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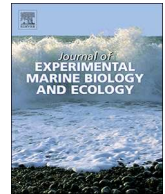
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ENVIRONMENTAL DRIVERS OF HUMPBACK WHALE FORAGING BEHAVIOR IN THE REMOTE SOUTHERN OCEAN

Environmental drivers of humpback whale foraging behavior in the remote Southern Ocean

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ABSTRACT

Satellite telemetry and animal movement models advance our ability to remotely monitor the behavior of wide-ranging species. Understanding how different behaviors (e.g. foraging) are shaped by dynamic environmental features is fundamental to understanding ecological interactions and the impact of variability. In this study we deployed satellite-linked tags on humpback whales (Megaptera novaeangliae) and used state-space models to estimate locations and to infer underlying behavioral states. We then modelled the association between whale behavior (e.g. foraging or transiting) and environmental variables using linear mixed-effect models. We identified the importance of two recently discovered Southern Ocean feeding areas for Oceania humpback whales as well as the key environmental drivers affecting whale behavior. We detected behavioral differences between whales utilizing the two adjacent feeding regions (~2000 km apart), which were likely caused by animals trying to efficiently locate prey in relation to the dynamic environmental characteristics of each habitat. We observed a seasonal pattern in foraging behavior, with the peak occurring in the middle of summer. Whales also foraged more intensively with increasing proximity to areas from which the ice edge had recently retreated, suggesting heightened productivity in these areas. The relationship between the animals and the physical features of the seascape, as well as the behavioral plasticity observed, could have implications for the future recovery of these whales in a changing Southern Ocean.

1. Introduction

Many animal behaviors, such as movement and habitat use, are driven by responses to internal cues as well as the external conditions experienced by the animal (Nathan et al., 2008). Understanding how the physical environment shapes the behavior and distribution of animals as they try to satisfy their resource requirements is a fundamental topic in behavioral ecology (e.g. Ballance et al., 2006; Aarts et al., 2008; Davies et al., 2012). A wide range of animals from moths to caribou (Rangifer tarandus) migrate between critical habitats following pulses in resource availability and abundance (Jiang et al., 2011; Le Corre et al., 2017). In many terrestrial and aquatic taxa the decision to depart for a new habitat is often controlled by variables such as photoperiod, temperature, snow fall and severe weather at the initial location, at which

point the animals cannot predict the habitat conditions at the end destination (Jonsson and Ruud-Hansen, 1985; Vøllestad et al., 1986; Cotton, 2003; Balbontín et al., 2009; Jiang et al., 2011; Rivrud et al., 2016). Memory of long-term average conditions may also play a role in directing migrants to their destination (Bracis and Mueller, 2017; Abrahms et al., 2019). Upon arrival at a new location resources, such as prey, are often patchily distributed throughout space and time, at which point animals initiate search strategies to locate and secure prey (Benhamou, 1992; Boyd, 1996; Sims et al., 2008; Humphries et al., 2010; Carroll et al., 2017). In marine systems specifically, biological productivity can be highly variable due to the heterogeneity of the many physical processes in the environment (Haury et al., 1978). This results in some habitats being more productive than others, which in turn influences prey availability and predator behavior. To forage
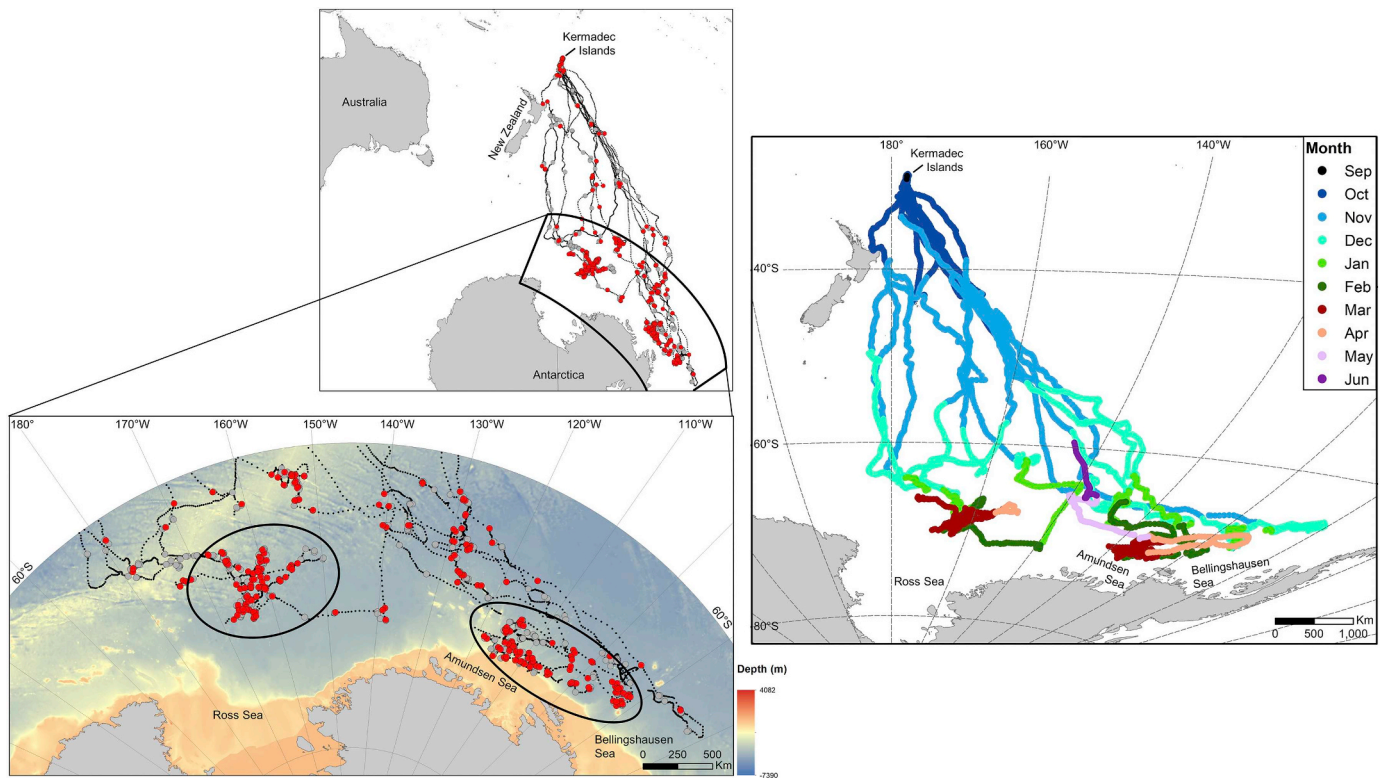
Fig. 1. Migration pathways for 18 Oceania humpback whales satellite-tagged at the Kermadec Islands, New Zealand. Left column: State-space model estimated behavioral states: red dot = area restricted search (ARS; inferred foraging); black dot = inferred transit; grey dot = uncertain behavioral mode. Bottom left: Tracks of 14 whales whose tags transmitted on their Southern Ocean feeding grounds with circles denoting the approximate locations of the two key foraging grounds. The background color scale indicates the bathymetric depth (derived from the International Bathymetric Chart of the Southern Ocean (IBCSO) digital bathymetric model of the circum-Antarctic waters). Right column: Satellite tracks color coded by month. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

efficiently predators must move through their dynamic environment in search of prey while maximizing time spent foraging in the most productive areas (Stephens and Krebs, 1986; Fauchald and Tveraa, 2006). In patchy environments individuals may even adjust aspects of their foraging behavior depending on the external environmental conditions (Weimerskirch, 2007; Sebastiano et al., 2012; Kirchner et al., 2018).

