Managing for change: Using vertebrate at sea habitat use to direct management efforts

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Running title: Using seal habitat use to direct management

Highlights

- Reconstruction of likely historical foraging habitat of key Southern Ocean consumer.

- Assessment of decadal changes to habitat quality and temporal variability in use.

- Habitat quality consistent or improved despite notable physical ocean changes.

- Overlap with fisheries with core habitat also falling outside management areas.

- Results applicable to Southern Ocean MPA plans and ecosystem monitoring programs.

Summary

To understand and predict current and future distributions of animals under a changing climate it is essential to establish historical ranges as baselines against which distribution shifts can be assessed. Management approaches also require comprehension of temporal variability in spatial distributions that can occur over shorter time scales, such as inter-annually or seasonally. Focussing on the Southern Ocean, one of the most rapidly changing environments on Earth, we used Species Distribution Models (SDMs) and satellite ocean data to reconstruct the likely historical foraging habitats of Antarctic fur seals (*Arctocephalus gazella*) from three populations during the non-breeding winter (Marion Island, Bird Island and Cape Shirreff), to assess whether habitat quality has changed in recent decades. We then quantified temporal variability in distributions to assess overlap with management areas (CCAMLR – Commission for the Conservation of Antarctic Marine Living Resources) and the potential for competition with fisheries. Despite notable physical ocean changes, the quality of foraging habitat during the non-breeding season has remained relatively consistent over 20 years at Marion and Bird Islands, but less so at Cape Shirreff, where reduced sea ice cover has improved habitat accessibility. Spatio-temporally explicit SDMs identified variability in habitats across the winter. Some areas overlapped significantly with fisheries activities, suggesting a potential for competition for prey resources at several key periods. A significant component of core habitat at all populations was not within the CCAMLR Convention Area. Although organisations such as CCAMLR adopt a precautionary, ecosystem-based approach to fisheries management, changes to the physical environment and developments in the fishing industry can affect how dependant species are impacted. The hindcasting of historical spatial distributions shown here are baselines against which future changes

can be assessed. Given recent proposals for a system of marine protected areas (MPAs) in the Southern Ocean, our results can be used in the design and evaluation of MPAs, be they static or dynamic. Our study also demonstrates that the core habitat of species may fall outside of areas of active management, providing an important context for the interpretation of monitoring programs and management efforts.

Key words: Spatial distribution, species distribution model, fisheries competition, baseline, distribution shift, animal tracking, geolocation, Southern Ocean.

1. Introduction

Recent changes to the Earth's climate are well documented, unequivocal and are effecting a wide range of species and communities from the equator to the poles in both terrestrial and marine ecosystems (e.g. Parmesan 2006). Polar regions are experiencing some of the strongest and fastest large-scale physical changes anywhere on Earth, with rapid rises in atmospheric and oceanic temperatures (Meredith & King 2005; Chapman & Walsh 2007) and accelerating loss of ice sheet mass (Pritchard *et al.* 2012). In the Southern Ocean, there is increasing evidence of the impacts of such changes on biological systems at various trophic levels (e.g. McMahon & Burton 2005; Montes-Hugo *et al.* 2009; Flores *et al.* 2012; Ropert-Coudert *et al.* 2015). Despite this, the links between physical changes and biological productivity remain poorly understood. However, any biological effects will ultimately be reflected in the responses of higher-trophic level species (seals, seabirds and whales) because they integrate and amplify the effects occurring at lower trophic levels (Hindell *et al.* 2003; Costa *et al.* 2010), often making them useful indicators of wider ecosystem change.

A change in distribution is one potential response to climate change (Walther *et al.* 2002; Mueter & Litzow 2008; Trathan & Agnew 2010) as species are forced towards higher latitudes or altitudes. Recently, studies into the distribution of highly mobile marine predators have focussed on predicting species responses to future climate change (e.g. Péron *et al.* 2012; Hazen *et al.* 2013; Spencer *et al.* 2016). However, to properly understand current and future distributions it is essential to establish historical distributions as baselines against which changes can be assessed (Lotze & Worm 2009). Historical records are often brief or fragmented (Swetnam *et al.* 1999) and biased towards terrestrial ecosystems (Elith & Leathwick 2009). For marine environments, historical distributions are mostly available for species of commercial interest (Bellier *et al.* 2007; Nye *et al.* 2009) and typically do not exist for remote regions such as the Southern Ocean. Conversely, baseline environmental data from remotely sensed sources (satellite) have been available since the 1980's, before the widespread use of animal-tracking devices to observe habitat use and at-sea distributions. Environmental data can be used to construct habitat models or Species Distribution Models (SDMs), which correlate species occurrence with environmental variables to explain or predict a species' distribution (Robinson *et al.* 2011). The inclusion of historical environmental data has the potential to hindcast SDMs to the likely historical distribution of top predators (Louzao *et al.* 2013), providing a baseline to assess future change and inform and appraise management decisions.

