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INTERNATIONAL WHALING COMMISSION

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Ari S. Friedlaender[1], Susan G. Heaslip[1,2], David W. Johnston[2], Andy Read[2], Doug Nowacek[2], John W. Durban[3], Robert L. Pitman[4], Logan Pallin[1], Jeremy Goldbogen[5], and Nick Gales[6]

1. Marine Mammal Institute, Oregon State University, Hatfield Marine Science Center, 2030 SE Marine Science Drive, Newport, OR 97365, USA

2. Division of Marine Science and Conservation, Nicholas School of the Environment, Duke University Marine Laboratory, 135 Duke Marine Lab Road, Beaufort, NC 28516, USA

3. National Marine Mammal Laboratory, Alaska Fisheries Science Center, NOAA Fisheries, 7600 Sand Point Way NE, Seattle, WA

4. Southwest Fisheries Science Center, NOAA Fisheries, 8604 La Jolla Shores Dr., La Jolla, CA 92037, USA

5. Hopkins Marine Station, Stanford University, 120 Oceanview Boulevard, Pacific Grove, CA 93950, USA

6. Australian Antarctic Division, 203 Channel Hwy, Kingston, Tas 7050, Australia

Introduction

A central focus of the IWC/SC/EM agenda at SC65b was to discuss methods to model the potential for competition and competitive interactions between baleen whales. For models to be accurate detailed knowledge about the foraging behavior of individuals within a species is paramount. However, critical information gaps exist in our understanding of the species-specific energetic costs of feeding, location and duration of foraging bouts, and how these relate to measures of prey availability. To that end, this report uses state-space animal movement models to determine the foraging effort and locations of Antarctic minke whales and humpback whales in the nearshore waters of the western Antarctic Peninsula. This information will help to determine the amount of sympatry in the foraging locations of these two species and the relationship to environmental co-variates (e.g. sea ice).

Clapham and Brownell (1996) discussed criteria necessary to demonstrate if, in fact, competition among cetaceans exists. The species in question must be resource limited (Milne 1961), have substantial spatio-temporal overlap in their distribution, and must occupy similar ecological niches. The former is predicated on having similar prey types (e.g. age class of common prey item), as well as foraging on prey patches of similar characteristics (e.g. patch depth, size, etc.). Although the potential for some direct competition may exist, the influence of any such interaction on depleted and recovering whale populations in the Antarctic is difficult to assess, given the paucity of appropriate data for analysis (Clapham and Brownell, 1996). Nonetheless, Clapham and Brownell (1996) postulate that competition is unlikely between Antarctic baleen whale species due in part to probable resource partitioning mediated by food preferences and, potentially, the biomechanics of body size. It has been suggested, but not substantiated, that baleen whales in the Southern Ocean are not resource limited, because their prey exists in densities exceeding their requirements (Kawamura, 1978). The lack of information on the fine-scale distribution of whales, their prey, and estimates of food consumption has prevented a full examination of interspecific relationships in the Antarctic whale community (Friedlaender *et al*., 2008).

Until recently, logistical constraints limited our ability to test many of the ecological criteria to determine the likelihood of direct competition between cetaceans. However, a growing body of literature provides insights that, in combination, provide a framework for a greater understanding of this question. Friedlaender *et al*. (2008, 2011) use a spatially-explicit modeling approach to determine the oceanographic/environmental variables that best predict habitat for sympatric humpback and minke whales and how each species distributes itself in relation to krill patches. One key parameter used in this analysis was a quantitative measure of prey biomass and distribution collected concurrent to whale observations, and whales appear to partition resources vertically at broad spatial scales. Similarly, Friedlaender *et al*. (2011) conducted an exploratory analysis of the ecological niches of sympatric krill predators to determine the amount of niche overlap among cetaceans, penguins, and seals. The results of this work indicate that humpback and minke whales have substantial overlap in their ecological niches which may indicate lower likelihood of competition via evolved means to partition resources: humpback whales appear to be distributed primarily in relation to their prey while minke whales are more strongly associated with sea ice and secondarily to prey. Compared to other krill predators, humpback and minke whale niches appear more stable across years.

Friedlaender et al. (2013, 2014, 2016) and Tyson et al. (2106) use multi-sensor movement tag data to provide quantitative measures of humpback and minke whale feeding behaviour in the Antarctic. Minke whales feed at unprecedentedly high rates compared to other baleen whales, however they filter significantly less water than other whales over the same period of time (Friedlaender et al. 2014). These differences are directly related to the anatomical scaling of the feeding apparatus in baleen whales. In relation to prey, humpback whales in fall only feed during night-time hours when prey are most abundant in the upper 50 meters of the water column (Friedlaender et al. 2014) and do so in a manner that is consistent with optimal foraging theory (Tyson et al. 2016). However, within this paradigm, the whales mediate their foraging behavior by targeting denser krill the deeper they feed, likely optimizing their energetic gains (Friedlaender et al. 2016). One of the main differences however between humpback and minke whale foraging is the ability of the latter to feed directly under sea ice. This strategy is particular to Antarctic minke whales in this region and is likely one of the means by which these two species partition resources.

The information from short-term tags provides novel insights into the underwater behaviour of these whales but critical gaps still exist in our knowledge of the longer-term movement and behaviour patterns of these whales and how they relate to each other and environmental features. Several studies have used ship-based (e.g. Murase et al. 2002, Santora 2014, SOCEP) or aerial surveys (Williams et al. 2014, Herr et al. 2016) to link the distribution of whales to sea ice and other physical features but these lack detailed information about the behaviour of individual whales and provide a snap-shot of animal distribution over a short temporal scale.

Here, we present progress on a project to analyze movement patterns, habitat use, and foraging bout duration of humpback and Antarctic minke whales from telemetry data. We report on hierarchical state-switching modeling analysis using satellite-derived telemetry data for both species to determine the proportion of time spent foraging, the location of where foraging occurs and the spatial relationships between foraging and sea ice. This information will be used to help develop individual-based models of cetacean foraging and generate specific hypotheses regarding competition between species from fine-scale foraging observations. This is a unique opportunity to achieve the analytical goals discussed within EM, provide new information to better understand competition between baleen whales, and stimulate further collaborative research.

Methods

Study Area

Tag deployments occurred over two weeks during the austral summer of February 2013 in the vicinity of the Gerlache Strait on the western side of the Antarctic Peninsula (Figure 1). A 6 m inflatable boat with a 40 horsepower 4-stroke engine and raised tagging pulpit was used to approach the animals for tag deployments from a perpendicular or oblique rear angle and at idle speed to reduce the potential disturbance of the animal prior to tag attachment. Placement of the tag was aimed to be high on dorsal surface of the whale, close to the dorsal fin, to maximize antenna exposure during surfacing. Photos of the dorsal fin and flukes of each tagged animal were taken to aid in individual identification.

Tags

Trans-dermal Argos-linked satellite tags were custom-designed, with an implantable housing containing a Wildlife Computers (Redmond, WA) Spot 5 transmitter or a SIRTRACK KiwiSat 202 (Cricket) platform transmitting terminal (PTT). Tag housings were built from surgical grade stainless steel and sterilized before deployment on humpback and minke whales (e.g. Gales et al. 2009). Tags were programmed to activate after attachment with a conductivity switch and duty-cycled to transmit over 3 or 6-hour intervals. A single AA battery provided up to ~270 days of active life.

Tags were deployed using a Restech modified compressed air line launcher (750-1000 kPa), with a projectile housing to aid in accuracy, from a distance of 3-8 m. Tags penetrated beneath the skin and hypodermis and anchored in the tissue beneath the underlying blubber with stainless steel barbs (Gales et al. 2009). This work was permitted under the U.S. Marine Mammal Protection Act by the National Marine Fisheries Service, Antarctic Conservation Act and Duke University Institutional Animal Care and Use Committee.

State-space behavioral switching model

We fit a Bayesian hierarchical switching state-space model (hSSSM, as described by Jonsen et al. 2005) to satellite location data from minke and humpback whales. This model was used to take into account error in Argos location estimates, normalize the data so that there were 4 locations per day, and to infer either transiting or area-restricted search (ARS) behavior from animal movements. Location data were derived from Argos' Kalman filter positioning algorithm (Lopez & Malardé 2011). The R package bsam was used for fitting the hDCRWS model, a hierarchical first-difference correlated random walk with switching model, to estimate movement parameters across multiple animals. Tracks were split into five groups for humpback whales and three groups for minke whales to reduce model run time. Groups contained one sex if information was available from progesterone assays (Pallin and Friedlaender unpublished data). Tracks with gaps equal to or greater than two days in length were split into subtrips and modelled separately. Tracks were modelled in R (R Development Core Team 2015) with a six-hour time step for 60,000 iterations; 40,000 sample burn-in; and with a retention of every 20th sample to reduce sample autocorrelation. The models were fit via Markov Chain Monte Carlo (MCMC) implemented in JAGS (Plummer 2015). Model parameters and location estimates were calculated using a total of 2000 MCMC samples. Model convergence and sample autocorrelation were assessed by visually inspecting autocorrelation and trace plots.