Obtaining direct observations of movement and behavior in wide-ranging predators can be challenging, and more indirect techniques, such as animal-borne transmitters and data loggers, are often required to detect and identify behavior. Advancements in satellite telemetry and tagging technology have improved the ability to remotely collect animal movement data at high spatial and temporal resolutions (Hussey et al., 2015; Gurarie et al., 2016; Chimienti et al., 2017). Different movement models can be applied to these remotely collected data to identify underlying behavioral states such as foraging (Morales et al., 2004; Jonsen et al., 2005, 2006; Michelot et al., 2017). Various statistical models can then be used to link animal locations and behavior with ecological variables. Such models are useful tools for explaining spatial distribution patterns of highly mobile animals, for identifying critical habitats, and they have many applications including addressing management and conservation questions (Mandel et al., 2008; Gregr et al., 2013; Guisan et al., 2013).

In the Southern Hemisphere, humpback whales (*Megaptera novaeangliae*) migrate thousands of kilometers annually from the tropics to the Southern Ocean to feed on their main prey, the Antarctic krill (*Euphausia superba*; Kawamura, 1994; Murase et al., 2002). The endogenous and exogenous cues used by the whales to navigate to the feeding grounds and to search for prey remains unresolved (Horton et al., 2011, 2017; Torres, 2017). Directly observing the foraging behavior and characterizing the foraging habitat of large marine

predators, such as humpback whales, in the Southern Ocean is notoriously difficult due to the logistical challenges associated with accessing this remote and vast area (Griffiths, 2010). Therefore, our knowledge of the fine-scale behavior and patterns of habitat use by humpback whales in this region remains limited, compared to for example the more accessible Antarctic Peninsula (e.g. Friedlaender et al., 2013, 2016).

During the commercial whaling era, Southern Hemisphere humpback whale stocks were highly overexploited and hunted to near extinction (Ivashchenko and Clapham, 2014; Clapham and Baker, 2017). Since being granted protection from whaling, humpback populations have shown variable recovery. The Oceania humpback whales, comprising whales from multiple breeding ground subpopulations from the Pacific Islands (spanning New Caledonia to French Polynesia) are estimated to be < 50% of pre-exploitation numbers and recovering more slowly than the neighboring east Australian population (Childerhouse et al., 2008; Constantine et al., 2012; International Whaling Commission, 2015). To date there has been little information available on the Oceania humpback whales within the Southern Ocean feeding grounds, and we only recently revealed their migration paths and location of the feeding grounds (Riekkola et al., 2018). As a consequence, we do not know whether the feeding behavior and patterns of habitat use by these humpback whales could be linked to the different population recovery rates (International Whaling Commission, 2015).

Here we applied a movement model to satellite tagging data of humpback whales on their Southern Ocean feeding grounds to infer underlying behavioral states: transiting and area restricted search (ARS), a behavior indicative of foraging (Weinstein et al., 2017; Andrews-Goff et al., 2018). We expected that aspects of whale foraging behavior would change throughout the feeding season. For example, we hypothesized that there would be an increase in foraging effort as prey

becomes more abundant with the onset of spring and summer. We then used a statistical model to investigate the relationship between the inferred behavioral states (specifically the occurrence of ARS-foraging) and different environmental variables. We expected the whales' behavior to be affected by different environmental factors, and that behavioral differences would exist between animals utilizing different regions of the Southern Ocean. By linking whale movement data and behavioral changes to the conditions of their foraging habitat, this study ultimately contributes to a better understanding of the behavior of wide-ranging predators.

2. Materials and methods

2.1. Satellite tag deployment

Wildlife Computers (Redmond, WA, USA) SPOT 5 Platform Transmitting Terminals (PTTs) were attached to 25 adult humpback whales during the peak of their southern migration past the Kermadec Islands, New Zealand, between September and October 2015 (Fig. 1). The tags were deployed using a modified version of the Air Rocket Transmitter System (Heide-Jørgensen et al., 2001) at a pressure of 10–12 bars. Observed locations were calculated by the Argos System using the Doppler Effect on transmission frequency when multiple messages from a tag were received by a satellite. An estimated error and a location class (in descending order of accuracy: 3, 2, 1, 0, A, B, Z) were assigned to each location (see Argos user's manual, 2016). Location classes A and B have no accuracy estimation and Z is an invalid location. The tags were duty cycled to transmit for 21 h each day to maximize the time with overhead Argos satellites. The maximum number of transmissions per day was set to 600 at a repetition rate of 45 s. Reproductive status (mother with a calf, or adult) of the tagged whales was inferred in the field based on the presence of a calf closely associated with the satellite tagged animal (Clapham et al., 1999). Molecular sex identification was conducted using tissue samples collected at the time of tagging (Riekkola et al., 2018).

2.2. Data processing and hierarchical state-space model

Raw Argos locations were speed filtered using the R package *argosfilter* (Freitas et al., 2008) at a conservative maximum speed of 36 km/h to remove only highly erroneous and unrealistic locations. We used a hierarchical version of a Bayesian state-space model (SSM; Jonsen et al., 2005, 2006) to estimate locations (via an observational model) and behavioral states (via a movement model). We used a 6-h time-step in the model to provide detailed whale movement data. Obtaining whale data on an even finer scale was not necessary given the low resolution of some of the environmental covariates (see section 'Explanatory variables for statistical model' and Table 1). The SSM was fitted in R (version 3.5.1, R Core Team, 2018) using the software JAGS (Plummer, 2013) and the R packages *rjags* (Plummer, 2016) and *bsam* (Jonsen et al., 2015). Where a gap of > 1 day existed in the satellite data transmission, the individual track was split and ran as segments to avoid interpolating over long periods of time with no data. Two Markov chain Monte Carlo (MCMC) chains were run in parallel, each for a total of 200,000 simulations. The first 100,000 samples were discarded as a 'burn-in', and the remaining samples were thinned, retaining every 100th sample to reduce autocorrelation. The final 2000 samples were used to compute the posterior distribution of the model parameter estimates: the mean turning angles, and movement persistence (i.e. the autocorrelation in speed and direction). The behavioral mode estimate (b), ranging between 1 and 2, was inferred from the means of the MCMC samples. A behavioral mode close to 1 ($b < 1.25$) indicates transiting behavior, which is persistent and highly directional movement with low turning angles (near 0°). Animals are expected to be in transiting mode during migration or when traveling between favorable locations (e.g. prey patches). A behavioral mode close to 2 ($b > 1.75$)

indicates area-restricted search (ARS) behavior, a more variable movement with large turning angles (near 180°) and increased rate of turning. ARS is generally considered to be indicative of foraging, resting or breeding behavior (e.g. Weinstein et al., 2017; Andrews-Goff et al., 2018). Locations with a mean b estimate between 1.25 and 1.75 were treated as 'uncertain'.

