 30-day window was calculated across simulations.

Results

Satellite-linked tagging

Between 2012 and 2016 satellite tags were deployed on eight SRKW (Table 1). Three tags were deployed on J pod members, two on K pod, and three on L pod. All tags were deployed on adult males. One of the tag deployments (L88) occurred while K25 was tagged, but because K and L pods were together during the duration of this deployment the L88 data were not included in these analyses. A total of 323 days were monitored for these unique whales (duration of signal contact ranged 3-96 days) yielding 3,145 locations for all whales. The seasonal duration of satellite tag data spanned from late December to mid-May.

Overall Coastal Distribution

The predictions from our state-space movement model suggest that in the winters of 2013 and 2015, SRKWs spent the highest density of time located off the Columbia River and near Westport (Figure 3). Other areas with concentrated occurrence included the northern coasts of Washington and California.

Acoustic recorder deployment effort

Annual

Acoustic data were obtained from six to thirteen recorders deployed off the Washington, Oregon, and California coast each year from 2011–2015. Data were collected throughout every year resulting in a total of 11,718 days monitored (Table 2). The number of days monitored each year was a function of the number of recorders that were deployed, delays in deployment schedules, mooring failures, instrument failures, instrument service life limitations, or fishing gear interactions, resulting in a range from 1,568 days to 3,186 recording days for each year. Although the focus of the study was from January to June, some data were collected in every month of the year.

Location

Most of the recorder data were collected from moorings located off the Washington coast which represented 15 of the 21 unique sites used (Figure 1, Table 2). The number of days monitored for sites ranged from 72 (Willapa) to 1,636 days (Cape Flattery Offshore). Of the 11,718 total monitoring days, over a third (4,314) were from the two to five sites that were deployed in NWTW237 between 2011 and 2016.

Southern resident killer whale acoustic detections

Annual

SRKWs were detected on 246 days between 2011 and 2016 (Table 3). The annual number of days with SRKW detections ranged from a high of 71 in 2014 to a low of 37 detections in 2011, with 2013, 2015, and 2012 yielding 54, 45, and 39 detections, respectively. In 2014, the year with the greatest monitoring effort (3186 days at 13 sites, average 245 days/site), we detected SRKW on 71 days, which represents approximately a little less than one third of the days/site during this period.

After weighting for the variation in effort (recording days) among years, detection rates per month of recorder effort (Table 4) were higher in 2012 (0.75) and 2014 (0.67) than in 2015, 2013, and 2011 (0.60, 0.58, 0.58, respectively).

Location

SRKW were detected at 13 of the 21 unique sites. Five sites had no detections and three sites were either not recovered or suffered instrument failure (Table 3). The furthest offshore site that SRKW were detected was the Cape Flattery Offshore site which is approximately 62km (176 m depth) off the coast. No SRKW detections occurred on any of the sites that were located off the continental shelf which had data available (Quinault Deep, Westport Deep).

Nine of the 21 sites were located in W237, but SRKWs were detected at only four of these nine sites. 67 detections occurred in W237 representing only about 25% of the total detections. When considered over the 4,314 days monitored in W237there between 2011 and 2016, the overall rate of detection was 0.43detections/month. Two of the sites had no detections (Cape Flattery Inshore, Cape Flattery mid-shelf). One site had a recorder failure in one year and was not recovered in another (Cape Flattery Deep) and one site the recorder was not recovered in either year (Quinault mid-shelf). Most of the detections in W237 were at the La Push site (26) which also had the highest average detection rate/month (1.27) of any of the sites in W237 (Table 4). La Push had the third highest average detection rate /month among all sites, only exceeded by Westport Inshore (1.75) and Columbia River North (1.57).

Detection Probability and Future Prediction

Our estimates of killer whale detection rates from the autonomous passive acoustic recorders suggest that the detection probability is approximately only 44% when an uninformative prior is used for *p*. The vocalization rate from the three winter research cruises were consistently less than that observed in the summer (Figure 4). This difference may be due to different survey methodology used during the winter coastal surveys versus the effort in their summer range, or differential vocalization rates in summer months when SRKW are primarily feeding on Chinook salmon compared to winter when prey are thought to be more scarce (Hanson et al. 2010).

Our updated predictive maps for SRKW occurrence from the acoustic recorder data in the winters of 2007-2011 (Figures 2 and 5) continued to show a concentration of utilization near the mouth of the Columbia River and Westport. The predictive maps developed on a monthly basis (based on the detections that occurred in at month and year) for each year (Figures 6-9) illustrate that while most months in most years exhibit the previously described annual pattern (Hanson et al. 2015), periodically substantial variations may occur, e.g. 2007, where the indication is that the whale may have spent more time in California. The coarseness of predictions in early years (e.g., 2007) is largely a function of the number of days with detections. For example, in 2007 SRKW were detected on only 2 days in February, but in 2009 and 2011, the detections increased to 12 and 11 days, respectively.

Optimal recorder deployment

Eight of the mooring sites deployed in 2014 and 2015 (Juan de Fuca, Sandpoint/Ozette, La Push, Quinault Inshore, Westport Inshore, Willapa, Columbia River North, and Columbia River South) were located near high density occurrence areas based on the satellite-tagged SRKWs (Figure 1). The average distance between these mooring locations was 33.1 km such that the given an average travel speed of approximately 6-7 km (Hanson et al. 2017) and the general linearity of the whales' travel patterns (NWFSC unpublished data) it was expected that detections would occur every about every 5 hours. However, the average duration between detections in 2014 averaged 3.4 days and 4.6 days in 2015. Consequently, the observed durations between detections were much greater than expected given the increase in the number of moorings. This greater than expected detection duration may have been a result of the lack of data from key high density sites each year (Westport Inshore– 2014, Columbia River North – 2015), or from the whales' vocalizing more infrequently, or the whales spent more time in areas not covered by recorders.

Results from our simulation analysis of recorder spacing suggest that the density of acoustic recorders would have to be spaced every 20 km (Figure 10) for whales to be detected consistently on a daily time step. At a spacing of 20 km, a whale would be continuously detected approximately 95% of the time, but the detection probability rapidly dropped off such that at a spacing of 60km, continuous probabilities of detection approached only 30%. The simulation indicates that at a spacing of approximately 33km spacing we would expect to detect SRKW on about 70% of days. In 2014 SRKW were detected on 29.4% of days and 22.1% of days in 2015.

Discussion

As the use of passive acoustic recorders has increased rapidly in ecology, one of the fundamental uncertainties is the acoustic detection probability (Alldredge et al. 2007). Detection is a function of several factors: the peak transmission frequency of the species of interest (Mellinger et al. 2007), ambient noise (Clark et al. 2009), and the detection range of the instrument to the animal – but one of the most important determinants is likely the behavioral characteristics that influences the acoustic production of the focal species (Oswald et al. 2003). In other words, the use of passive acoustic recorders to quantify presence / absence or density is most effective for species that vocalize frequently, and may be uninformative for species that rarely vocalize. Based on the combination of confirmed visual sightings of a tagged whale (or pod members) while within detection range of a towed hydrophone array, we estimate that these fish-eating killer whales vocalize approximately only 44% of the time while in the vicinity of the coastal recorders (Figure 4). These consistently low rates of vocalization in the winter, relative to those documented in the summer (Holt et al. 2009), were surprising. We hypothesize that these lower vocalization rates are likely due to the whales spending less time in two activities that typically involve vocalizing: foraging and socializing.

We considered the inclusion of several other datasets on vocalization rates from ship-based acoustic data collection, and these data were used to construct priors in our Bayesian modeling. Ultimately we used the posterior result from an uninformative prior to generate spatial predictions because the posterior result from the uninformative case was centered between the two ship-based studies, and the data collection from ship-based platforms was potentially problematic. In each ship-based survey, acoustic data were collected for several days (generally only during daylight hours), and each 10-minute interval within this period was assumed to be independent. Extrapolating these short surveys to the much longer time scale used in our analysis (4 months) is potentially problematic, particularly if vocalization rate varies in space, or as a function of environmental conditions (such as prey). In addition, as the results between 2013, 2015, and 2016 suggest, there also may be inter-annual variability in vocalization rates.