Post-hoc Analysis and Environmental Covariates

Output from the hSSSM was used to infer the movement behavior of the whales at the resolution of the six-hour time step. The behavior at each location was estimated as the mean of the MCMC samples with estimates of $b<1.25$ assumed to represent transiting, $b>1.75$ ARS, and $1.75 \leq b \geq 1.25$ uncertain, the same categories used by Jonsen et al. (2007).

Time of departure from the foraging grounds was estimated from the timing of a switch to the inferred transiting behavioral state with a concurrent directional northward movement of the animal. For the post-hoc analysis of inferred foraging behavior, data prior to this directional northward movement was retained for analysis.

We used the General Bathymetric Chart of the Oceans (GEBCO) 2014 Grid, a global 30 arc-second interval grid to extract depth values (m) for each location estimate using the Extract Multi Values to Points tool from the Spatial Analyst extension of ESRI ArcGIS® Desktop software (ESRI 2014). Ice concentration and distance (m) to ice edge (15% ice concentration contour) was estimated for each location from images of daily radiometer measurements of sea ice concentration at a resolution of 6.25 km from the Advanced Microware Scanning Radiometer-E using the ARTIST sea ice algorithm (Spreen 2008). The Extract Multi Values to Points tool and Spatial Join tool (Spatial Analyst extension) were used to extract ice concentration values and distance to ice edge for each location estimate using ESRI ArcGIS® Desktop software (ESRI 2014).

We then investigated the relationship between the two inferred behavioral states (transiting vs. ARS) and environmental covariates using generalized additive mixed models (GAMMs) for each species and the R package 'mgcv' with quasibinomial error distributions (logit link function) fit by maximum likelihood methods. A random effect of PTT ID accounted for within-individual variance in behavior. Temporal correlation in model residuals was assessed with the plotting of autocorrelation functions (ACF) in R. Descriptive statistics and GAMM results are reported as estimates ± standard errors (S.E.).

Home Range Estimation

Locations corresponding with inferred ARS behavior were used to construct a kernel utilization distribution for each animal and for each species to test if differences in foraging between species are related to environmental covariates. Home-ranges were based on the 90% isopleth from kernels created using a bivariate normal kernel estimated using the package adehabitatHR with the proportion of home range overlap assessed using the function 'kerneloverlaphr' (Fieberg and Kochanny 2005). Home ranges are presented between 25-99% isopleths.

Results

Tag Deployments

PTTs were deployed on humpback (n=17; Table 1) and minke (n=9; Table 2) whales in the vicinity of the Gerlache Strait on the western side of the Antarctic Peninsula between February 5–12, 2013. PTT deployments ranged from locations in Flandres Bay to Andvord Bay, the Gerlache Strait, and in Wilhelmina Bay (Figure 1). Track durations ranged from 4.6–265.6 days (mean 98.1 ± 19.6 days) for humpbacks and 1.4–179.3 days (mean 53.9 ± 21.1 days) for minkes. There were 7/17 tracks for humpbacks that were longer than 100 days (Table 1 and Figure 2) and 3/9 tracks from minke whales that were longer than 100 days (Table 2 and Figure 2).

Timing of Departure from Foraging Grounds

There were seven tracks from humpback whales and three tracks from minke whales with durations until the end of May or later (Tables 1 and 2). The departure from the foraging grounds was between April 23 and May 22, 2013 for humpback whales (Table 1) and between May 21 and June 7 for minke whales (i.e., 112745 and 112750 respectively; Table 2) and was estimated using the timing of a switch to transiting behavior (as inferred from the hSSSM), a concurrent directional movement to lower latitudes, and increase in swimming speed (e.g., Figure 3). The departure timing of minke whale 112747 was unclear given the eastward and then westward movements of this animal and a 29-day gap in the location data from April 25–May 24, 2013 (Figure 2). The movement and space use of individual whales during the foraging season are shown in Figure 2-5 with points representing the filtered locations from the hSSSM with a six-hour time step.

Movement Behavior

Tracks from the 17 humpback whales (9 females, 5 males, and 3 unknown sex) ranged from 4.6 to 265.6 days in length with an average of 98 days (98.1 ± 19.6 SEM; Table 1). Tracks from the 9 minke whales (3 females and 6 unknown sex) were relatively shorter in length and ranged from 1.4 to 179.3 days in length with an average of 54 days (53.9 ± 21.1; Table 2). The mean number of locations received per day and mean time step was comparable between humpback and minke whales, except for minke whale 112732 (Table 2). Few locations were received for 112732 likely as a result of poor tag transmission.

The hSSSM models were fit to the tracks of the 17 humpback whales and 9 minke whales, and results from the diagnostic plots suggest convergence of the MCMC chains. The transiting behavioral state was characterized by high persistence in move speed and direction with small turning angles (relatively straight track segments), while the ARS behavior was distinguished by lower persistence in speed and direction and frequent reversals (Tables 3 and 4). The estimated movement parameters from the models imply that minke whales are less likely to remain transiting and more likely to switch to transiting from the ARS state (Table 3) than humpback whales (Tables 4). Transiting animals had high move persistence with turning angles near zero, while animals in the ARS state had low autocorrelation in move speed and direction (Tables 3 and 4). Minke whales had relatively lower move persistence for the transiting state, relatively higher move persistence in the ARS state, and relatively greater turning angles for the transiting state compared to humpback whales (Tables 3 and 4).

For the pre-migration period of the tracks, the hSSSM results inferred 19% of humpback whale locations as transiting, 69% as ARS, and 7% as uncertain (Table 5). Close to 16% of minke whale locations were inferred as transiting, 33% as ARS, and 51% as uncertain (Table 6). The models had some difficulty in distinguishing between the two behavioral modes (state estimates between 1.25 and 1.75; Percent Uncertain, Tables 5 and 6), which could potentially be improved by setting a time step shorter than 6 hours. Posterior distributions of the movement parameters that represent turning angle (θ) and autocorrelation in move speed and direction (γ) did not overlap between the two behavioral states.

During the foraging period (pre-migration), bouts of inferred ARS behavior for humpback whales were 18.9 days long on average (range 0.25 to 71.75 days; Table 5) while transiting bouts were 1.36 days on average (range 0.25 to 6.75 days; Table 5). Bouts of inferred ARS behavior for minke whales for the foraging period were 4.6 days long on average (range 0 to 52.25 days; Table 6) while transiting bouts were 0.84 days on average (range 0.25 to 7.75 days; Table 6). The length of transiting bouts were similar between humpback and minke whales, but the variability in ARS bout lengths both within and between species and the small sample size for minke whales does not allow us to conclude whether there are any clear differences in bout lengths between species.

Inferred ARS locations for humpback and minke whales for the foraging period (pre-migration) are shown in Figures 4 and 5 respectively. ARS locations span the length of the Western Antarctic Peninsula for both humpback and minke whales (Figures 4 and 5 respectively), but are more dispersed for minke whales (Figures 5 and 6). Humpback whale ARS locations range further offshore with a few isolated ARS locations located off the coast (e.g., 121208 and 123236, Figure 4 insets), while minke ARS locations tend to be concentrated close to shore (Figure 5). Minke whales traveled farther than humpback whales during the foraging period with travel extending from the northeast tip of the Peninsula for 112745 and west along the continent for 112747 (Figure 5 insets and Figure 6). Although minke whale transit locations were located further from the grounding line on average compared to humpback whales (Figure 5), both transit and ARS locations were located closer to the 15% ice contour for minke whales (Figure 6).

Results for the generalized additive mixed model exploring the relationship between inferred behavioral state and the continuous explanatory variables distance to grounding line and distance to 15% ice contour, the factor variable species, and interactions between these variables are shown in Table 7 and Figures 8 and 9. This model explained 31.9% of the variation, with significant relationships (and species interactions) between inferred behavioral state and distance to grounding line and distance to 15% ice contour (Table 7). However, the smooth term for distance to 15% ice contour was not significant (p = 0.1310) for humpback whales (Table 7 and Figure 8). In contrast with humpback whales, the occurrence of ARS locations for minke whales varied with distance to 15% ice contour, decreasing with distance from the ice edge and then increasing at distances greater than 4 decimal degrees (though there were few ARS locations at this distance; Figure 8). The relationship between inferred behavioural state and distance to grounding line differed between humpback and minke whales, with the number of ARS locations decreasing non-linearly with distance to grounding line for humpbacks and decreasing and then increasing for minke whales (Figure 9).

For just the ARS points (Figures 10 & 11), the volume of intersection is 0.3699830 between minke and humpbacks (0.2831530 for all points during the pre-migration period) and the overlap of home range is 100% for humpbacks and 13% for minkes (minkes have a home range area that is 13% larger) based on the 90% isopleth (Figure 12). These values are based on home range estimates calculated using a fixed kernel home range with default bandwidth selection and a grid cell size of 1 km.