2.3. Explanatory variables for statistical model

We used both static and dynamic variables estimated at each state-space modelled location as explanatory variables to identify those that had most effect on the whales' behavioral mode (specifically the occurrence of ARS-foraging). We selected environmental variables which, based on prior knowledge, are likely to be biologically relevant (e.g. Friedlaender et al., 2011; Bombosch et al., 2014; Trudelle et al., 2016; Andrews-Goff et al., 2018; Table 1), and that were available for the entire spatial extent of location data.

Daily sea ice concentration data were obtained from the National Snow and Ice Data Center (NSIDC, https://nsidc.org/data). Distance to the ice edge was calculated from the daily ice concentration as the minimum distance between whale locations and the 15% sea ice concentration contour (e.g. Gloersen et al., 1992; Stammerjohn and Smith, 1997). One month and two-month lags were calculated as the distance of each SSM-estimated whale location to where the ice edge was one month and two months prior. It takes approximately one to two months after ice melt for productivity to peak in the marginal ice zone (Lehodey et al., 1998; Arrigo et al., 2008; Dalpadado et al., 2014). Altimeter derived daily sea surface heights (SSH) and daily sea surface current velocity data were obtained using E.U. Copernicus Marine Service Information (http://marine.copernicus.eu). SSH and sea surface current velocity gradients can be used to trace the locations of the Antarctic Circumpolar Current fronts, and therefore by using these variables we could account for possible interactions with the fronts (e.g. Sokolov and Rintoul, 2009). Sea surface current velocity was log transformed prior to analysis. Data on sea ice, SSH, and sea surface current velocity were obtained through the Australian Antarctic Data Centre and extracted using the R package *raadtools* (Sumner, 2016).

Bathymetry was obtained from the International Bathymetric Chart of the Southern Ocean (IBCSO) digital bathymetric model of the circum-Antarctic waters (Arndt et al., 2013). IBCSO is a regional mapping project of the General Bathymetric Chart of the Oceans (GEBCO) and the digital bathymetric model is publicly available (www.ibcso.org). Slope was derived from the IBCSO digital bathymetric model using the 'slope' tool in ArcGIS (version 10.5, Esri, Redlands, CA, USA) and was log transformed prior to analysis.

Month for each point was obtained from the SSM estimated locations. We chose to include month as a continuous variable in the model. Therefore, November, the first month for which there were data within the feeding grounds, was labelled '0' (followed by December = 1 through to June = 7) in order to set November as the baseline and to maintain chronological order.

Prior analysis of the satellite tags had revealed that the whales diverged to two broad feeding regions (Riekkola et al., 2018). To make comparisons between these feeding areas, each location was assigned a 'region' based on whether it occurred west (Ross Sea) or east (Amundsen and Bellingshausen Seas) of the 130°W meridian (Fig. 1). Studies have identified regional trends in the Antarctic sea ice variability, with increasing sea ice extent occurring in the Ross Sea region, and contrasting decrease in sea ice extent occurring in the Amundsen and Bellingshausen Seas region (e.g. Zwally et al., 2002; Turner et al., 2009). Future ocean and sea-ice changes are also projected to affect the growth rates of krill (the whales' main prey), with modelled high potential growth rates in Ross Sea, and low or negative potential growth rates in the Amundsen and Bellingshausen Seas (Murphy et al., 2017).

Table 1
The unit of measure, source and resolution of the environmental predictor variables used to construct the species distribution models.

Variable	Definition and unit	Source	Resolution	
			Spatial	Temporal
Dynamic				
Ice concentration (ice conc)	Percentage of ocean area covered by sea ice	National Snow and Ice Data Center (NSIDC)	25 × 25 km	Daily
Distance to ice edge (dist ice)	Distance of whale location to ice edge (15% ice concentration; km) on the same day	Derived from ice concentration	25 × 25 km	Daily
Distance to ice edge – 1-month lag (dist ice lag 1)	Distance of whale location to where the ice edge was 1 month prior	Derived from ice concentration	25 × 25 km	Daily
Distance to ice edge – 2-month lag (dist ice lag 2)	Distance of whale location to where the ice edge was 2 months prior	Derived from ice concentration	25 × 25 km	Daily
Sea surface height (SSH)	Sea surface height (m)	E.U. Copernicus Marine Service Information (CMEMS)	0.25 × 0.25°	Daily
Sea surface current velocity (current)	Surface current velocity (m/s)	Derived from SSH	0.25 × 0.25°	Daily
Static				
Bathymetry (bathy)	Depth (m)	International Bathymetric Chart of the Southern Ocean (IBCSO)	500 × 500 m	
Slope	Topographic gradient (degrees)	Derived from bathymetry	500 × 500 m	
Other				
Month	Month	SSM estimated locations		
Region	Ross Sea or Amundsen and Bellingshausen Seas cut-off at 130°W	SSM estimated locations		

2.4. Environmental drivers of behavior

To assess the influence of the explanatory variables on the SSM estimated behavioral modes, we fitted a series of linear mixed-effect models (LMMs) by maximum likelihood (ML) using the R software package *nlme* (Pinheiro et al., 2018). Similar to previous studies, we adjusted the behavioral mode (*b*) to range between 0 and 1 (by subtracting 1 from each value), after which the variable (continuous) was logit transformed (O'Toole et al., 2015; Cerchio et al., 2016). We dealt with sample proportions equal to exactly zero or one by adding the smallest non-zero proportion (ε) to the numerator and denominator of the logit function (i.e. $\log(y + \varepsilon / 1\text{-}y + \varepsilon)$) as per Warton and Hui (2011). Individual whales (i.e. unique tag numbers/PTTs) were fitted as a random effect to account for individual variation, and a first order AR (1) autocorrelation structure for each individual whale was assumed. We first built LMMs with the full data set using region as a factorial variable, and then split the data to build region specific models.

The remotely sensed variables SSH and sea surface current speed included missing values ($n = 31$ and $n = 35$ respectively, representing 0.9% of the data), most likely due to sea ice coverage. To maintain the same number of observations between models, the rows including missing values were removed from the data set prior to model fitting. The variables sea surface current velocity and slope were log transformed prior to analysis. A quadratic term was included for month and the different 'distance to ice edge' candidate variables following examination of the relationships visually. All continuous variables were tested for pairwise correlation (Electronic Supplementary Material, Figure ESM 1). SSH and log transformed sea surface current velocity had a Spearman correlation of 0.66. All other variables showed a Spearman correlation of ≤ 0.5.