Our predictive maps for SRKW occurrence from the acoustic recorder data in the winters of 2007-2011 (Figures 2 and 5) show a similar pattern to the distribution of satellite tagged SRKW in 2012-2016 (Hanson et al. 2017)). The inclusion of acoustic recorder data with other data types (satellite tracks, visual sightings) offers the opportunity to improve precision of estimates (Barlow and Taylor 2005, Akamatsu et al. 2008), and identify opportunities for improvements in future study design. Each of these data types has strengths and weaknesses, as well as economic costs. Although opportunistic visual sightings can be obtained at no cost, they potentially have inaccurate spatial locations and times and are obtained only very infrequently. However, even dedicated visual surveys are costly and limited in their effectiveness by short day length and inclement weather in winter. Satellite tags provide high resolution spatial information that is unbiased, but deployed tags may not remain attached on animals for more than a few weeks, and tagging small or endangered populations, such as the one included in our analysis, may be logistically challenging. Finally, although acoustic recorders have a limited detection range, they possess the ability to sample for extensive durations (up to a year). Integrating these three types of data, our analysis highlighted that for time periods when continuous satellite tag data doesn't exist, acoustic recorders should be deployed in a manner to minimize the number of days between detections. This objective can likely be achieved by reallocating the spatial distribution of recorders to match regions of high habitat use, or by increasing the total number of recorders. We estimated that an increase in the number recorders (7 to 17), if strategically placed to coincide with areas where high use was previously observed, had the potential to allow multiple detections per day (Hanson et al. 2015). The average duration between detections increased from 2.2 days in 2009 with five recorders and 2.8 days in 2011 with seven recorders (Hanson et al. 2015), to 3.4 days in 2014 with 13 recorders and 4.6 days in 2015 with 9 recorders. Even though there was an increase in detections in 2014, the distribution of detections was somewhat clumped with a greater average time interval between detections despite the increase in number of recorders. This may have been due to the loss of key recorders (Westport Inshore, Columbia River North) or a decreased rate of vocalizing by the whales.

We estimated in a simulation that a recorder spacing of 20km, even with only 50% vocalization rate, would be sufficient to consistently detect the whales. While the estimated spacing of 20km might appear to be require a large number of recorders to cover the continental shelf it is important to note that 95% of SRKW locations are within a 34 km wide band parallel to the coast (Hanson et al. 2017). Thus, a pair of recorders positioned 20 km apart east to west would cover the 34km band. Given the Washington coast is 265 km long from the western entrance of the Strait of Juan de Fuca to the entrance of the Columbia River, we estimate that a total of approximately 28 recorders would be required to achieve a high probability of detection with this grid. However, it is important to note that different levels of detections may occur as a result of the whales foraging in some areas, where they would be more likely to vocalize, than in other areas. Such a situation seems to exist when comparing the detection rates at La Push compared to its neighboring sites, Ozette and Quinault inshore. Despite being only 41.9 km north of LaPush, Ozette's monthly detection rate was only a third (0.66) of LaPush's (1.62). Similarly, Quinault Inshore's (located 65.5 km south of LaPush) detection rate was less than 1/3 (0.45) of LaPush in 2014, and 1/10 in 2015 (0.08 versus 0.94). In addition, potential differences in environmental conditions may exist between years that affect animal movements, and thus detections (Hanson et al. 2013).

An additional consideration is that acoustic monitoring efforts are potentially constrained by factors inherent to the study area that may affect the ability to maintain a mooring at a site for an extended duration. For example, in some portions of this study area, commercial fishing activity, which has the potential to damage or free the recorder moorings is high. Despite efforts to position recorder moorings in areas of SRKW high habitat use while mitigating for high fishing activity (Figure 11), four of the 17 recorders deployed in 2014 , and three of the 15 recorders in the 2015 season were lost due to fishing activity during the deployment season. These losses occurred despite positioning the moorings adjacent to areas of relatively low fishing effort.

The methods developed here for integrating animal tracks, acoustic recorders, and visual sightings are widely applicable to other species where acoustic data are collected in parallel with other data types. Examples include applications to other marine mammals, including other killer whale populations (resident and transient whales in the NE Pacific), pilot whales, sperm whales, or beaked whales. Our approach could also be extended to better address questions about habitat use in terrestrial species, including elephants (Thompson et al. 2010), birds (Alldredge et al. 2007), and bats(Adams et al. 2012).

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We thank the crews of the R/V Centennial and F/V Cape Windy for deployment and recovery of the acoustic recorder moorings. The officers and the crew of the NOAA R/V Bell M. Shimada assisted in the PODs 2013, 2015, and 2016 cruises where we collected killer whale vocal activity on a towed hydrophone array. We thank the staff of Biowaves, Inc. for their assistance collecting the killer whale vocal activity and to Arial Brewer and Dave Haas for help with its analyses. D. Holzer provided Figures 1 and 11.

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Table 1. Satellite-linked tags deployed on Southern resident killer whales 2012-2016.

Whale ID	Pod association	Date of tagging	Duration of signal contact (days)
J26	J	20 Feb. 2012	3
L87	J	26 Dec. 2013	31
J27	J	28 Dec. 2014	49
K25	K	29 Dec. 2012	96
L88*	L	8 Mar. 2013	8
L84	L	17 Feb. 2015	93
K33	K	31 Dec. 2015	48
L95	L	23 Feb. 2016	3

*whale was tagged and monitored during K25 deployment when K and L pods were together and therefore not included analyses

Table 2. Acoustic recorder deployment effort, 2011-2016.

Year		2011-2012			2012-2013			2013-2014			2014-2015			2015-2016	
	Start Date	End date	# days	Start Date	End date	# days	Start Date	End date	# days	Start Date	End date	# days	Start Date	End date	# days
Location															
Juan de Fuca							30-Oct-13	23-Jul-14	266	02-Oct-14	23-Jul-15	294	05-Sep-15	28-May-16	267
Cape Flattery Inshore	01-Oct-11	04-Apr-12	187	22-Aug-12	30-Nov-12	100									
Cape Flattery Midshelf															
Cape Flattery Offshore	01-Oct-11	22-Aug-12	327	22-Aug-12	01-Sep-13	374	30-Oct-13	01-Oct-14	336	02-Oct-14	15-Aug-15	317	05-Sep-15	12-Jun-16	282
Cape Flattery Deep													06-Sep-15	19-May-16	257
Sand Point/Ozette							30-Oct-13	17-Jul-14	260	02-Oct-14	15-Aug-15	317	05-Sep-15	08-Sep-15	3
La Push										02-Oct-14	26-Jul-15	297	05-Sep-15	18-Jul-16	318
Quinault Inshore										31-Oct-14	23-Jul-15	265	05-Sep-15	20-Jul-16	365
Quinault Midshelf															
Quinault Deep										01-Nov-14	24-Jul-15	265	09-Mar-16	22-Apr-16	44
Westport Inshore	30-Sep-11	23-Aug-12	343	09-Nov-12	06-Jun-13	208	22-Oct-13	02-Jan-14	374	31-Oct-14	15-Nov-14	15	15-Sep-15	08-Aug-16	329
Westport Mid Shelf										31-Oct-14	23-Jul-15	265	08-Jan-16	28-Jul-16	202
Westport Deep													19-Mar-16	07-Sep-16	172
Willapa										31-Oct-14	11-Jan-15	72			
Columbia River North	30-Sep-11	22-Nov-11	53	09-Nov-12	19-Nov-12	10	22-Oct-13	01-Oct-14	344	01-Nov-14	07-Sep-15	320			
Columbia River South							23-Oct-13	01-Nov-14	374	01-Nov-14	04-Jun-15	225			
Newport	13-Sep-11	14-Sep-12	368	14-Sep-12	05-Mar-13	171									
Brookings							23-Sep-13	27-Jan-14	126	31-Dec-14	01-Jun-15	200			
Fort Bragg	27-Oct-11	12-Sep-12	322	12-Sep-12	20-Aug-13	341	04-Feb-14	30-Dec-14	329						
Sea Ranch							22-Sep-13	18-Oct-14	391	20-Nov-14	13-Oct-15	334			
Point Reyes	24-Oct-11	12-Sep-12	325	12-Sep-12	12-Sep-13	364									

Table 3. Number of days with acoustic detections ('detection days') of SRKW, 2011-2016.