Discussion

The results of our tagging study provide quantitative information about the movement and behavior of Antarctic minke and humpback whales in the nearshore waters around the Western Antarctic Peninsula. In general, we find differences in the timing, duration, and location of area-restricted search (ARS) for each species and the relationship with physical environmental features such as the marginal ice edge and shore.

Our behavioral state-switching model found that humpback whales spend a greater proportion of their time in ARS than minke whales (69% versus 33%). Similarly, humpback whales remained in bouts of ARS for much longer than minke whales. That the average transit time between ARS bouts was not dissimilar indicates that humpback whales tend to remain in a general foraging mode for longer than Antarctic minke whales throughout the feeding season. This information is consistent with the presumed energetic demands of these whales based on differences in their body size. Combined previous knowledge or the feeding rates (Friedlaender et al. 2014) and partitioning of prey vertically (Friedlaender et al. 2008), it appears that the potential for competition between Antarctic minke and humpback whales is unlikely in this region.

In terms of space use, we find that humpback whales foraged broadly across a large extent of the continental shelf area of the Western Antarctic Peninsula. In contrast, minke whale foraging locations were generally located inshore or where sea ice persisted, however these areas spanned a greater spatial extent than for humpback whales (Figures 10-12). Whereas humpback whales are known to forage across a broad area in summer and then focus their foraging to smaller areas closer to shore in fall (Curtice et al. 2015), minke whales appear to increase their movements in nearly all directions from summer to fall and winter. The result of this is that minke whales have a home range (at the 90% isopleth) for ARS that is 13% larger than that of humpback whales. This movement of minke whales is likely a reflection of their affinity for sea ice and the lack of sea ice found around the western side of the Antarctic Peninsula in summer. This relationship is borne out in our GAMM results. Compared to humpback whales, minke whales foraged significantly closer to shore and significantly closer to the marginal ice edge. Humpback whales do not show any change in the probability of foraging with increasing distance from the ice edge while minke whale foraging is significantly more probable close to the ice edge, diminishing with increasing distance. As both species decrease their foraging probability with increased distance to shore the conclusion can be drawn that humpback whales are not affected by proximity to ice, but rather distance to shore whereas minke whales forage in proximity to sea ice when it is available and when it is not, they are more likely to remain inshore. These relationships may be unique to the western side of the Antarctic Peninsula that is one of the few locations in Antarctica with substantial coastal habitat and ice-free waters. In contrast, in areas like East Antarctica, while the extent of sea ice varies significantly across seasons, there is little access to the coast and the bathymetry over which the sea ice covers extends out beyond the continental shelf.

At the very broad scale, the area of the entire home range of the whales, we find substantial overlap between humpback and minke whales on the western side of the Antarctic Peninsula. However, while we do not include any direct measurements of prey in the current study, we are able to show significant differences in the duration, timing, and location of habitat-driven ARS between Antarctic minke and humpback whales where they are sympatric. This information is critical when trying to determine if competition exists between baleen whales in the Southern Ocean. The climate-driven changes occurring around the Western side of the Antarctic Peninsula have resulted in increasing air temperatures and a concurrent decrease in the number extent, duration, and number of ice covered days in the region (e.g. Vaughn et al. 2003, Stammerjohn et al. 2008). Our results indicate that in areas where little sea ice exists, minke whales remain close to shore in ARS, whereas humpback whales distribute themselves more broadly in open water. When sea ice is available, minke whales ARS is in close proximity to it while we observed no change in humpback whale ARS based on proximity to this feature. The decrease in sea ice appears to decrease the available foraging habitat for minke whales in the region, which could reduce the relative abundance of the species locally. Our tag data support this and show that minke whales eventually move from areas without sea ice to those where it is more prevalent and where the whales can forage/survive successfully.

Antarctic minke whales must balance the need for energy gain with the risk of predation from killer whales. It is very likely that the areas in which minke whales distribute themselves offers the greatest combination of success in each respect. Humpback whales on the other hand, are not at predation risk from killer whales and their distribution is likely unaffected by areas of high killer whale abundance. In the future, habitat models comparing the distribution and ecology of baleen whales in the Antarctic should consider the distribution and abundance of killer whales as a driver for some species (e.g. Antarctic minke whales).

Table 1. Tracking data for PTTs (Spot 5, Wildlife Computers and *KiwiSAT 202, SIRTRACK) deployed on humpback whales (n=17) in the Western Antarctic Peninsula in the austral summer of 2013. *denotes SIRTRACK tags, all others are Wildlife Computers. There was a gap in the transmission of the location data for 123232 and the timing of departure from the foraging grounds occurred sometime during this gap.

PTT ID	Sex	Deployment Date	Latitude (˚S)	Longitude (˚W)	Track start	Departure from foraging grounds	Track duration (days)	Total number of locations	Mean number of locations per day	Mean time step (hours)
112737	NA	2013-02-06 17:02	64.652	62.216	2013-02-06 18:48	—	68.7	2056	29.3	0.8
112738	M	2013-02-06 18:04	64.645	62.269	2013-02-06 18:44	—	63.8	1770	27.2	0.9
112746	F	2013-02-07 16:47	65.001	63.313	2013-02-07 18:31	—	61.0	1995	32.2	0.7
113206*	F	2013-02-07 16:21	65.000	63.324	2013-02-06 18:43	2013-04-23	215.8	3249	15.5	1.6
113207*	M	2013-02-07 18:54	64.980	63.267	2013-02-07 19:16	—	37.9	1139	29.2	0.8
113208*	F	2013-02-08 17:03	64.642	62.609	2013-02-08 18:22	2013-05-09	198.3	3877	19.3	1.2
113210*	M	2013-02-12 17:17	64.620	62.182	2013-02-12 17:52	—	41.5	1203	27.9	0.8
113211*	NA	2013-02-11 16:07	64.672	62.275	2013-02-11 23:54	2013-05-02	125.1	2996	23.5	1.0
121207	F	2013-02-12 16:40	64.634	62.209	2013-02-12 17:42	2013-05-06	130.3	2933	25.9	1.1
121208	F	2013-02-05 19:32	64.789	62.771	2013-02-05 23:25	—	21.3	179	9.4	2.9
121210	M	2013-02-05 18:51	64.806	62.745	2013-02-05 18:58	2013-04-29	195.7	4109	20.8	1.1
121211	F	2013-02-06 13:58	64.699	62.260	2013-02-06 23:55	—	37.5	1096	28.1	0.8
121212	M	2013-02-06 15:40	64.651	62.236	2013-02-06 17:01	—	4.6	152	25.3	0.7
123224	F	2013-02-05 17:47	64.834	62.699	2013-02-05 23:30	2013-05-22	141.5	2736	21.0	1.2
123231	F	2013-02-05 22:20	64.773	62.742	2013-02-05 23:26	—	8.3	125	12.5	1.6
123232	NA	2013-02-06 16:16	64.640	62.183	2013-02-06 17:03	2013-04-25 ≤ and ≥ 2013-06-09	265.6	4170	18.1	1.5
123236	F	2013-02-05 16:55	64.830	62.603	2013-02-05 17:16	—	50.8	1418	27.2	0.9

Table 2. Tracking data for PTTs (Spot 5, Wildlife Computers) deployed on minke whales (n=9) in the Western Antarctic Peninsula in the austral summer of 2013. There was a gap in the transmission of the location data for 112747 and the timing of departure from the foraging grounds occurred sometime during this gap. Percent of positions in transit, ARS, and uncertain behavior modes are for the period prior to the departure from the foraging grounds.

PTT ID	Sex	Deployment Date	Latitude (˚S)	Longitude (˚W)	Track start	Departure from foraging grounds	Track duration (days)	Total number of locations	Mean number of locations per day	Mean time step (hours)
112731	NA	2013-02-09 12:24	64.692	62.262	2013-02-09 18:12	—	13.7	298	22.8	1.1
112732	NA	2013-02-09 12:44	64.697	62.273	2013-02-25 1:35	—	6.9	30	4.3	5.7
112733	NA	2013-02-08 12:38	64.790	62.736	2013-02-08 19:59	—	1.4	39	13.0	0.9
112734	NA	2013-02-08 14:45	64.801	62.699	2013-02-09 5:57	—	13.1	363	25.9	0.9
112736	NA	2013-02-09 12:20	64.694	62.266	2013-02-09 12:32	—	35.7	888	23.9	1.0
112745	F	2013-02-09 12:32	64.697	62.262	2013-02-09 12:35	2013-05-21	108.7	2672	24.7	1.0
112747	NA	2013-02-09 12:27	64.693	62.263	2013-02-09 12:32	2013-04-21 ≤ and ≥ 2013-05-24	110.5	1748	21.3	1.5
112748	F	2013-02-09 16:01	64.665	62.238	2013-02-09 19:49	—	16.0	230	13.5	1.7
112750	F	2013-02-09 15:21	64.684	62.264	2013-02-09 18:10	2013-06-07	179.3	3001	18.9	1.4

Table 3. Estimated parameter means for each of the 5 groups of humpback whale tracks modelled. α_1 is the probability of remaining in the transiting state at time *t* if in the transiting state at time *t*-1 and α_2 is the probability of switching to the transiting state at time *t* if in the ARS state at time *t*-1. γ_1 and γ1 are the mean autocorrelations in move speed and direction for transiting and ARS behavioral states respectively and θ1 and θ_2 are the mean turn angles (in degrees) for the transiting and ARS behavioral states.