As the different 'distance to ice edge' candidate variables represent the same environmental process, we included each of these terms sequentially during the model building (Table 2). Several model combinations of the different main effects and various interaction terms were run (Table 2). For model selection we explored both backward selection following Zuur et al. (2009; starting with a full model with all explanatory variables included, dropping individual variables one by one until all remaining variables are significant) and automated model selection (function *dredge* in R package *MuMIn*; Bartoń, 2018) to check for all possible variable combinations. We used the Akaike Information Criterion (AIC) to select the most parsimonious (lowest AIC value) model as the criterion penalizes for the use of more variables (Burnham and Anderson, 2002; Burnham et al., 2011). The best model based on AIC was then run using restricted maximum likelihood (REML) to obtain the final parameter estimates (as per Zuur et al., 2009). The normality of residuals was checked graphically.

3. Results

3.1. Whale movement and behavior

Out of 25 tags deployed, 18 transmitted sufficient data for the SSM analysis (Table 3). This included 5 females without calves, 6 females with calves, 5 males and 2 individuals of unknown sex (PTT102211 had no tissue sample; molecular sex identification for PTT112722 was unsuccessful). Ten tags had data gaps of > 1 day (range: 2–76 d), excluding those tags that did not begin transmission straight after deployment. The average number of location fixes per day received from a tag was 22 (range: 10–42).

The tags of 14 individual humpback whales transmitted data within the feeding grounds south of 60°S, covering a temporal period from November 2015 to June 2016 and a spatial range from 175°E to 80°W. The number of active tags transmitting data varied between months (range: 1–14; Table 4). The SSM distinguished well between the two behavioral states (Electronic Supplementary Material, Table ESM 2) and classified 6.3% of locations as ARS-foraging, and 79.3% of locations

Table 2
Model selection results of the best linear mixed-effect models to explain the effects of different variables on humpback whale behavioral mode (*b*).

Variables	K	AIC	ΔAIC
Comparison of different ice distance variables			
Month + Month^2 + Region + dist ice lag 2 + dist ice lag 2^2 + Ice conc + SSH + bathy + slope(log)	13	18,471.5	
Month + Month^2 + Region + dist ice lag 1 + dist ice lag 1^2 + Ice conc + SSH + bathy + slope(log)	13	18,475.2	3.7
Month + Month^2 + Region + dist ice + dist ice^2 + Ice conc + SSH + bathy + slope(log)	13	18,475.6	4.1
Comparison of different interaction terms			
All models have the same base: Month + Month^2 + Region + dist ice lag 2 + dist ice lag 2^2 + Ice conc + SSH + bathy + slope(log)			
+ Region × Month + Region × Month^2	15	18,449.9	
+ Region × SSH	14	18,468.9	19.0
+ Region × dist ice lag 2 + Region × dist ice lag 2^2	15	18,471.2	21.3
Reduced version of the best model			
Month + Month^2 + Region + dist ice lag 2 + dist ice lag 2^2 + SSH + Region × Month + Region × Month^2	12	18,447.5	

All models include the individual whale (unique tag number, PTT) fitted as a random effect. For each candidate model we report the Akaike's Information Criterion (AIC) and the change in AIC (ΔAIC) compared to the best model of each scenario. K = number of parameters.

as transiting behavior, with the remaining 14.4% classified as uncertain (Fig. 1). The average behavioral mode (i.e. likelihood of ARS-foraging behavior) increased as the feeding season progressed, peaking in March (February–March for whales on the Ross Sea side only; Fig. 2a). Overall, the whales on the Ross Sea side were consistently farther away from the continental shelf break (Fig. 1) and from the ice edge than the whales in the Amundsen and Bellingshausen Seas region (Fig. 2b). In general, the whales' distance from the ice edge increased between December and January (December–February for Ross Sea whales) and decreased between January and April (February–May for Ross Sea whales; Fig. 2b).

3.2. Environmental drivers of behavior

Out of the highly correlated variables SSH was identified as being a more important predictor than log transformed sea surface current speed and was therefore kept in the model. Examination of the different 'distance to ice edge' scenarios resulted in 2-month lag being identified as the most relevant, and out of several trials with different interaction terms interaction between month (representing time) and region was found to be most significant (Table 2). The most parsimonious model identified month, 2-month lag in the distance to the ice edge, SSH and the interaction between region and month as important predictors of the behavioral state of humpback whales within their Southern Ocean feeding grounds (Table 2, Table 5). Non-linear relationships indicated that the whales were more likely to exhibit ARS-foraging behavior during the middle of the summer feeding season, and near where the marginal ice-edge had been two months prior. Humpback whales were also more likely to exhibit ARS-foraging behavior at lower SSH values, and there was a significant interaction between region and month (Table 5, Fig. 3). The model provided some indication of possible differences between regions. The variable 'region' was marginally significant (F-test *p* = .06), although the coefficient estimate was not significantly different from zero (*t*-test *p* = .36). Dredge automated model selection identified region to be a significant variable in 70% of 1664 model variations.

4. Discussion

Humpback whales foraging in the Southern Ocean changed their ranging behavior and habitat use patterns throughout the summer feeding season suggesting that behavioral plasticity is important for this large predator. The changes were related to the environmental features of the different habitats, in particular to an important lag effect in the ice edge dynamics, and consequently the whales ended up utilizing these areas very differently. Similar to other long-distance migrants that move between critical habitats for different life functions (Both and Visser, 2001; Le Corre et al., 2017), these whales time their arrival at their feeding grounds to exploit the habitat optimally without knowing

the precise habitat conditions when beginning their migration ~7000 km north. The large-scale sensitivity to environmental cues enabling prediction of conditions in another geographic location is key to the success of migratory animals, e.g. barn swallow (*Hirundo rustica L.*, Balbontín et al., 2009), caribou (Le Corre et al., 2017).

4.1. Characterizing whale movement and behavior on the Southern Ocean feeding grounds

The SSM results revealed two important resource sites for Oceania humpback whale foraging; one within the Amundsen and Bellingshausen Seas and one north of the Ross Sea, ~2000 km west (Fig. 1). The majority of ARS-foraging locations for the whales within the Amundsen and Bellingshausen Seas occurred near the continental shelf break (within ~200 km) where high densities of krill are expected to be found due to life history related movement (e.g. Pauly et al., 2000; Nicol, 2006; Davis et al., 2017), as well as near the ice edge (~210 km on average) where ice melt stimulates primary production which in turn supports elevated concentrations of higher trophic level organisms (e.g. Brierley et al., 2002; Nicol, 2006; Meyer et al., 2017). In contrast, the main aggregation of ARS-foraging locations north of the Ross Sea did not occur near the shelf break (> 500 km away; Fig. 1) nor the ice edge (~370 km on average; Fig. 2b). However, the ARS-foraging locations of the Ross Sea whales occurred in a reported hotspot, with increased chlorophyll *a* as an indicator of primary production (Schine et al., 2015). The observed differences between the foraging regions suggest that humpback whales utilize different environmental cues, with some cues being of greater importance for whales in one area than the other.