Year	2011-12	2012-13	2013-14	2014-15	2015-16	Total
EAR Location						
Western Juan de Fuca			2	9	14	25
Cape Flattery Inshore	0	0				0
Cape Flattery Midshelf				NR	0	0
Cape Flattery Offshore	3	6	2	1	3	15
Cape Flattery Deep				NR	ND	NR/ND
Sand Point/Ozette			9	7	ND	16
La Push				16	10	26
Quinault Inshore				4	1	5
Quinault Midshelf				NR	NR	NR
Quinault Deep				0	0	0
Westport Inshore	21	22	20	ND	11	74
Westport Mid Shelf				3	6	9
Westport Deep				NR	0	0
Willapa				ND	ND	ND
Columbia River North	0	0	11	27	NR	38
Columbia River South			7	3	NR	10
Newport	7	6				13
Brookings			3	1		4
Fort Bragg	2	5				7
Sea Ranch			0	0		0
Point Reyes	4	0				4
Total	37	39	54	71	45	246

NR – Recorder not recovered ND- No data recovered Gray boxes – no recorder deployed

Table 4. Monthly detection rate of SRWK at each recorder location by year, 2011-2016.

Year	2011-12	2012-13	2013-14	2014-15	2015-16	Average
EAR Location						
Western Juan de Fuca			0.23	0.92	1.57	0.91
Cape Flattery Inshore	0.00	0.00				0.00
Cape Flattery Midshelf				NR	0.00	0.00
Cape Flattery Offshore	0.28	0.48	0.18	0.09	0.35	0.28
Cape Flattery Deep				NR	ND	
Sand Point/Ozette			1.04	0.66	ND	0.83
La Push				1.62	0.94	1.27
Quinault Inshore				0.45	0.08	0.24
Quinault Midshelf				NR	NR	
Quinault Deep				0.00	0.00	0.00
Westport Inshore	1.84	3.17	1.60	ND	1.00	1.75
Westport Mid Shelf				0.34	0.89	0.58
Westport Deep				NR	0.00	0.00
Willapa				ND	ND	
Columbia River North	0.00		0.96	2.53	NR	1.57
Columbia River South			0.56	0.40	NR	0.50
Newport	0.57	1.05				0.72
Brookings			0.20	0.15		0.18
Fort Bragg	0.19	0.44				0.32
Sea Ranch			0.00	0.00		0.00
Point Reyes	0.37	0.00				0.17
Annual	0.58	0.75	0.58	0.67	0.60	

NR – Recorder not recovered ND- No data recovered Gray boxes – no recorder deployed

Figure 1. Locations of 2014 -2016 season acoustic recorders and 2013 track of satellite-tagged SRKW K25 relative to Navy training ranges. Density 5x5 km grid cells based on duration of occurrence are shown in red.

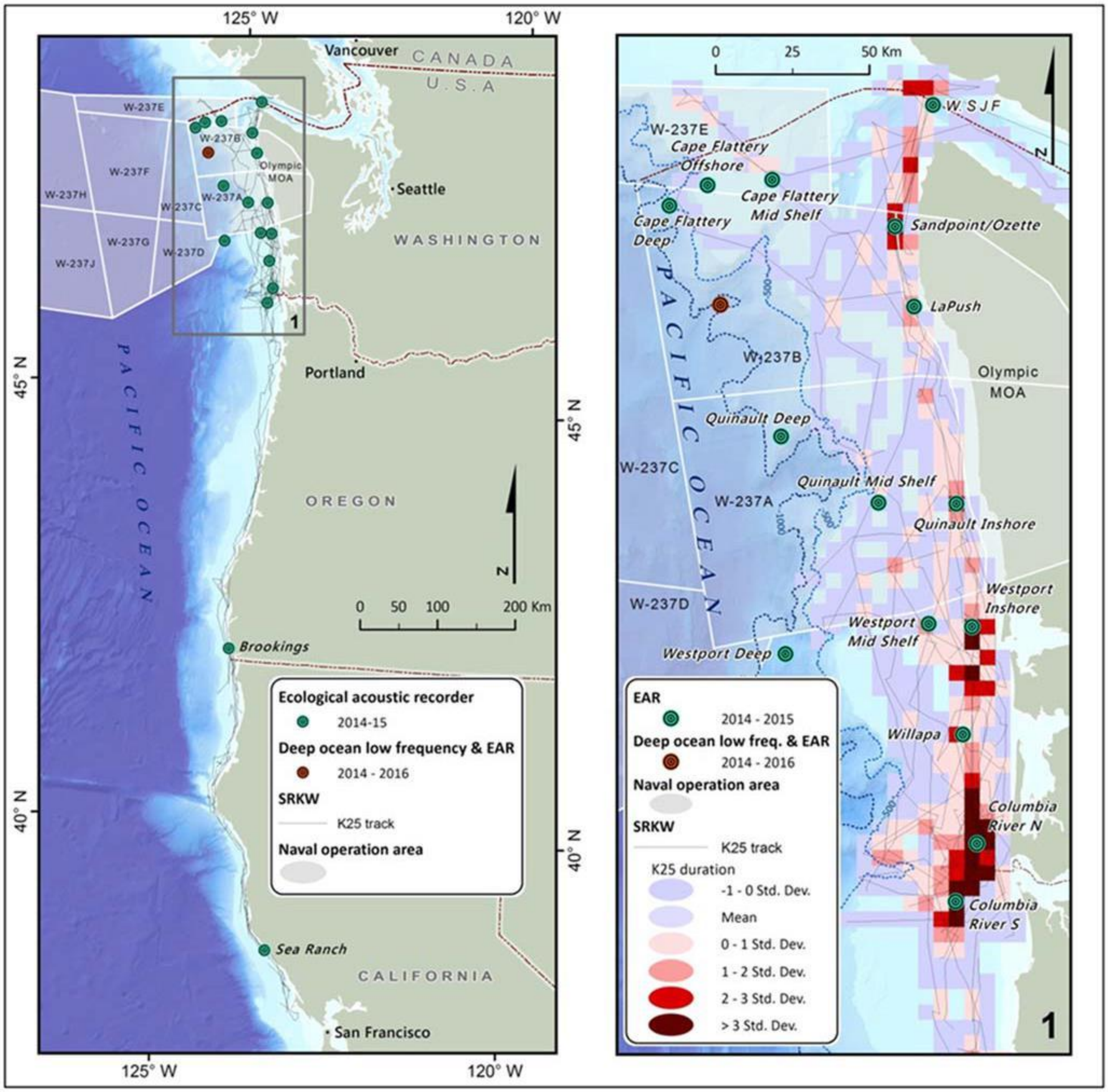

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Figure 2. Estimated probability of occupancy around a single recorder (in this instance, the recorder near Westport). The heat map is scaled relative to a uniform distribution of habitat use (e.g. dark red values indicate 15x higher than expected by chance). The quartered circle represents the location of the acoustic recorder – in this instance there's a 26% probability that the whale is within 8km of the recorder in a given 10-minute segment.