Model run	α_1	α_2	γ_1	γ_2	θ_1	θ_2	PTT Tracks
Female Mn	0.928	0.023	0.9046	0.0136	-0.73	187.38	112746, 121207a, 123231, 123236
Female 2 Mn	0.975	0.018	0.9294	0.0459	0.92	185.18	113206a, 121208a, 121208b, 121211
Pregnant Mn	0.965	0.021	0.9029	0.0264	2.89	177.76	113208, 123224a, 123224b
Male Mn	0.949	0.030	0.9245	0.0273	0.03	236.37	112738, 113207, 113210, 121210, 121212
Unknown Mn	0.979	0.013	0.9216	0.0133	1.06	191.56	112737, 113211, 123232a, 123232d, 123232e

Table 4. Estimated parameter means for each of the 3 groups of minke whale tracks modelled. α_1 is the probability of remaining in the transiting state at time *t* if in the transiting state at time *t*-1 and α_2 is the probability of switching to the transiting state at time *t* if in the ARS state at time *t*-1. γ_1 and γ1 are the mean autocorrelations in move speed and direction for transiting and ARS behavioral states respectively and θ1 and θ_2 are the mean turn angles (in degrees) for the transiting and ARS behavioral states.

Model run	α_1	α_2	γ_1	γ_2	θ_1	θ_2	PTT Tracks
Female Bb	0.883	0.043	0.8536	0.1130	5.60	242.46	112745a, 112745b, 112748, 112750a
Unknown Bb1	0.714	0.644	0.6209	0.2833	-3.17	192.08	112731a, 112732, 112733, 112736
Unknown Bb2	0.883	0.172	0.8380	0.0312	1.03	178.07	112734, 112747a, 112747b

Table 5. Bout characteristics for humpback whales during the foraging period (pre-migration) along the Western Antarctic Peninsula in the austral summer of 2013. Percent of positions in transit, ARS, and uncertain behavior modes are for the period prior to the departure from the foraging grounds.

PTT ID	Duration of track on foraging grounds (days)	ARS bouts (days)				Transiting bouts (days)				Transit (%)	Uncertain (%)	ARS (%)
		Minimum	Maximum	Mean	*N*	Minimum	Maximum	Mean	*N*			
112737	68.7	23.75	43.25	33.50	2	1.00	1.00	1.00	1	1.5	1.1	97.5
112738	63.8	0.25	10.50	4.20	10	0.75	1.75	1.13	6	10.5	23.8	65.6
112746	61.0	3.50	56.25	30.00	2	1.00	1.00	1.00	1	1.6	0.4	98.0
113206	75.2	0.75	37.25	18.00	4	0.25	0.75	0.50	3	2.0	2.6	95.4
113207	37.9	3.00	16.00	7.00	4	0.75	4.50	2.08	3	16.4	9.9	73.7
113208	89.2	12.50	69.50	41.00	2	0.25	1.00	0.58	3	2.0	6.4	91.6
113210	41.5	2.00	19.50	9.30	4	0.25	1.50	0.75	3	5.4	4.8	89.8
113211	79.0	3.50	53.50	24.68	3	0.25	1.75	0.92	3	3.4	4.4	92.2
121207	82.3	0.25	27.25	7.20	9	0.25	4.00	1.25	7	10.5	12.0	77.5
121208	21.3	3.00	4.75	3.88	2	1.00	1.25	1.13	2	15.8	29.8	54.4
121210	82.2	1.75	71.75	36.75	2	0.25	0.25	0.25	1	0.3	10.9	88.8
121211	37.5	36.00	36.00	36.00	1	1.00	1.00	1.00	1	2.6	2.0	95.4
121212	4.6	4.75	4.75	4.75	1	—	—	—	0	0.0	0.0	100.0
123224	105.0	0.25	46.75	7.55	11	0.25	3.25	1.64	7	11.1	8.5	80.4
123231	8.3	8.50	8.50	8.50	1	—	—	—	0	0.0	0.0	100.0
123232	77.3	11.25	65.75	38.50	2	0.25	0.50	0.38	2	1.0	0.3	98.7
123236	50.8	1.00	25.00	10.50	4	6.75	6.75	6.75	1	13.2	4.4	82.4

Table 6. Bout characteristics for minke whales during the foraging period (pre-migration) along the Western Antarctic Peninsula in the austral summer of 2013. Percent of positions in transit, ARS, and uncertain behavior modes are for the period prior to the departure from the foraging grounds.

PTT ID	Duration of track on foraging grounds (days)	ARS bouts (days)				Transiting bouts (days)				Transit (%)	Uncertain (%)	ARS (%)
		Minimum	Maximum	Mean	*N*	Minimum	Maximum	Mean	*N*			
112731	13.7	—	—	—	0	0.25	0.75	0.40	5	18.6	81.4	0.0
112732	6.9	—	—	—	0	—	—	—	0	0.0	100.0	0.0
112733	1.4	—	—	—	0	—	—	—	0	0.0	100.0	0.0
112734	13.1	1.50	3.75	2.13	4	0.75	0.75	0.75	1	5.7	30.2	64.2
112736	35.7	0.25	0.25	0.25	6	0.25	4.00	0.78	17	37.1	58.7	4.2
112745	100.5	0.25	10.75	4.08	15	0.25	4.25	1.63	14	23.2	14.3	62.5
112747	70.5	0.25	2.75	0.86	7	0.25	7.75	1.75	15	34.9	57.1	8.0
112748	16.0	1.00	4.00	2.25	6	0.25	0.25	0.25	2	3.1	12.5	84.4
112750	117.2	1.75	52.25	18.05	6	0.25	0.50	0.31	4	1.1	7.4	91.5

Table 7. Parameter estimates and approximate significance of smooth terms for the fitted generalized additive mixed model.

Parametric coefficients	Estimate	Standard error	*z*	*p*	Approximate significance of smooth terms	Estimated d.f.	*Chi square*	*p*
Intercept (humpback)	2.6551	0.1335	19.882	<0.0001	Distance to grounding line (humpback)	6.996	147.644	<0.0001
Species (minke)	-1.0698	0.1871	-5.718	<0.0001	Distance to grounding line (minke)	5.883	250.314	<0.0001
					Distance to 15% ice contour (humpback)	1.000	2.286	0.1310
					Distance to 15% ice contour (minke)	3.952	62.306	<0.0001

Figure 1. Map of the study area with location of PTT deployments in the vicinity of the Gerlache Strait, Western Antarctic Peninsula, February 5–12, 2013 for humpback (n=17) and minke (n=9) whales.