As well as potential changes over decadal time scales, the spatial distribution of many pelagic predators can be highly variable over shorter periods, such as inter-annually or seasonally (Forney & Barlow 1998; Pettex *et al.* 2012). This temporal variability is a major source of uncertainty in marine resource management and the effectiveness of SDMs as a management tool is determined in part by their ability to

capture year-round habitat conditions (Becker *et al.* 2014). For species known to have pronounced seasonality in distribution, as is the case for many Southern Ocean predators (Cockell *et al.* 1999), SDMs that are spatio-temporally explicit at scales relevant to species movements and management objectives, will likely prove more informative. Although SDMs are under-utilised in marine species (Robinson *et al.* 2011) they have been effectively employed to inform habitat conservation, understand fisheries interactions and investigate the impacts of climate change in pelagic predators (See Robinson *et al.* 2011). Yet often, many do not consider the temporal shifts in habitat use and spatial distribution that can occur in wide-ranging animals.

In highly variable environments such as the Southern Ocean, significant environmental changes including the growth and decay of sea ice, seasonal movement of fronts, and fluctuations in primary productivity can occur on relatively short time scales of weeks to months (Gordon 1981; Clarke 1988; Sokolov & Rintoul 2009). Such rapid environmental change can alter prey availability and the distribution of foraging predators (Cockell *et al.* 1999). Therefore, incorporation of temporal variability into SDMs for Southern Ocean predators is important for a variety of management approaches such as the design of marine protected areas, quantification of potential fisheries interactions and development of accurate ecosystem models.

Within this context, we studied the winter distribution of female Antarctic fur seals (*Arctocephalus gazella*, Peters, 1875), a highly mobile pelagic predator, from three Southern Ocean populations. In the context of the current biogeography of the species, following recovery after massive exploitation in the 18th and 19th centuries (Payne 1977) and by expanding SDMs previously established for each population (Arthur *et al.* 2017) this study aims to: (1) Establish likely historical fur seal foraging habitat as a baseline to assess whether habitat quality has changed over recent

decades, (2) describe temporal variability in foraging habitats across the non-breeding period and (3) assess the degree of spatio-temporal overlap with Southern Ocean management areas and the potential for interaction with fisheries during winter.

2. Materials and methods

2.1. TRACKING INSTRUMENTATION AND ANALYSIS

Female Antarctic fur seals were tracked during their non-breeding winter migrations (April-December) at three colonies: Marion Island (Prince Edward Islands, 2008-13), Bird Island (South Georgia, 2008-11) and Cape Shirreff (South Shetland Islands, 2008-10) (Fig. 1a). Seals were equipped with a global-location sensing logger (GLS; British Antarctic Survey, Cambridge UK, 2.5-3.6 g) towards the end of lactation that was recovered when animals returned to pup the following season (n=184). Animal handling, device attachment and calibration procedures followed those outlined in Arthur *et al.* (2015). Non-breeding winter foraging trips encompassed the female's first post-weaning excursion until return to the colony in December. Individual foraging trips were identified and analysed separately (n=320). Location estimates were produced from the raw light and temperature data using the Bayesian approach of Sumner *et al.* (2009) in the R software (R Core Team 2014) package 'tripEstimation' (Sumner & Wotherspoon 2010) following the approach detailed in full in Arthur *et al.* (2016, Supporting Information).