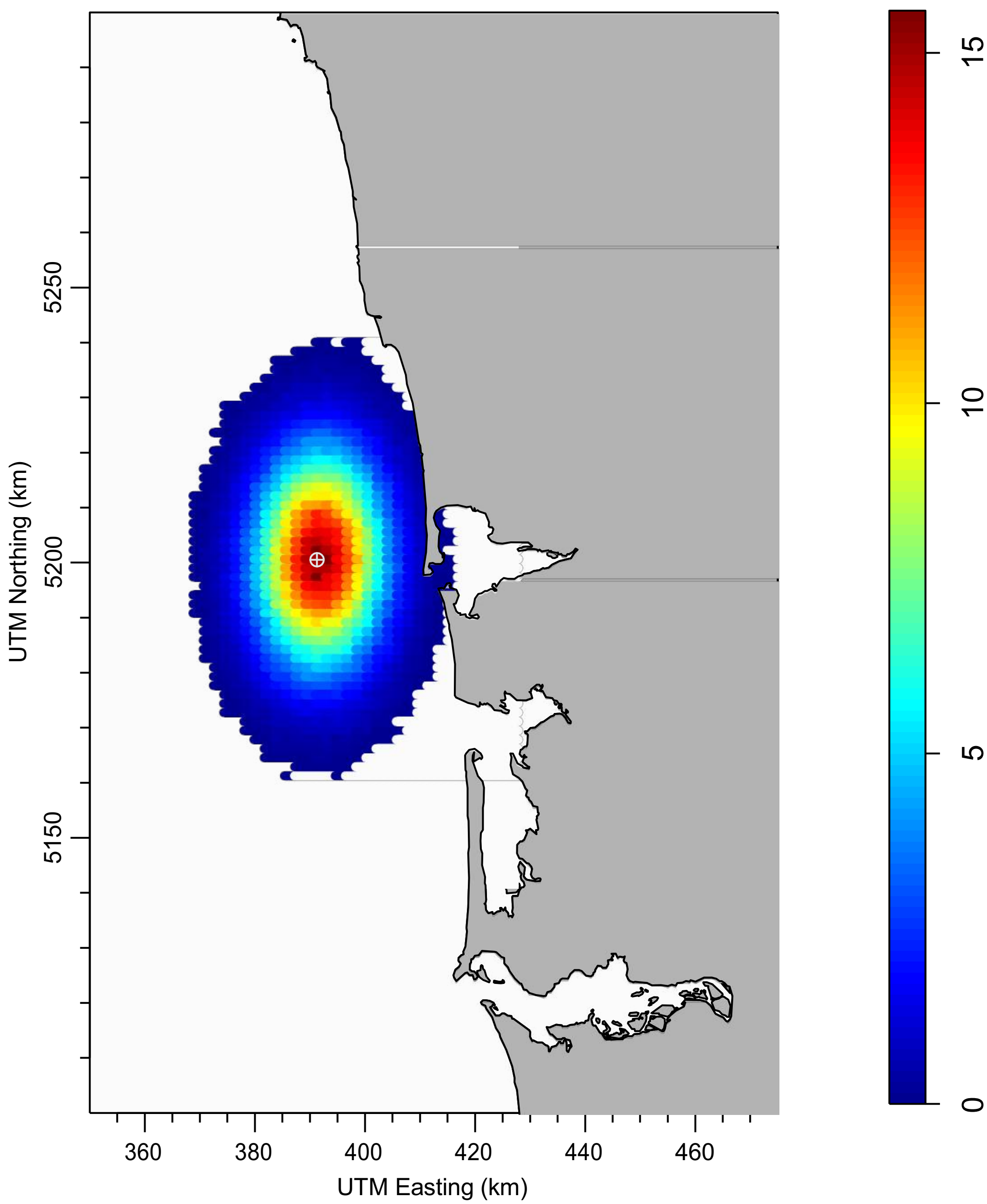


Figure 3. Estimated density for the K25and L84 movement tracks using a state space movement model, with 10-minute intervals. The heat map is scaled relative to a uniform distribution of habitat use (e.g. dark red values indicate 35x higher than expected by chance).

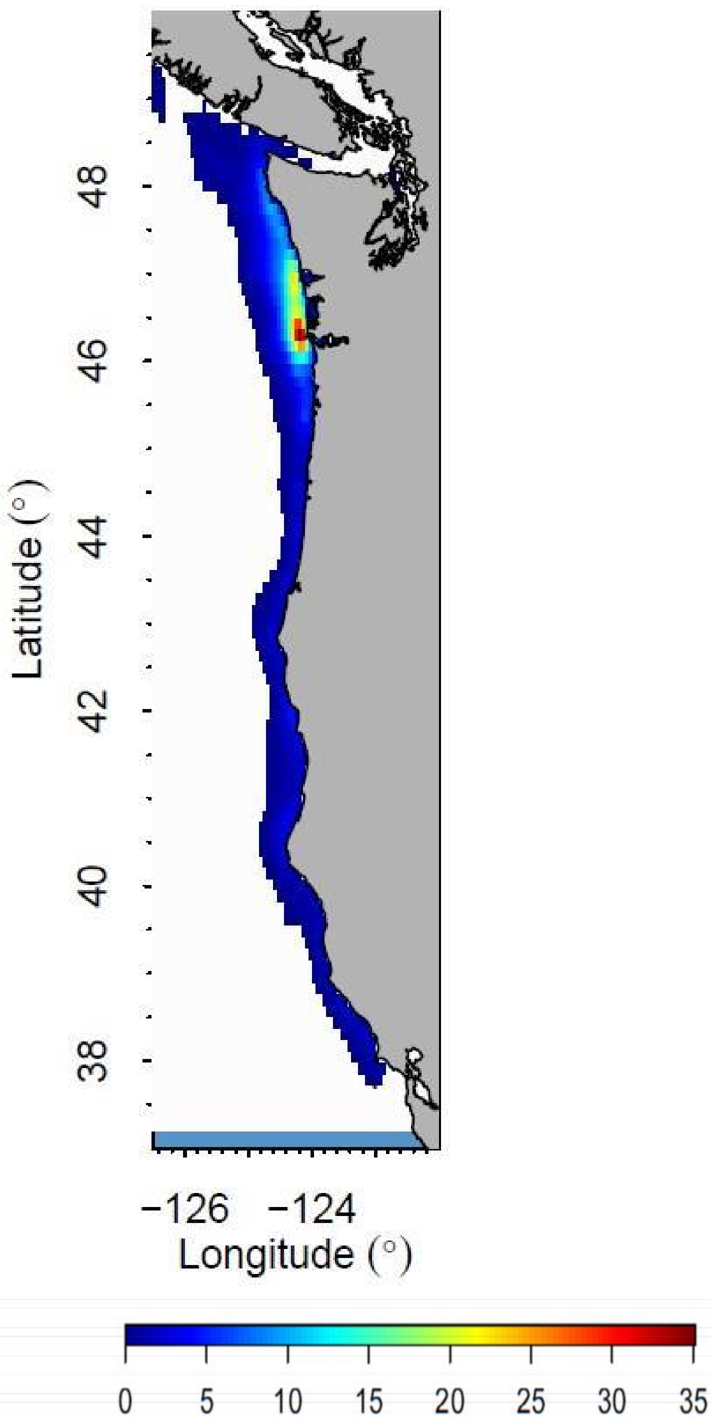


Figure 4. Prior distributions of Southern Resident killer whales detection probabilities derived from a towed hydrophone array paired with visual follows (within 2km) in coastal waters during winter cruises in 2013, 2015, and 2016 as compared to summer habitat. Red – 2013, green -2015, blue -2016, purple - summer (Holt et al. 2009).