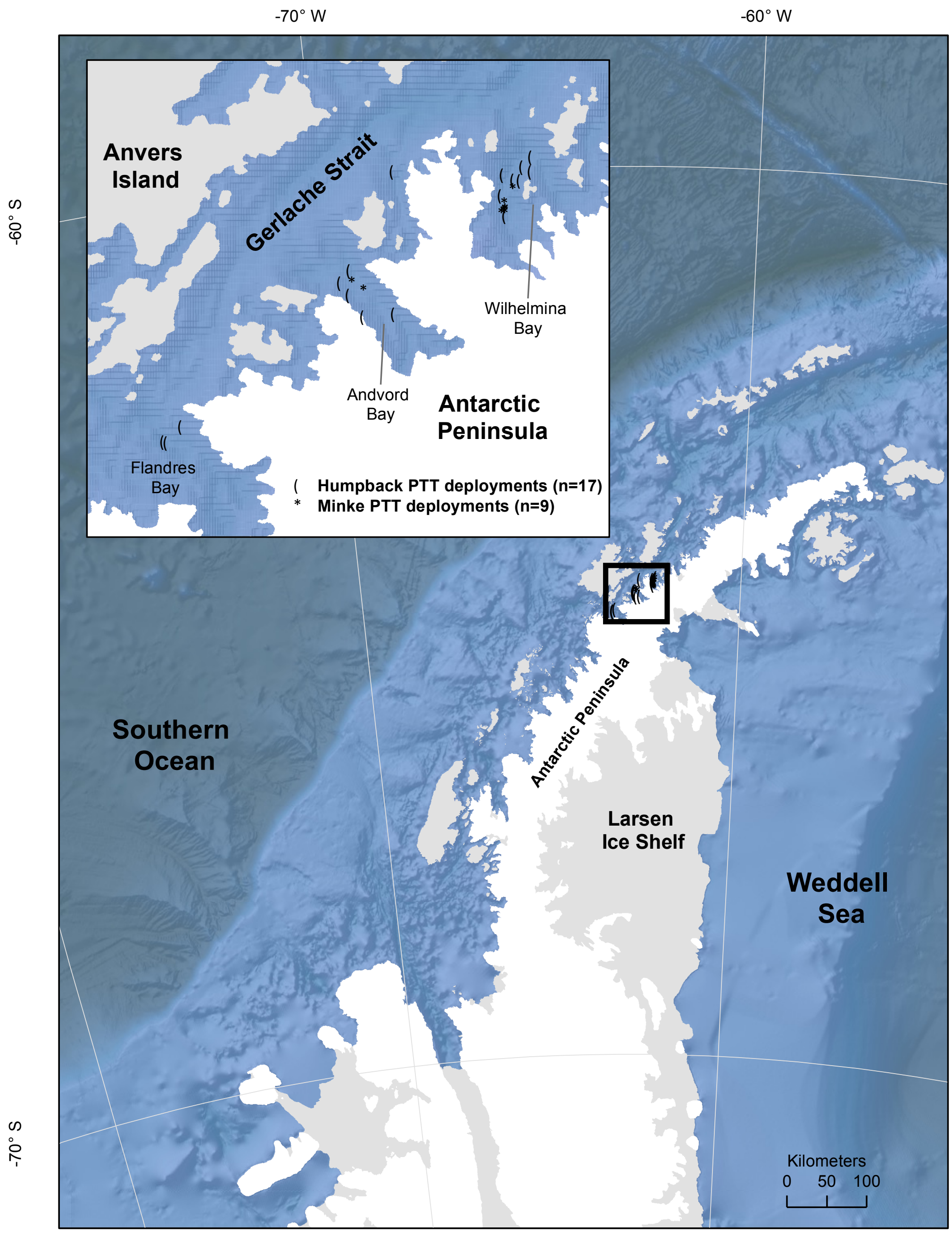


Figure 2. Map with location of PTT tracks for humpback (n=17) and minke (n=9) whales.

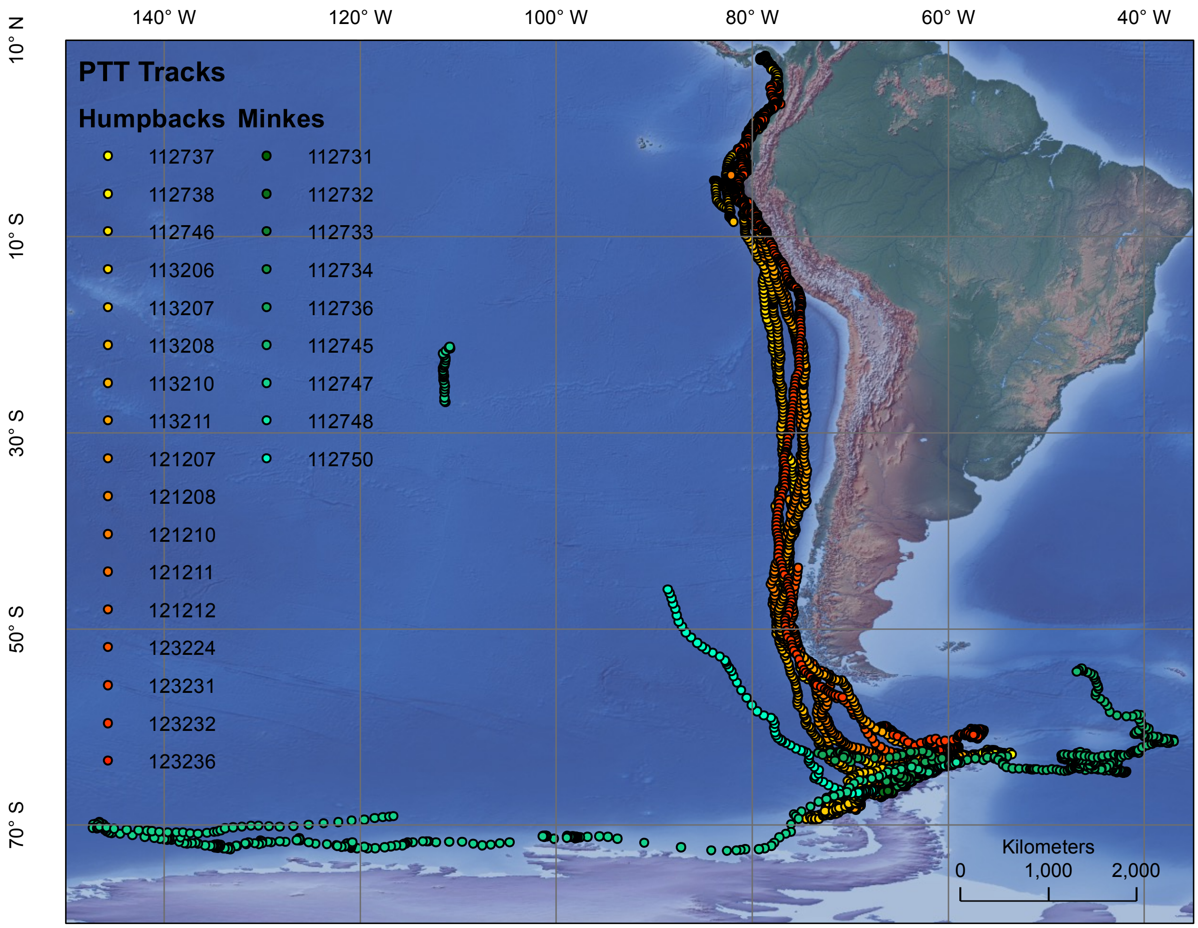


Figure 3. Example plot showing estimated departure date from foraging grounds on April 23, 2013 as a concurrent switch to transiting from area restricted search behavior (ARS; as inferred from the hSSSM), an increase in speed, and a directional movement to lower latitudes for humpback whale 113206.

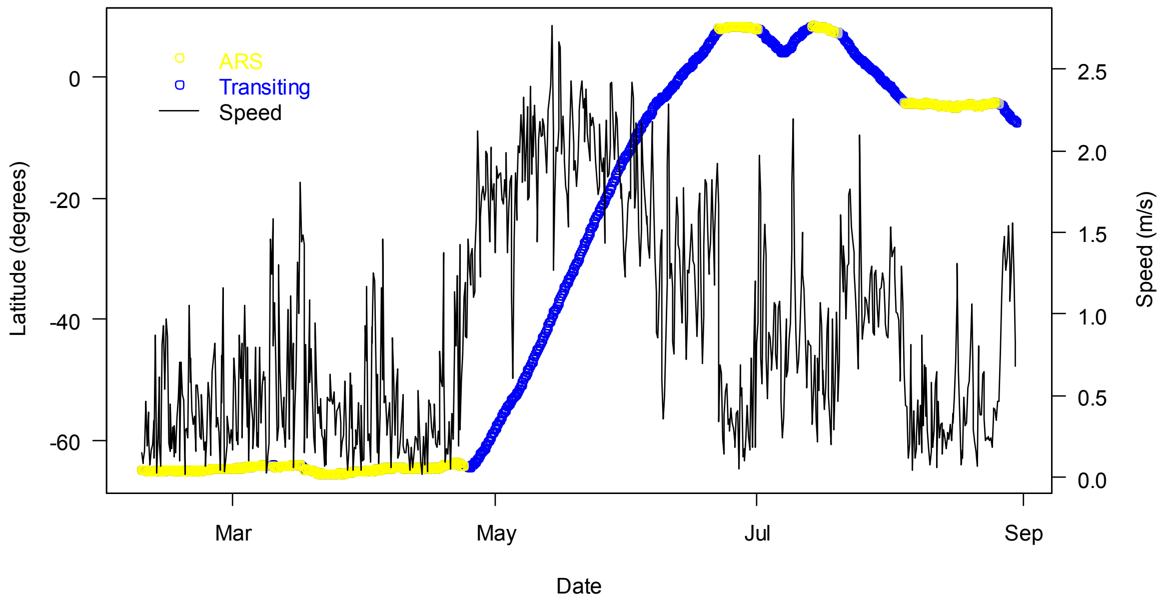


Figure 4. Locations of transiting behavior (blue) and area restricted search behavior (yellow; ARS) for humpback whales as inferred from the hSSSMs during the foraging period (pre-migration). Insets show ARS bouts for each animal.