Although we were not able to confirm ARS behavior identified by our SSM as foraging, both previous studies and the general knowledge about humpback whale behavior south of 60°S suggest that ARS behavior identified by the SSM is largely foraging (Chittleborough, 1965; Weinstein et al., 2017; Andrews-Goff et al., 2018). With this assumption in mind, the high overall amount of transiting behavior south of 60°S might serve as an indicator of prey distribution, whereby whales may have to move quite long distances between prey patches. For instance, the Amundsen and Bellingshausen Seas reportedly have generally low chlorophyll *a* concentration with only isolated pockets of high productivity (e.g. Constable et al., 2003; Stambler, 2003). This could result in smaller prey aggregations that are highly spread out, increasing the whales' need to transit between foraging patches.

Humpback whales in the northern hemisphere have been shown to exhibit strong maternally inherited feeding ground fidelity (Palsbøll et al., 1995; Stevick et al., 2006; Baker et al., 2013). In contrast, humpback whales from discrete Oceania breeding grounds do not show such clear patterns of feeding ground fidelity (Rosenbaum et al., 2017). Additionally, as satellite tagged Oceania mothers with calves migrated

Table 3
Summary of satellite tag deployments and tracking data for 18 humpback whales used in the state-space model.

PTT	Transmitted south of 60°S	Sex (* = with calf)	Deployment date	First location	Last location	Transmitting days	Data gaps (d_1,d_2,d_n)	Total no. of locations	Mean no. locs/day (± SE; range)	% Argos location class							Mean time (h) between locs (± SE)
										3	2	1	0	A	B	Z	
88727	Yes	F*	08-Oct-2015	08-Oct-2015	14-Jan-2016	99		2665	27 (± 1.3; 1–64)	3.3	6.1	7.0	2.0	16.3	64.9	0.3	0.9 (± 0.02)
102211	Yes	U	10-Oct-2015	11-Oct-2015	19-Dec-2015	57	14	594	10 (± 0.9; 1–26)	0.2	0.2	0.0	0.2	4.7	94.1	0.7	2.8 (± 0.57)
102218	Yes	M	10-Oct-2015	11-Oct-2015	20-Jun-2016	249	2,4	8659	33 (± 1.1; 1–85)	4.1	10.1	12.2	3.8	15.1	54.7	0.0	0.7 (± 0.02)
111866	Yes	F	04-Oct-2015	06-Nov-2015	15-Mar-2016	130	2	3820	29 (± 1.1; 4–65)	2.1	4.3	5.7	2.2	13.5	72.1	0.1	0.8 (± 0.02)
112722	Yes	U	10-Oct-2015	11-Oct-2015	03-Apr-2016	174	2,2	6390	37 (± 1.0; 3–71)	12.8	17.0	11.4	2.5	18.9	37.4	0.0	0.7 (± 0.02)
131173	Yes	M	30-Sep-2015	30-Sep-2015	08-Apr-2016	184	8,2	5925	32 (± 1.1; 2–70)	2.9	7.9	11.1	3.9	16.7	57.5	0.1	0.8 (± 0.04)
131175	Yes	M	04-Oct-2015	04-Oct-2015	18-Jan-2016	97	11	2077	21 (± 1.1; 4–47)	0.7	1.7	1.7	1.1	11.2	83.4	0.2	1.2 (± 0.13)
131178	Yes	F*	08-Oct-2015	09-Oct-2015	17-Jan-2016	101		2167	21 (± 1.1; 2–58)	0.8	1.7	4.7	1.6	14.4	76.7	0.2	1.1 (± 0.03)
131179	Yes	M	02-Oct-2015	07-Dec-2015	22-Mar-2016	84	23,2	1785	21 (± 0.9; 6–50)	0.3	0.6	1.6	0.3	6.2	90.9	0.2	1.4 (± 0.30)
131182	Yes	F	01-Oct-2015	02-Oct-2015	02-Apr-2016	150	30,5,2	6264	42 (± 1.2; 11–90)	10.0	27.9	22.0	5.8	12.1	22.1	0.0	0.7 (± 0.12)
131185	Yes	F	02-Oct-2015	27-Nov-2015	06-Jan-2016	41		886	22 (± 1.4; 1–44)	0.1	0.3	1.0	0.2	6.2	91.6	0.5	1.1 (± 0.06)
131187	Yes	F	30-Sep-2015	01-Oct-2015	02-Jan-2016	94		1876	20 (± 0.9; 6–51)	1.4	1.6	2.6	0.9	10.5	82.9	0.0	1.2 (± 0.04)
131188	Yes	F*	29-Sep-2015	30-Sep-2015	11-Dec-2015	73		1310	18 (± 0.7; 8–37)	1.0	2.8	2.3	0.8	13.4	79.7	0.0	1.3 (± 0.04)
131190	Yes	F*	08-Oct-2015	08-Oct-2015	20-Mar-2016	90	76	2334	26 (± 0.9; 1–45)	5.8	13.5	13.4	4.4	18.4	44.5	0.0	1.7 (± 0.78)
111871	No	F	08-Oct-2015	09-Oct-2015	04-Nov-2015	26	2	308	12 (± 1.1; 1–20)	1.9	4.5	4.2	1.0	14.0	74.4	0.0	2.1 (± 0.20)
112718	No	M	05-Oct-2015	05-Oct-2015	13-Nov-2015	40		562	14 (± 0.6; 2–21)	2.1	3.4	3.4	0.9	14.4	75.4	0.4	1.7 (± 0.08)
112721	No	F*	09-Oct-2015	10-Nov-2015	28-Nov-2015	19		224	12 (± 1.1; 5–24)	0.4	1.3	1.3	0.0	6.3	90.2	0.4	2.0 (± 0.16)
112723	No	F*	06-Oct-2015	07-Oct-2015	18-Oct-2015	12		204	17 (± 1.7; 2–24)	2.5	2.9	4.9	2.9	18.1	68.6	0.0	1.3 (± 0.08)

All tags were deployed at Raoul Island (Kermadec Islands, New Zealand). PTT = unique tag number. Only whales whose tags transmitted data south of 60°S were used in the linear mixed-effect model.
F = female, M = male, U = unknown sex, and * denotes animals that had a calf. All dates are in UTC. Transmitting days = number of days when one or more locations were received.
Data gaps = any gaps in data transmission > 1 day in length, data gap length is in days, multiple data gaps for the same animal are separated with a comma.
Percent of locations belonging to each of the seven Argos service provider assigned location classes. Location classes in a descending order of accuracy: 3, 2, 1, 0, A, B and Z. See Argos user's manual, 2016

Table 4
Number of unique tags transmitting in any given month, and the number of state-space modelled data points (in brackets) within the feeding grounds (south of 60°S).