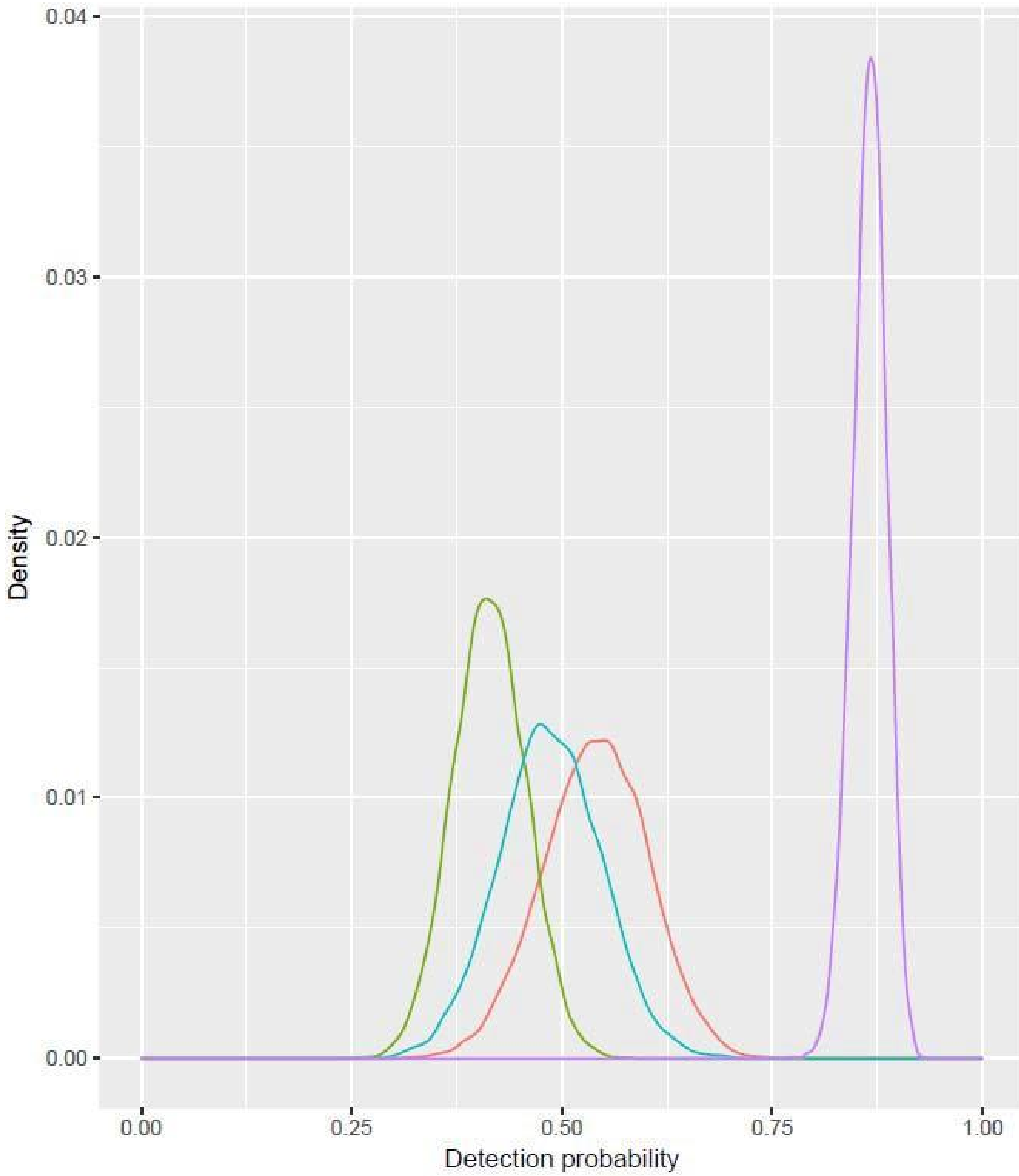


Figure 5. Spatial predictions of Southern Resident killer whale distribution in years without satellite tagged animals, based on acoustic recorder detections and visual sightings. All maps represent predictions for the month of February, and are shown on the same color scale relative to a uniform distribution (e.g. dark red values indicate 120x higher than expected by chance).

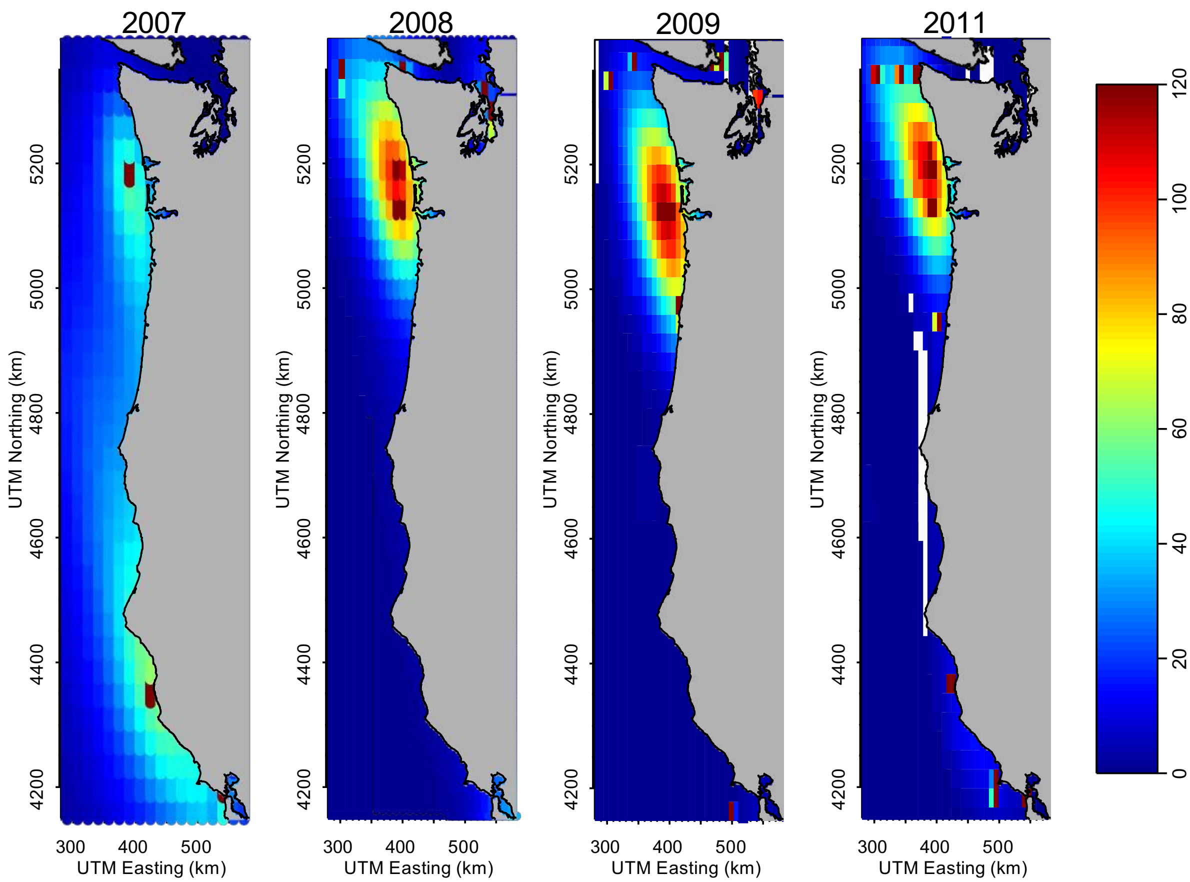
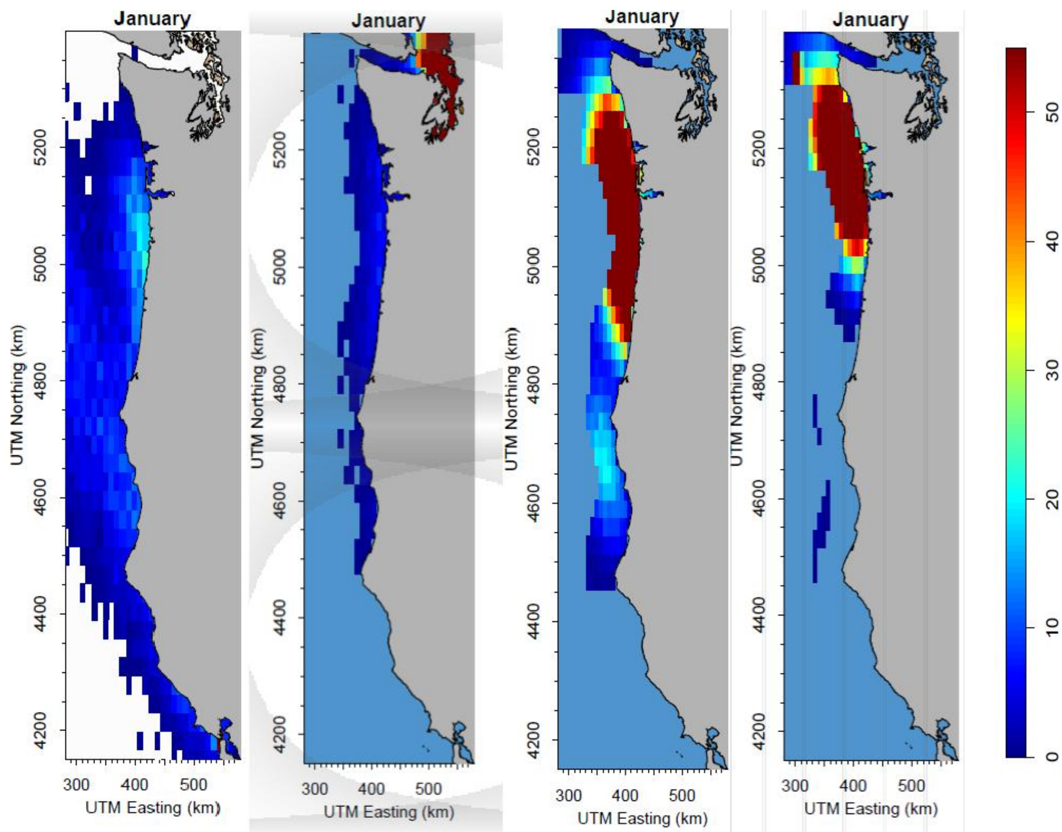