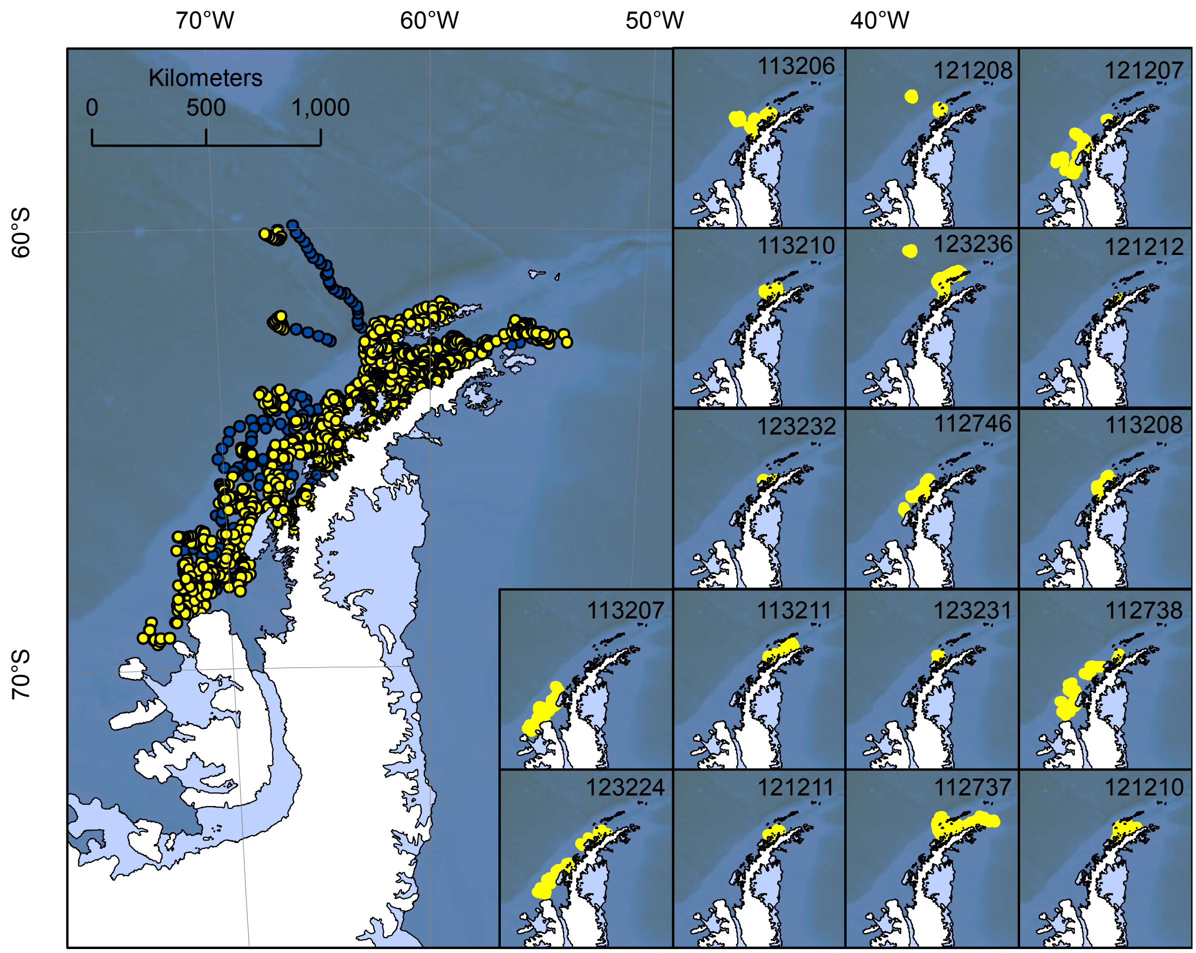


Figure 5. Locations of transiting behavior (blue) and area restricted search behavior (yellow; ARS) for minke whales as inferred from the hSSSMs during the foraging period (pre-migration). Insets show ARS bouts for each animal.

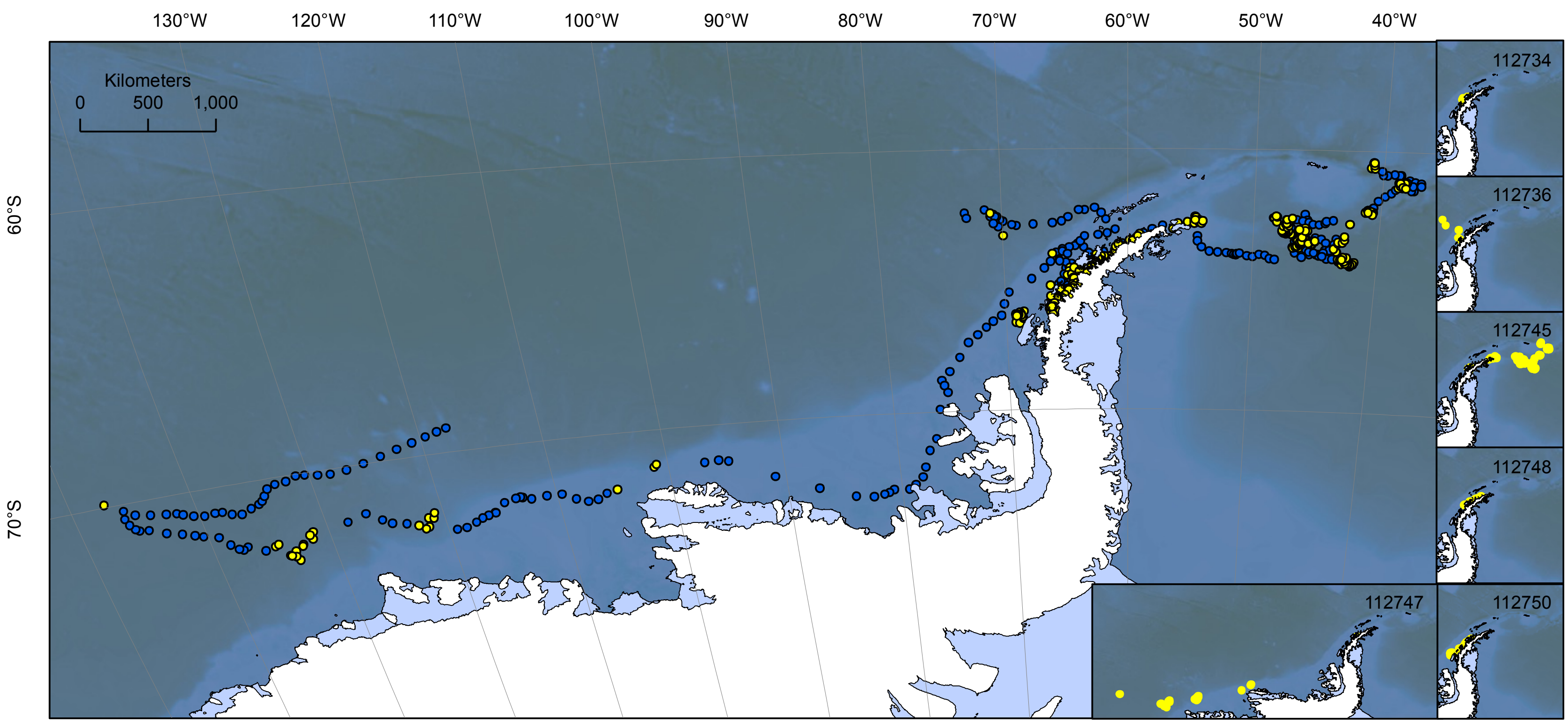


Figure 6. Boxplot of distance between grounding line/ocean edge and transit (blue) and ARS (yellow) locations for humpback and minke whales for the foraging period. The whiskers bound 1.5x the interquartile range (boxes) and the circles denote outliers.

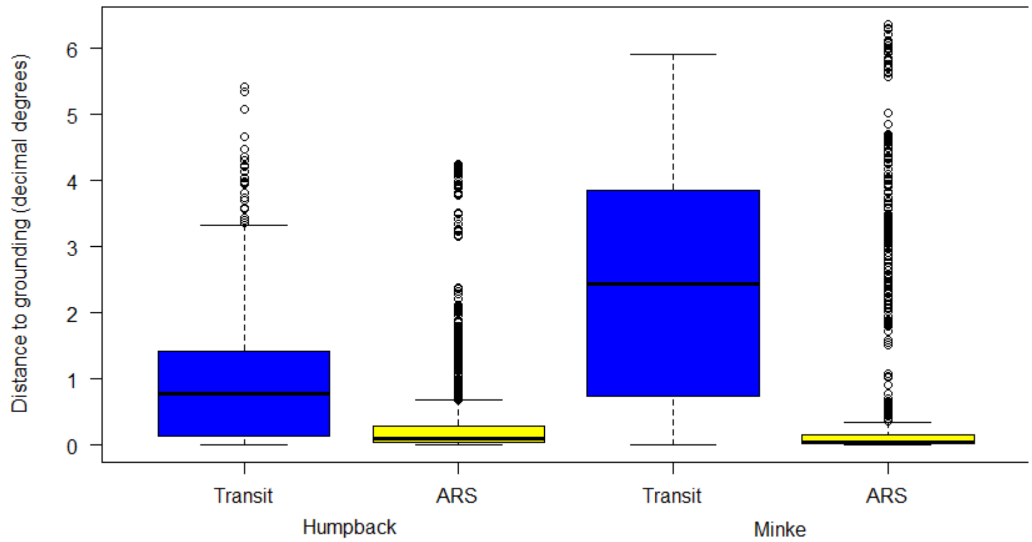


Figure 7. Boxplot of distance between 15% ice contour and transit (blue) and ARS (yellow) locations for humpback and minke whales for the foraging period. The whiskers bound 1.5x the interquartile range (boxes) and the circles denote outliers.