Year	Month	Ross Sea	A&B Seas	Total
2015	November	4[a] (119)	2[a] (48)	5 (167)
	December	11[b] (717)	6[b] (487)	14 (1204)
2016	January	5[c] (373)	7[c] (453)	11 (826)
	February	2 (187)	4 (365)	6 (552)
	March	3 (323)	4 (378)	7 (701)
	April	2 (45)	2 (127)	4 (172)
	May	1[d] (80)	1[d] (39)	1 (119)
	June	1 (77)	0 (0)	1 (77)

In total, the tags of 14 individual whales transmitted data within the feeding grounds.
A&B seas = Amundsen and Bellingshausen Seas.
[a] PTT131182 travels through both regions during the month of November.
[b] PTT102218, PTT131175 and PTT131187 travel through both regions during the month of December.
[c] PTT131175 travels through both regions during the month of January.
[d] PTT102218 travels through both regions during the month of May.

to the Ross Sea and given that whales still also migrate to the Amundsen and Bellingshausen Seas (Riekkola et al., 2018), these whales may not have maternally inherited feeding grounds. Knowing the approximate location of profitable foraging areas and consistently returning to them may increase foraging success and individual fitness, which could be highly advantageous for the slowly recovering Oceania population. Memory of long-term average conditions may be more important for cetaceans than previously thought (Abrahms et al., 2019), and some marine species in the Southern Ocean have been found to consistently return to foraging areas that may have arisen as a consequence of predictable oceanographic conditions (Weimerskirch, 2007; McIntyre et al., 2017; Sztukowski et al., 2018). Data on the Oceania whales across multiple years could help identify persistent patterns in the whales' behavior to determine the role of memory, and assess the stability of the two feeding areas over time, especially given the predicted future changes in ice dynamics due to climate change (de la Mare, 1998; Turner et al., 2009). Changes in global oceanographic events are becoming more common, for example they are likely to have disrupted the long-term feeding ground fidelity in humpback whales in southern Alaska (Neilson and Gabriele, 2019).

4.2. Environmental effects on whale movement and behavior on the Southern Ocean feeding grounds

Because large baleen whales have very high energetic demands (Lockyer, 1981), we expect that humpback whale behavior on the feeding grounds is largely driven by the distribution and availability of krill; especially given they effectively undertake all foraging during the ~five months they spend in the Southern Ocean. Previous studies have linked the behavior and distribution of humpback whales to krill abundance and distribution (e.g. Friedlaender et al., 2006, 2011, 2013; Curtice et al., 2015). However, as obtaining reliable data on krill abundance and distribution for the large temporal and spatial extent covered by our satellite telemetry data is all but impossible, we examined how the behavior of these whales was affected by more easily recorded, remotely sensed environmental parameters. In the absence of easily obtained prey field data understanding how marine top predators, such as whales, pinnipeds and seabirds, respond to more easily recorded variables (which act as proxies for prey availability) is often the only approach available (Raymond et al., 2015; Reisinger et al., 2018).

The best LMM indicated that the inferred behavioral states of humpback whales within the Southern Ocean feeding grounds were most affected by timing within the feeding season (month), where the

marginal ice edge was two months prior, SSH, and to some extent the region (Table 5, Fig. 3). All these variables are thought to be linked to krill availability and distribution associated with local and regional scale oceanographic features. By targeting and favoring areas with environmental conditions that are associated with increased prey availability, large marine predators, such as humpback whales, can improve their foraging opportunities (Heerah et al., 2016). In the absence of prior knowledge regarding potential prey locations, whales might use environmental cues to place themselves in likely profitable foraging areas.

As the feeding season progressed the likelihood of adopting ARS-foraging behavior increased, peaking in February–March (Fig. 2a). This was expected as the whales would be finding sufficient prey to feed on after several months of fasting, and as productivity should increase following the spring/summer ice melt (Lehodey et al., 1998; Arrigo et al., 2008; Dalpadado et al., 2014). After the peak, the likelihood of ARS-foraging behavior decreased likely in response to productivity declining in late summer-autumn months, however data for the last two months came from only one whale (Table 4).

The results indicated that foraging behavior was more likely to occur near where the ice edge was two months prior. As the sea ice melts, the ice-free waters promote phytoplankton blooms which in turn trigger grazers such as krill to aggregate at the sea ice edge (Nicol, 2006; Arrigo et al., 2008). This link between humpback whales and the ice indicates that the whales do not actively track the ice edge itself, but instead the productivity that occurs following ice melt (i.e. after a time lag). Organisms do not always respond immediately to changes in the physical or biotic environment. Animal population trends respond to fluctuations in the environment after appropriate time lags (e.g. Baker et al., 2007; Walker et al., 2013), however distribution and foraging behavior can also show lagged responses to environmental conditions (Pinaud and Weimerskirch, 2005). Our findings therefore support the importance of including time-lagged variables when modelling the relationships between animals and their environment, which is applicable to both aquatic and terrestrial species across a broad array of ecosystems.

The humpback whales were also more likely to exhibit ARS-foraging behavior at lower SSH values. Lower (more negative) SSH values are linked to meso-scale eddies, which stimulate productivity near the surface through vertical mixing of deep nutrient rich waters, and trap aggregations of buoyant and weekly swimming plankton and fish (Olson and Backus, 1985; Nel et al., 2001; Hyrenbach et al., 2006). However, whether the whales can detect changes in SSH and relate them to krill presence is unknown. As noted above, areas with lower SSH are generally linked to productivity and prey, and SSH is therefore functioning as a proxy for prey in our model.