2.2. SPECIES DISTRIBUTION MODELS

Arthur *et al.* (2017) built SDMs for each colony to explain the relationship between the environment and the spatial distribution of Antarctic fur seal habitat during the non-breeding winter period. Briefly, the time spent per trip (hours) in each
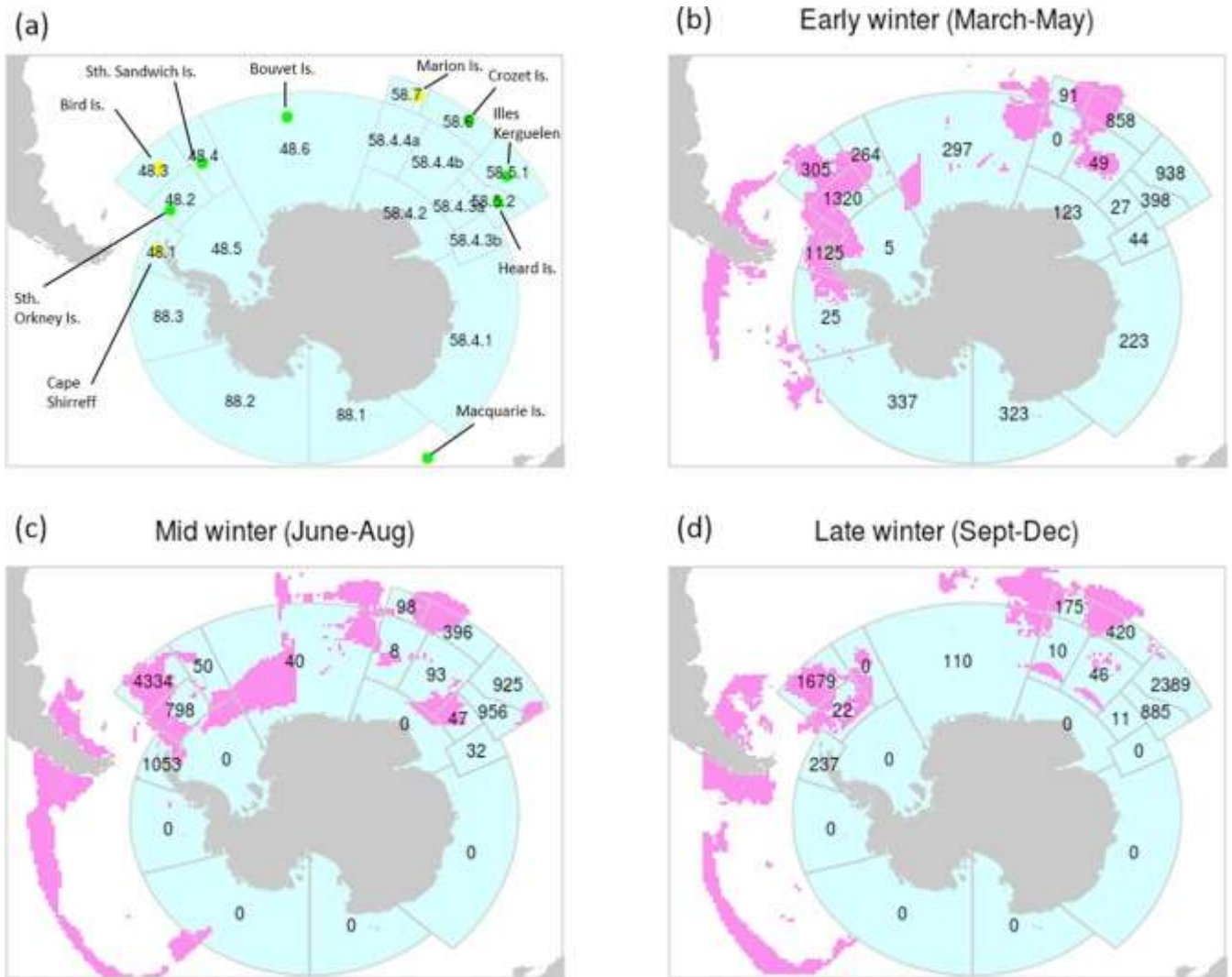
Fig. 1. (a) Location of Antarctic fur seal breeding colonies. Study colonies are represented by yellow circles while all other colonies are represented by green circles. The CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources) Convention Area is shown in light blue. Numbers represent the names of subareas and divisions comprising the Convention Area. (b–d) Seasonal Antarctic fur seal habitat in relation to the CCAMLR Convention Area and fishing effort for (b) early, (c) mid and (d) late winter. Core foraging areas for the Marion Island, Bird Island and Cape Shirreff colonies combined is represented pink shading. CCAMLR subareas and divisions are shown in light blue, overlaid with the cumulative total number of winter fishing days 2008–13.