Figure 6. Estimated spatial distribution for January 2007-2011, using (1) simulated movement tracks from the state space models of previously tagged Southern Resident killer whales, and (2) acoustic detections and confirmed sighting reports as data. The spatial locations across simulations have been aggregated into 2-km grid cells. Scale colors are proportional to the maximum counts (i.e., a relative scale, not probabilities of occurrence) with dark blue, gray blue, and white areas all equal to zero.



2007 2008 2009 2011

Figure 7. Estimated spatial distribution for February 2007-2011, using (1) simulated movement tracks from the state space models of previously tagged Southern Resident killer whales, and (2) acoustic detections and confirmed sighting reports as data. The spatial locations across simulations have been aggregated into 2-km grid cells. Scale colors are proportional to the maximum counts (i.e., a relative scale, not probabilities of occurrence) with dark blue, gray blue, and white areas all equal to zero.

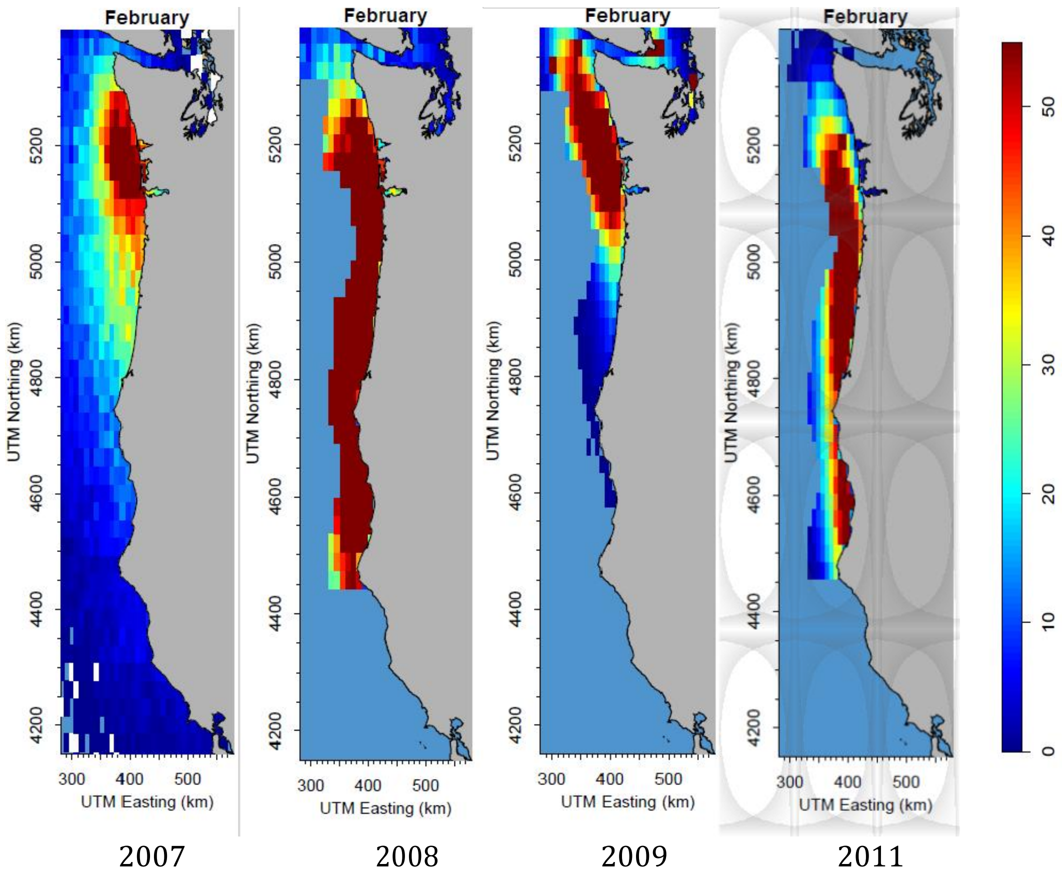
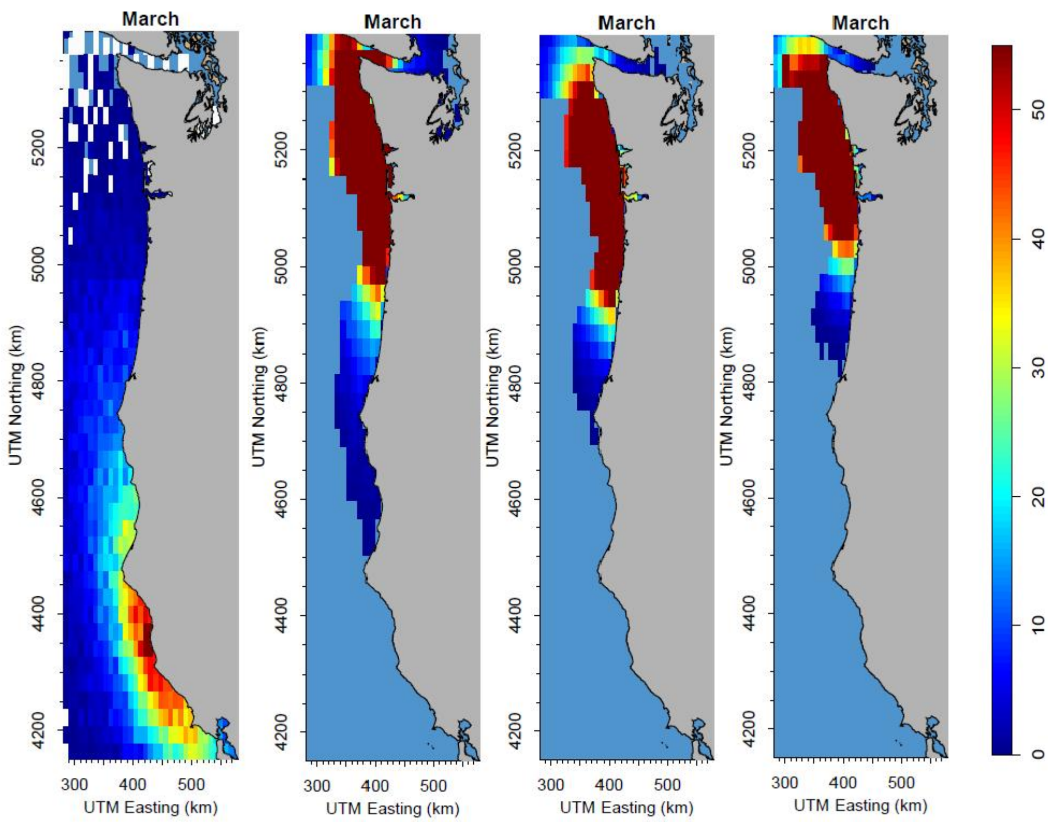


Figure 8. Estimated spatial distribution for March 2007-2011, using (1) simulated movement tracks from the state space models of previously tagged Southern Resident killer whales, and (2) acoustic detections and confirmed sighting reports as data. The spatial locations across simulations have been aggregated into 2-km grid cells. Scale colors are proportional to the maximum counts (i.e., a relative scale, not probabilities of occurrence) with dark blue, gray blue, and white areas all equal to zero.