There was some evidence that the behavioral mode of the whales was affected by the feeding region they were in, and the interaction between region and month suggests that the whales behave differently in the different regions during different points of the season (Fig. 2a). Animals are expected to strive to maximize foraging success while minimizing the associated effort and costs (MacArthur and Pianka, 1966; Schoener, 1971). Predators foraging in complex and patchy environments should therefore adjust their movements and foraging behavior according to prey availability (and density) to maximize foraging efficiency. They might for instance employ distinct foraging strategies in different habitats (Arthur et al., 2016). We expect that the observed regional foraging behaviors by the humpback whales are the result of region-specific decisions made in response to the dynamic characteristics of the environment in each habitat, suggesting that there is behavioral plasticity in this population. Many ecological studies have treated conspecific individuals as ecological equivalents, but the existence of intraspecific plasticity in foraging behavior (in the form of dietary differences, variation in habitat use or foraging strategies for example) is widespread among taxonomic groups and can be ecologically important (Bolnick et al., 2003; Ceia and Ramos, 2015; McHuron
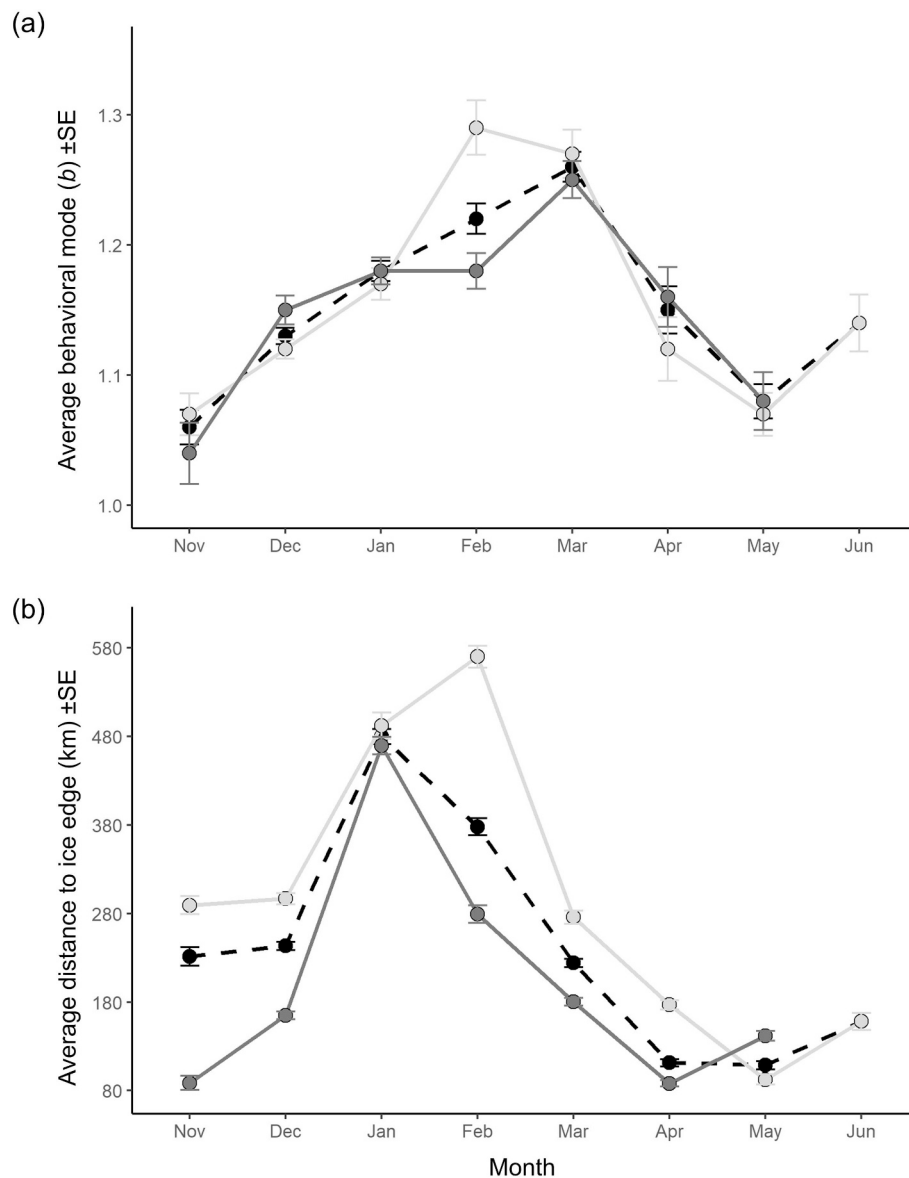
Fig. 2. (a) Average behavioral mode (*b*) by month. Values closer to 1 indicate transiting behavior and values closer to 2 indicate ARS-foraging behavior, and (b) distance to ice edge (km; all locations) by month. Black dashed = all whales, light gray = Ross Sea, dark gray = Amundsen & Bellingshausen Seas.

Table 5
Results of the best linear mixed-effect model, with logit transformed behavioral state (*b*) as a response variable and individual whales as a random effect. Higher *b*-values indicate an increasing likelihood of whales exhibiting ARS-foraging behavior.

Parameter	Estimate	SE	DF	t-value	p-value
Intercept	−9.49	1.10	3796	−8.61	**< .001**
Region_Ross Sea	−0.55	0.58	3796	−0.96	.34
Month	1.91	0.38	3796	4.99	**< .001**
Month^2	−0.35	0.06	3796	−5.40	**< .001**
dist ice lag 2	0.00	0.00	3796	0.26	.80
dist ice lag 2^2	−0.00	0.00	3796	−3.55	**< .001**
SSH	−4.92	1.08	3796	−4.57	**< .001**
Region_Ross Sea × Month	−0.93	0.48	3796	−1.95	**.05**
Region_Ross Sea × Month^2	0.24	0.08	3796	3.16	**< .01**

Estimates are in log-odds scale. During model selection all models were fitted using maximum likelihood for comparing models with different fixed effects. The best model was then fitted with restricted maximum likelihood to obtain final parameter estimates. Variables with a significant parameter estimate (< .05) are in bold.

et al., 2018). The predicted climate change induced spatial variability in factors that influence krill populations, such as sea ice characteristics and seasonal dynamics, are likely to result in region-specific responses in the whales' main prey (e.g. Constable et al., 2014), which might necessitate region-specific foraging strategies in the future.