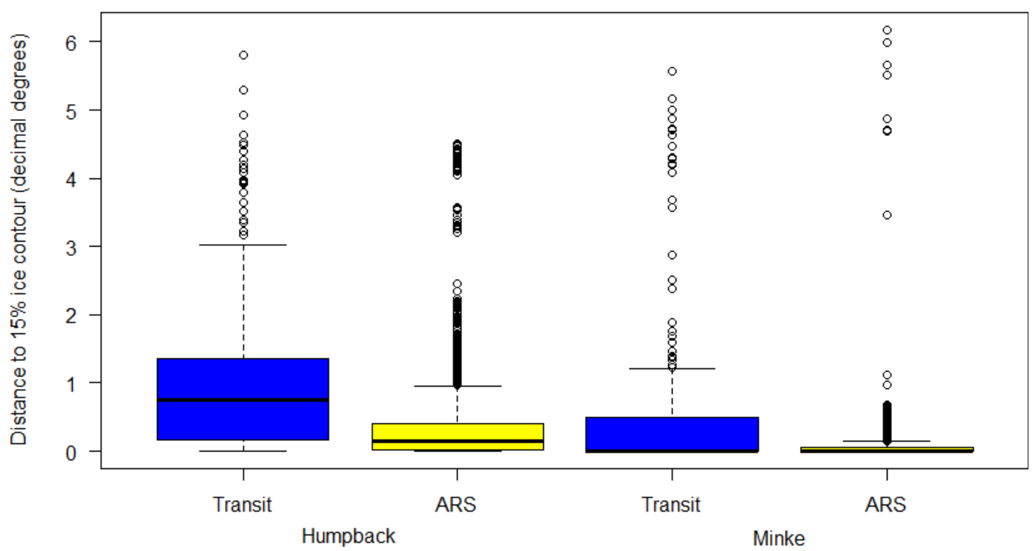
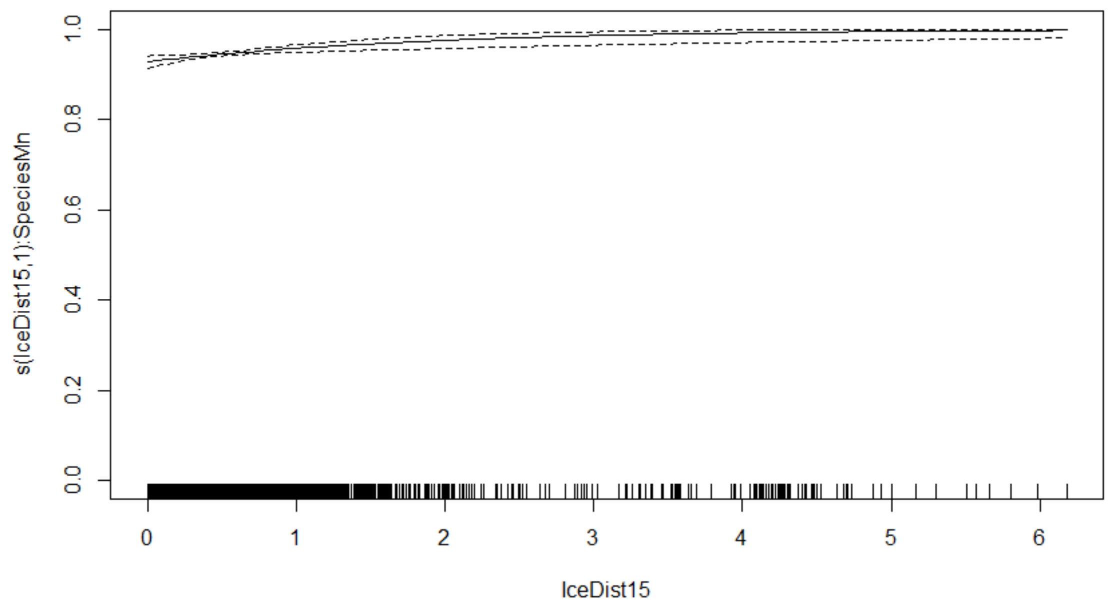


Figure 8. Predicted effects of distance to 15% ice contour (decimal degrees) on the inferred behavioural state of humpback whales (top) and minke whales (bottom). Inferred behavioral state is on the y-axis with values of 0.0 representing transiting and 1.0 representing ARS. Solid lines represent mean predicted values with dashed lines indicating ± 1 standard error. Rug plots across the bottom of the panel show sample size for all observations.



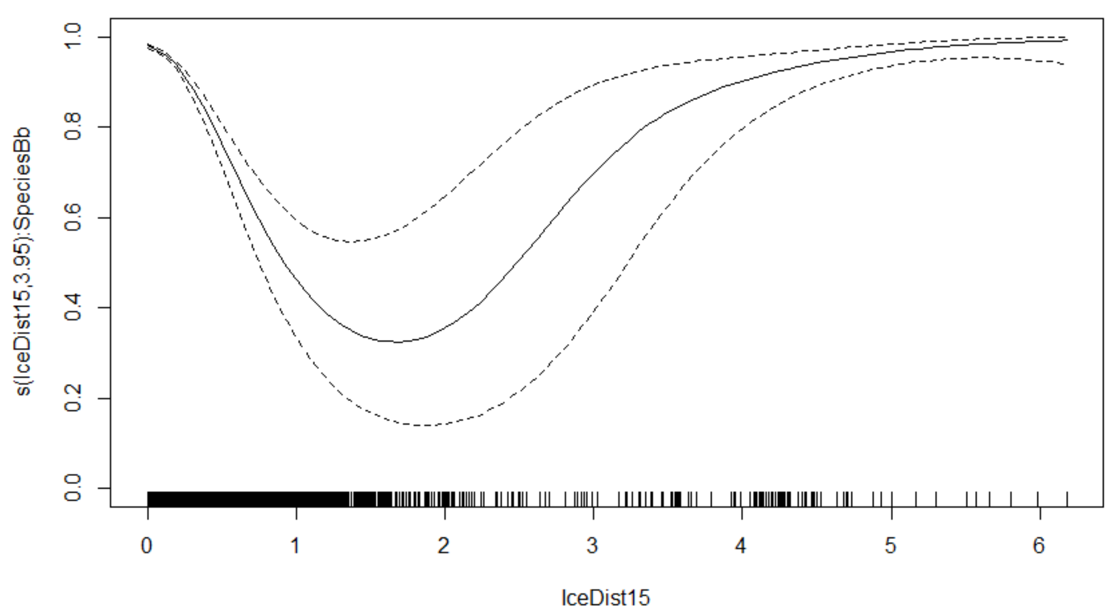


Figure 9. Predicted effects of distance to grounding line (decimal degrees) on the inferred behavioural state of humpback whales (top) and minke whales (bottom). Inferred behavioral state is on the y-axis with values of 0.0 representing transiting and 1.0 representing ARS Solid lines represent mean predicted values with dashed lines indicating ± 1 standard error. Rug plots across the bottom of the panel show sample size for all observations.