2007 2008 2009 2011

Figure 9. Estimated spatial distribution for April 2007-2011, using (1) simulated movement tracks from the state space models of previously tagged Southern Resident killer whales, and (2) acoustic detections and confirmed sighting reports as data. The spatial locations across simulations have been aggregated into 2-km grid cells. Scale colors are proportional to the maximum counts (i.e., a relative scale, not probabilities of occurrence) with dark blue, gray blue, and white areas all equal to zero.

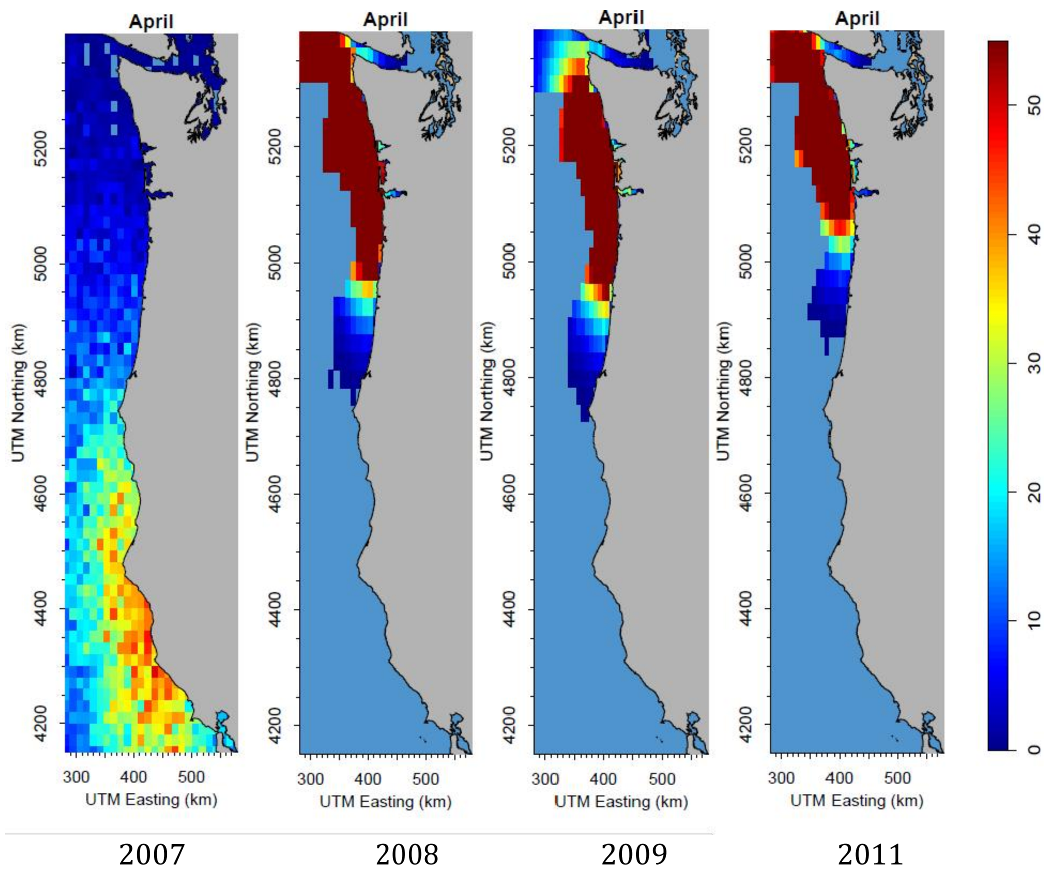


Figure 10. Probability function for optimal spacing of passive acoustic recorders to maximize detection SRKW recorders within their range in the coastal waters of the U.S.

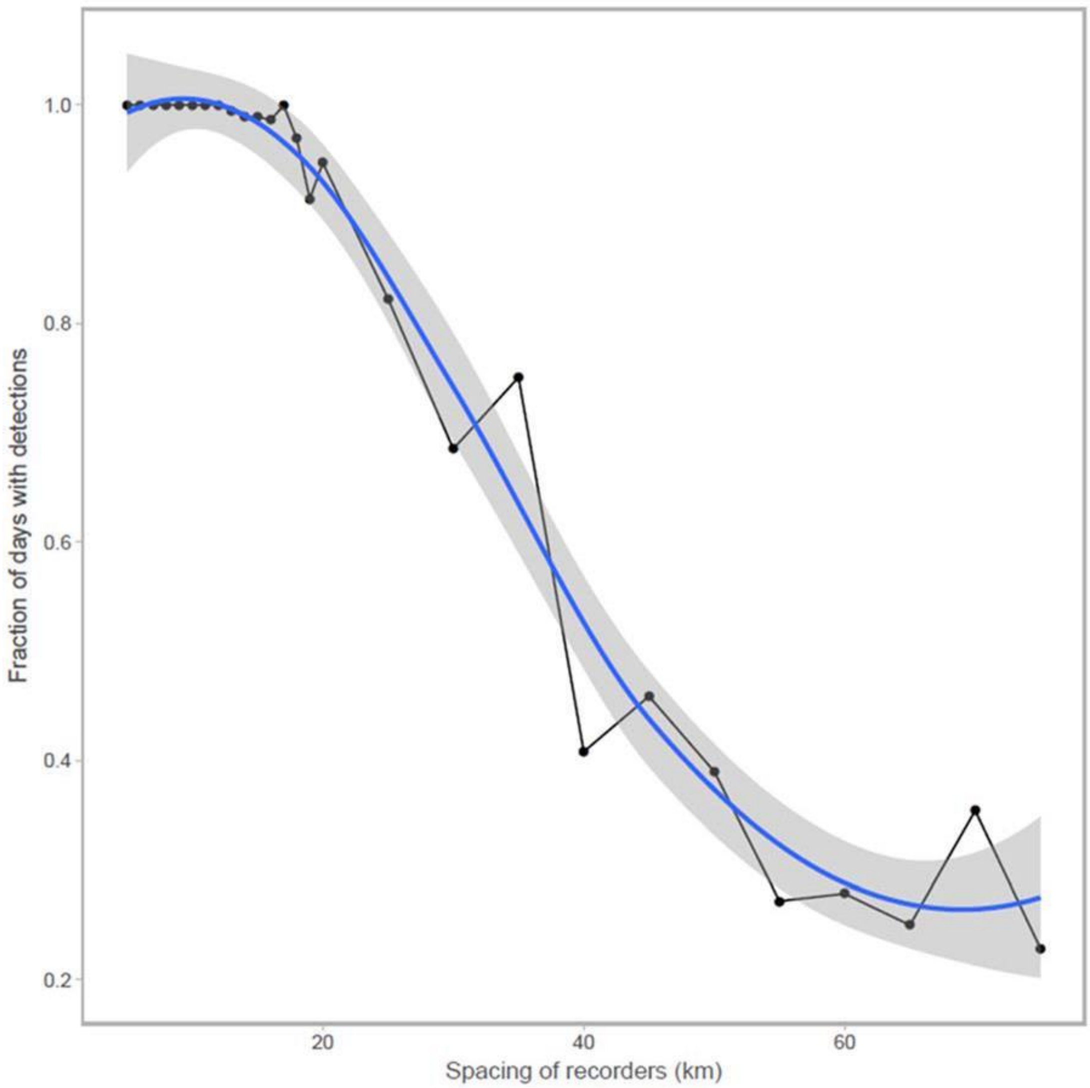


Figure 11. Locations of acoustic recorder mooring placement in 2014-2016 in relation to other SRKW location data sources and relative fishing intensity along the Washington coast.