In order to respond dynamically to sensory cues from the dynamic environment whales likely use multimodal sensory systems (Carroll et al., 2017; Torres, 2017). Additionally, species-habitat relationships are often scale dependent, and different environmental parameters may have a stronger influence on animals at different scales (Redfern et al., 2006; Ballance et al., 2006). For example, during long distance migration to the feeding grounds (thousands of kilometers) humpback whales, as well as other cetaceans, use large-scale oceanographic patterns and features to navigate (Horton et al., 2017; Torres, 2017). Once near or within the feeding grounds the whales are expected to change their movement to a smaller-scale prey search pattern, and will likely utilize different, finer-scale environmental cues (Ballance et al., 2006; Doniol-Valcroze et al., 2007; Torres, 2017; Kirchner et al., 2018). It is therefore important to use temporal and spatial scales that are appropriate for the main objectives of the analysis and relevant for the
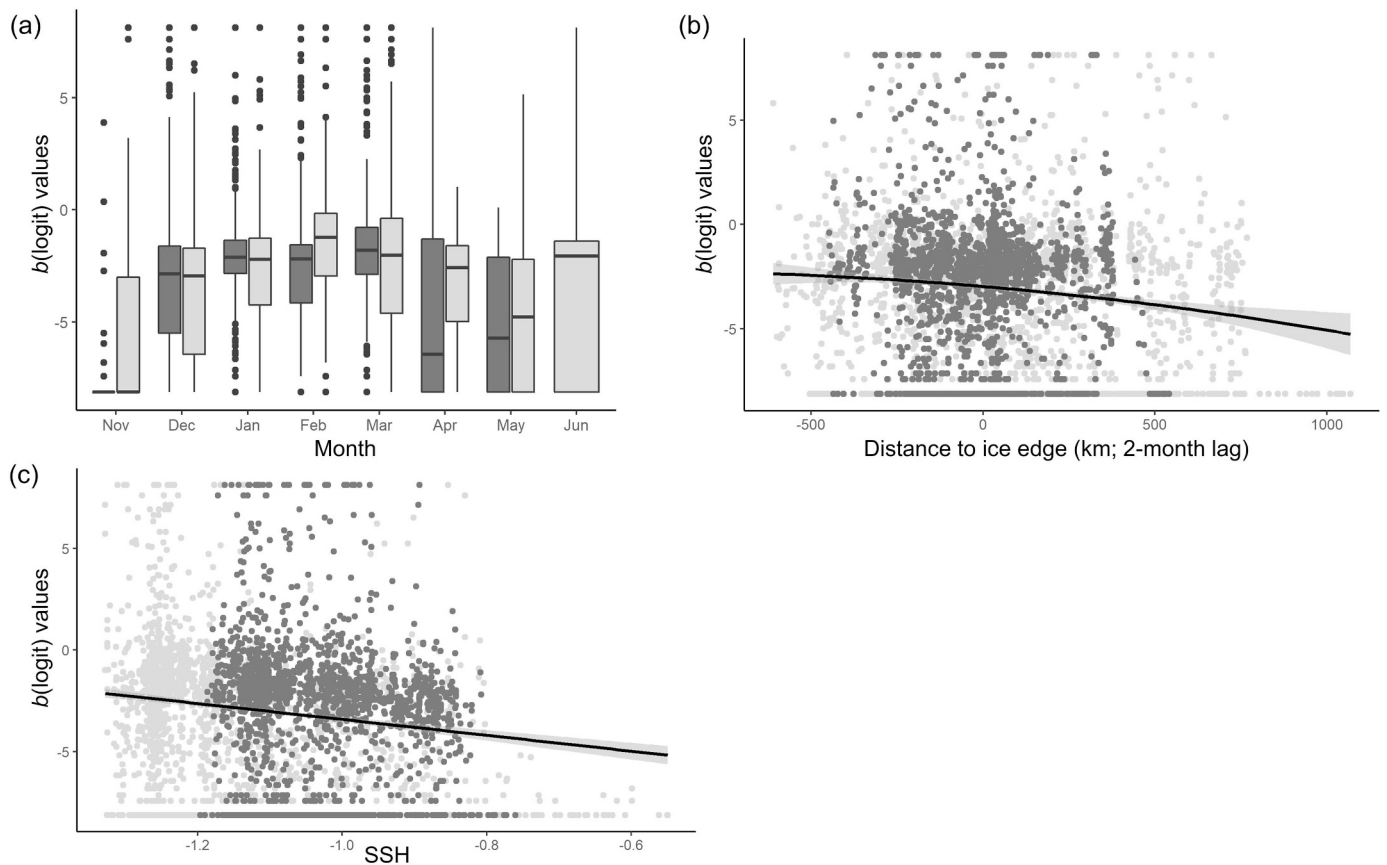
Fig. 3. The relationship between significant explanatory variables (a) month, (b) distance to the ice edge (2-month lag) and (c) SSH (sea surface height) and the logit transformed behavioral mode (*b*). Light gray = Ross Sea, dark gray = Amundsen and Bellingshausen Seas. Higher predicted *b*(logit) values indicate an increasing likelihood of whales exhibiting ARS-foraging behavior. A negative value for 'distance to ice edge' indicates that the whale has moved past the point where the ice edge was two months prior. Simplified univariate regression lines from the mixed-effect model analysis (without random effects and autocorrelation structure) were added to (b) and (c) to highlight the overall trend in the data for the sample population.

ecology of the target species (e.g. Ballance et al., 2006; Redfern et al., 2006; Fernandez et al., 2017). Unfortunately, the temporal and spatial scale used is often determined by the availability of the environmental data. We were not immune to this problem, yet we aimed to use resolutions closest to our modelled data to best capture the whales' behavior patterns. Using different movement/behavioral modelling techniques (e.g. McClintock et al., 2015; McClintock and Michelot, 2018) it can be possible to further improve the accuracy of the animal locations. In our case, due to the low resolution of many of the environmental covariates (raster data), improving the whale location estimates would have likely resulted in us sampling from the same environmental raster cell. In studies covering a smaller study area and having higher quality environmental data increasing the accuracy of the animal locations would be more paramount. Despite some caveats, using the available remotely sensed data and spatial modelling techniques enabled us to uncover the behavioral patterns of these whales spread over 4000 km across the Southern Ocean largely devoid of distinct land mass features, apart from the Antarctic continent. The whales' ability to detect and use environmental cues to locate patchily distributed prey in this vast ocean environment is remarkable and identifying the key variables for these animals will help us better understand their behavior and how they might respond to changes in their environment.

In many animal taxa (including insects, birds and mammals) the decision to begin migrating from one critical habitat to another often occurs in response to environmental conditions, social cues or sexual hierarchy, and is highly affected by individual variation (Chittleborough, 1965; Gunnarsson et al., 2006; Balbontín et al., 2009; Jiang et al., 2011; Rivrud

et al., 2016; Berdahl et al., 2017). Climate change has a variety of effects on the critical habitats of different animals, for example by altering the distribution and seasonal availability of food as well as the size of suitable breeding areas (Fitter and Fitter, 2002; Walther et al., 2002; Derville et al., 2019). If the timing of migration relies on endogenous cues that are not affected by climate change (compared to e.g. weather cues), the migration of such species will not advance even though they need to arrive earlier on their breeding or feeding grounds (Both and Visser, 2001). It is yet unclear whether climate change will influence whale arrival at the Southern Ocean feeding grounds, and whether this would have a positive or a negative effect on their fitness. Waiting for krill to become available could incur an energetic cost due to the wait time, yet the whales might adapt and prey switch to forage more on already available prey; this has been documented in different humpback whale populations (e.g. Weinrich et al., 1992; Fleming et al., 2015).

5. Conclusions

Here we used spatial modelling techniques to identify underlying behavioral states from movement data for a wide-ranging marine predator inhabiting a remote area, and related those behaviors with environmental conditions. We identified two important Southern Ocean feeding areas for humpback whales and observed differences in behavior, likely related to decisions made about the local environmental variation between the two adjacent habitats. Behavioral plasticity is critical to survive in environments that are unpredictable and changing (Stien et al., 2010; Wong and Candolin, 2015; Courbin et al., 2017). This could therefore be of advantage to whales in a changing Southern

Ocean, especially as the two feeding areas are experiencing different responses to climate change; sea ice increase in the Ross Sea, sea ice retreat in the Amundsen and Bellingshausen Seas (e.g. Zwally et al., 2002; Turner et al., 2009) and regional differences in food web structure (e.g. Murphy et al., 2012; Constable et al., 2014). Environmental changes may therefore elicit different behavioral and demographic responses for populations inhabiting different, yet adjacent, regions of the Southern Ocean. Having whales of the same population being subject to different environmental conditions provides an opportunity to study changes in their distribution and behavior within and between circum-Antarctic regions, which in turn can be used as indicators of change in the ecosystem (e.g. prey distribution) for all marine predators (Raymond et al., 2015). The phenomena of range shifts and behavioral adaptations in response to environmental change are better understood in the northern hemisphere where such events are more apparent (Both and Visser, 2001; Post et al., 2009).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jembe.2019.05.008.

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