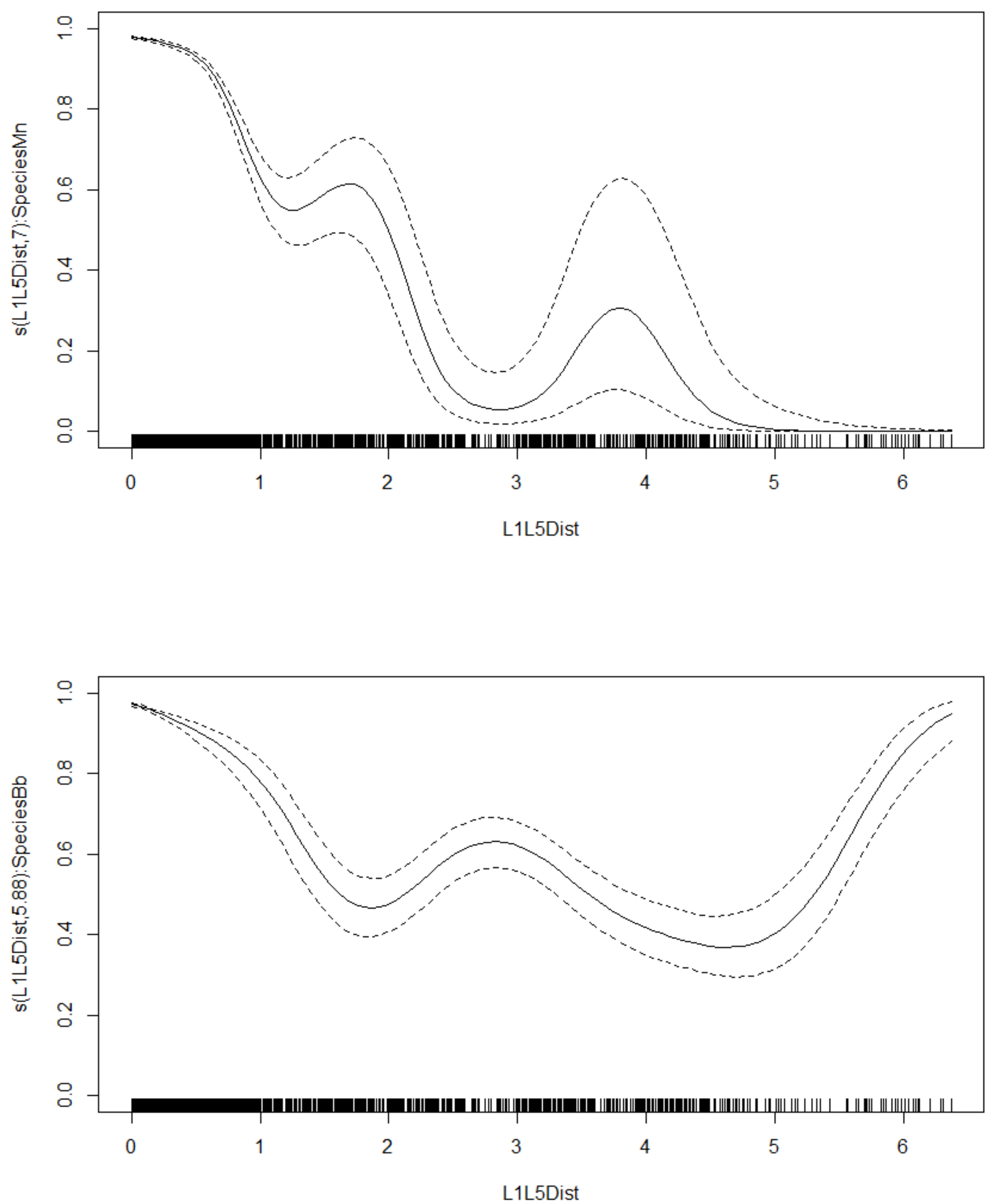


Figure 10. Humpback whale home range on the western side of the Antarctic Peninsula as calculated from ARS locations derived from satellite tag data. The 25, 50, 75, 90, 95, and 99% ispleths are shown.

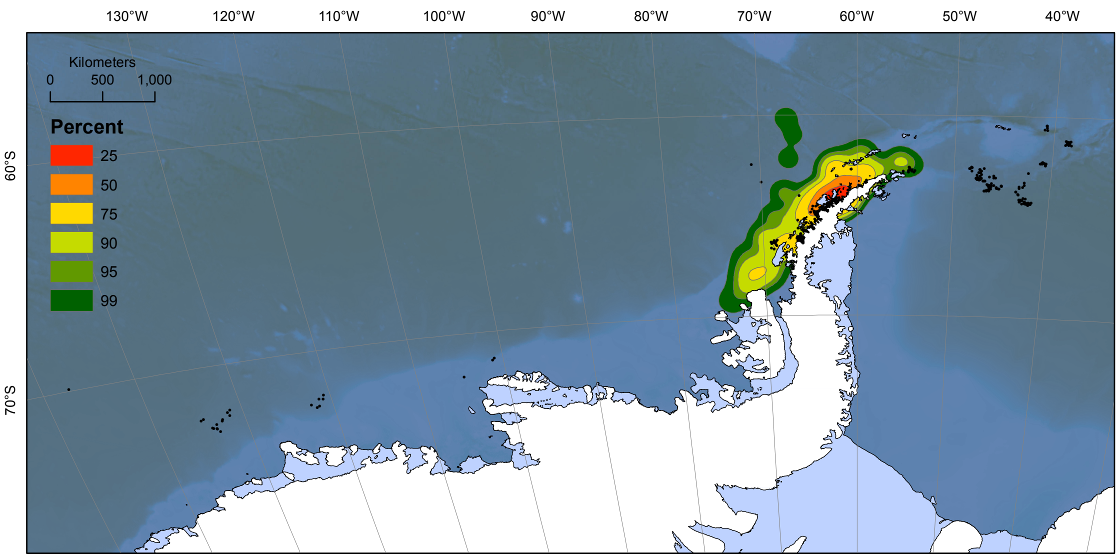


Figure 11. Antarctic minke whale home range on the western side of the Antarctic Peninsula as calculated from ARS locations derived from satellite tag data. The 25, 50, 75, 90, 95, and 99% ispleths are shown.

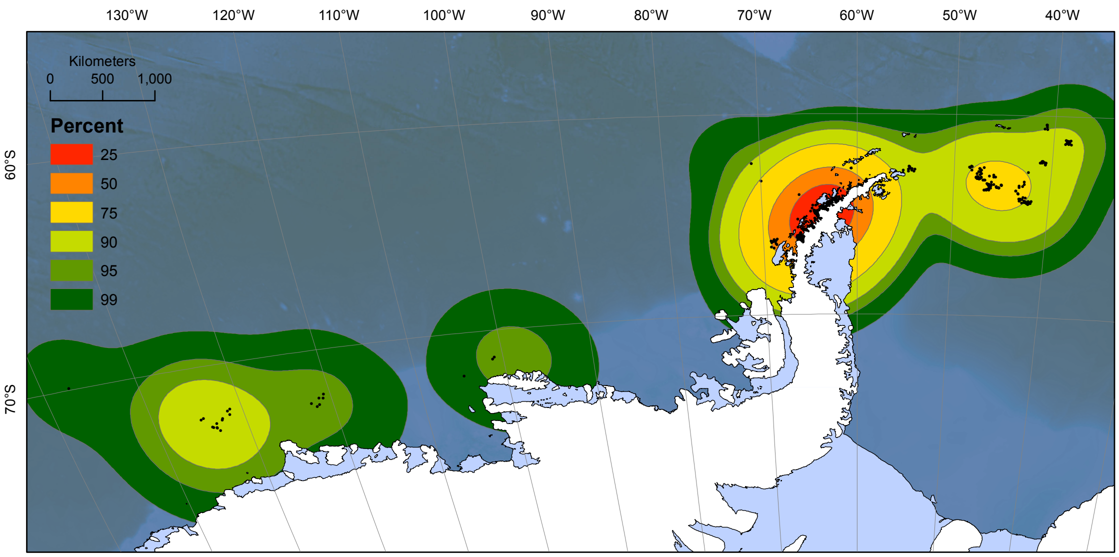
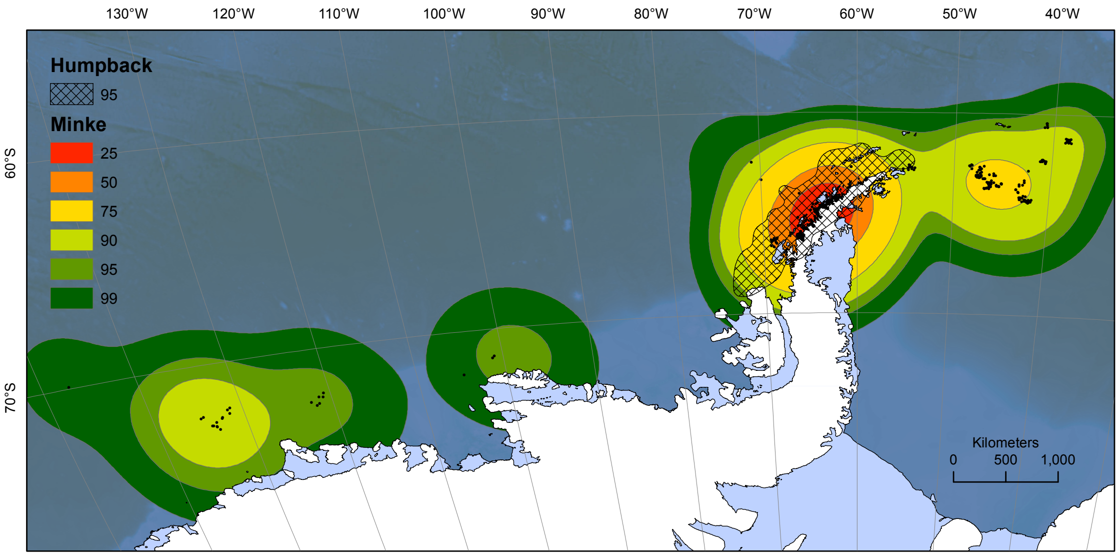


Figure 12. Antarctic minke whale ARS home range size with similar humpback whale ARS home range (90% isopleth) overlaid to show spatial overlap during the feeding season.



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