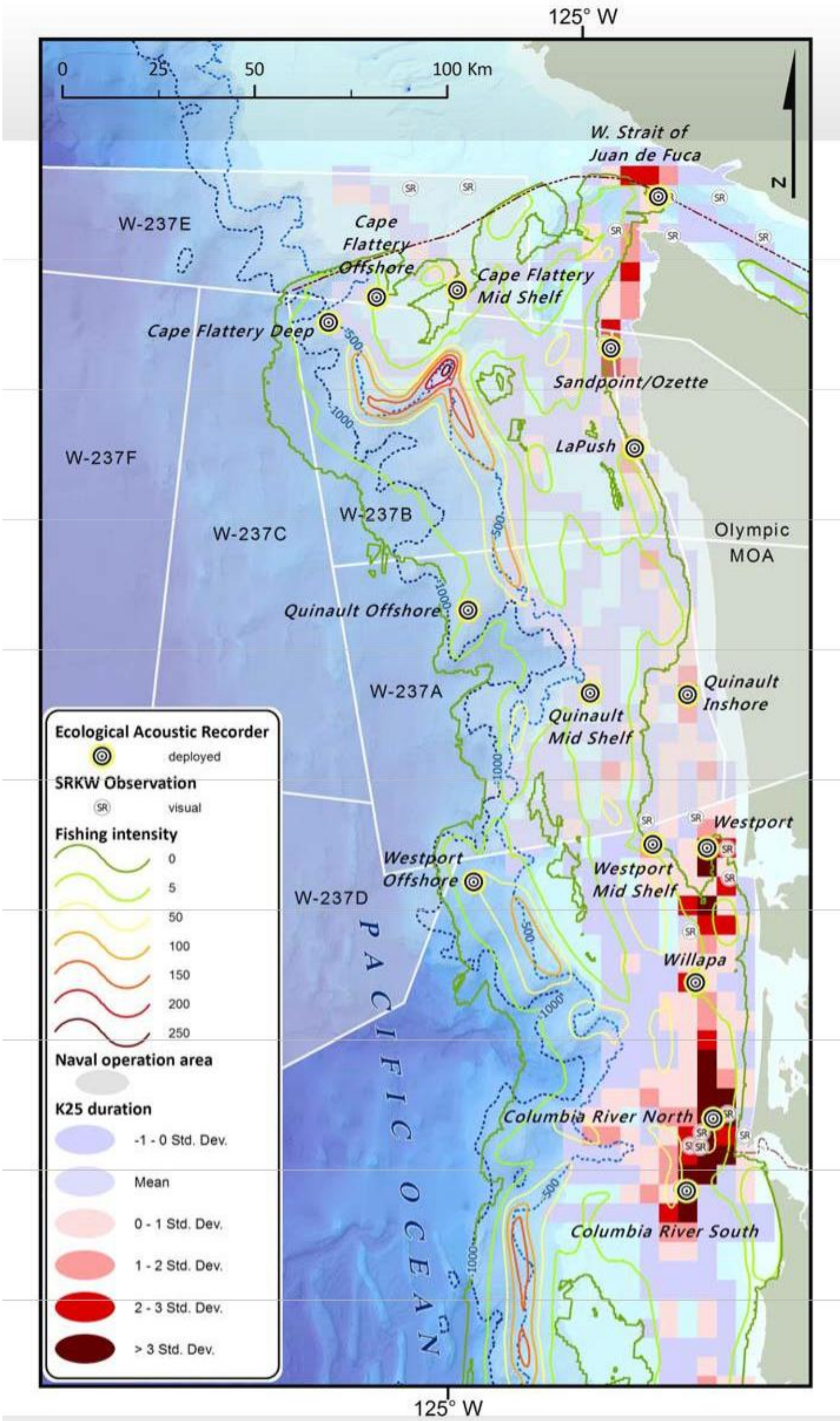


Table S1. Visual sighting records of SRKWs in U.S. coastal waters 2006-2011.

Year	Location	Latitude	Longitude	Julian day	Month	Day	Pod
2006	Pt Reyes	37.8956	123.0224	26	January	26	L pod
2006	Dana Passage	47.1628	122.8685	62	March	3	K,L12 pod
2006	Saratoga Passage	48.1853	122.5603	64	March	5	K,L pod
2006	Saratoga Passage	48.1853	122.5603	65	March	6	Prob SRKW
2006	Saratoga Passage	48.1853	122.5603	66	March	7	Prob SRKW
2006	Columbia River	46.1653	124.2848	89	March	30	K, L pod
2006	Columbia River	46.1653	124.2848	90	March	31	Prob SRKW
2006	Westport	48.9682	124.2353	94	April	4	L pod
2007	San Francisco	37.8167	122.4833	24	January	24	K pod
2007	Fort Bragg	39.3519	123.8831	77	March	18	L pod
2007	Gorda, CA	36.5833	121.85	79	March	20	Prob SRKW
2007	Monterey Bay	36.7083	121.91	83	March	24	K,L pods
2007	Monterey Bay	34.7477	121.8967	84	March	25	K,L pods
2007	Fort Bragg	39.3519	123.8831	88	March	29	Prob SRKW
2008	Puget Sound	47.8102	122.4274	1	January	1	K pod
2008	Puget Sound	47.8102	122.4274	2	January	2	Prob K pod
2008	Puget Sound	47.8102	122.4274	6	January	6	K pod
2008	Admiralty Inlet	47.9498	122.6013	7	January	7	Prob K pod
2008	Admiralty Inlet	47.9498	122.6013	8	January	8	Prob K pod
2008	Puget Sound	47.8102	122.4274	10	January	10	K pod
2008	Tacoma	47.2856	122.4446	11	January	11	Prob K pod
2008	Monterey Bay	36.9583	122.017	32	February	2	L pod
2008	Monterey Bay	36.9583	122.017	38	February	8	K,L pod
2008	Sekiu	48.261	124.3061	91	February	29	L pod
2009	Depoe Bay	44.808	124.061	21	Jan	21	L pod
2009	Depoe Bay	44.808	124.061	24	Jan	24	L pod
2009	Victoria	48.4079	123.39	37	Feb	6	J,K,L
2009	Gabriola	49.15	123.733	38	Feb	7	J,K,L

2009	Haro	48.5065	123.1786	40	Feb	9	K pod ?
2009	Puget Sound	47.8102	122.4274	50	Feb	19	K?,L pods
2009	Puget Sound	47.8102	122.4274	51	Feb	20	L pod
2009	Monterey Bay	36.9583	122.017	64	March	5	L pod
2009	Farrallones	37.6986	123.0022	66	March	7	L pod
2009	Westport	47.01167	124.5127	85	March	26	L pod
2009	Columbia River	46.263	124.2283	86	March	27	L pod
2011	Point Cabrillo, CA	39.3488	123.8234	39	2	8	20+ kw seen
2011	Fort Bragg, CA	39.3519	123.8831	39	2	8	"pod"
2011	10-12 mi W of Golden Gate Bridge	37.8167	122.4833	40	2	9	L
2011	Monterey Bay, CA	36.9583	122.017	41	2	10	L
2011	Just outside Golden Gate Bridge	37.8167	122.4833	43	2	12	12-15 whales
2011	San Fransisco Bay (NW)	37.8167	122.4833	45	2	14	L
2011	Umatilla Reef	48.1845	124.7544	83	3	24	K12s,K14s

Data source: Orca Network sighing archives - http://www.orcanetwork.org/Archives/index.php?categories_file=Sightings%20Archives%20Home

APPENDIX:

USING HIERARCHICAL MODELS TO ESTIMATE STOCK-SPECIFIC AND SEASONAL VARIATION IN OCEAN DISTRIBUTION, SURVIVORSHIP, AND AGGREGATE ABUNDANCE OF FALL RUN CHINOOK SALMON

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Abstract

Ocean fisheries often target and catch aggregations comprised of multiple populations or groups of a given species. Chinook salmon originating from rivers throughout the west coast of North America support mixed-stock ocean fisheries and other ecosystem components, notably as prey for marine mammals. We construct the first coastwide state-space model for fall Chinook salmon tagged fish released from California to British Columbia between 1977 and 1990 to estimate of seasonal ocean distribution along the west coast of North America. We incorporate recoveries from multiple ocean fisheries and allow for regional variation in fisheries vulnerability and maturation. We show that Chinook salmon ocean distribution depends strongly on region of origin and varies seasonally while survival showed regionally varying temporal patterns. Simulations incorporating juvenile production data provide proportional stock composition in different ocean regions and the first coastwide projections of Chinook salmon aggregate abundance. Our model provides an extendable framework that can be applied to understand drivers of Chinook salmon biology (e.g. climate effects on ocean distribution) and management effects (e.g. consequences of juvenile production changes).