cell of a 0.6^o x 0.6^o raster grid (60 km x 60 km) covering the spatial extent of

locations over all years (hereafter referred to as *time spent*) was modelled using winter

climatologies of biologically relevant environmental predictor variables in a

generalized additive modelling (GAM) framework. Climatologies of environmental

variables were calculated by averaging the weekly data across the period of the study,

producing one mean parameter value per cell for the period of interest. Environmental

variables retained in final models included both static; bathymetry (BATHY) and

distance to colony (d2col) and dynamic parameters; sea surface height anomaly

(SSHa), variability of sea surface height anomaly (SSHV), sea surface temperature

(SST), gradient of sea surface temperature (SSTG), chlorophyll a concentration

(CHLa), wind speed (WIND) and eddy kinetic energy (EKE). Models were fitted with

a Gamma error structure using a log-link function and including a spatial

autocorrelation term (Wood 2006). The best models for each colony are shown in

Table 1a. Model predictions interpolated across the entire spatial domain of locations

 for each colony revealed the likely habitat use of Antarctic fur seals during winter for

the years of study. We then defined core foraging areas as those within the 75%

distribution quantile (see Arthur *et al.* 2017, for full details)

2.3. PAST CHANGE AND RETROSPECTIVE HABITAT MODELLING

To assess whether the environmental characteristics of core foraging habitats

have changed in the past three decades, we extracted all available winter

environmental data for those variables retained in the final SDMs (Supporting

Information Table A1) across the combined spatial extent of the three colonies for all

years of study. We also included sea ice concentration (ICE). This parameter was not

used in initial habitat modelling to describe fur seal habitat, however large-scale

Table 1. Summary of generalised additive models (GAMs) of the relationship between foraging effort (time spent per grid cell) and environmental variables for: **(a)** global colony models (from Arthur et al. In press) and **(b)** period models. TS = time spent, SSTG = sea surface temperature gradient, SSHA = sea surface height anomaly, SSHV = sea surface height variance, WIND = wind speed, CHLa = chlorophyll a concentration, BATHY = bathymetry, d2col = distance to colony, (lon,lat) = spatial autocorrelation term, period = period term.

Colony	Model formula	k	% dev	r^2	RMSE
	(a) Fitted habitat models				
Marion Island	TS ~ SST + SSHA + SSHV + WIND + CHLa + BATHY + EKE + d2col + (lon,lat)	10	73.3	0.704	14.3
Bird Island	TS ~ SST + SSTG + SSHA + WIND + BATHY + EKE + d2col + (lon,lat)	9	85.3	0.828	13.2
Cape Shirreff	TS ~ SST + SSHA + SSHV + WIND + CHLa + EKE + d2col + (lon,lat)	9	72.5	0.701	15.6
	(b) Period habitat models				
Marion Island	TS ~ SST, by=period + SSHA, by=period + SSHV, by=period + WIND, by=period + CHLa, by=period + BATHY, by=period + EKE, by=period + d2col, by=period + (lon,lat)	10	65.4	0.653	17.7
Bird Island	TS ~ SST, by=period + SSTG, by=period + SSHA, by=period + WIND, by=period +	9	57.5	0.430	30.3

	BATHY, by=period + EKE, by=period + d2col, by=period + (lon,lat)				
Cape Shirreff	TS ~ SST, by=period + SSHA, by=period + SSHV, by=period + WIND, by=period +	9	53.1	0.525	22.9
	CHLa, by=period + EKE, by=period + d2col, by=period + (lon,lat)				

k, number of parameters; % dev, per cent deviance explained by model, RMSE, root mean-squared error (in hours) obtained through k-fold cross validation.

changes to sea ice impacting top predators have occurred in the Southern Ocean in the recent decade, especially in the Antarctic Peninsula where one of our colonies is located s (e.g. Ropert-Coudert *et al.* 2015). Environmental data from the Australian Antarctic Data Centre were extracted using the R package 'raadtools' (Sumner 2015) and aggregated and re-projected to match the 0.6^o x 0.6^o grid used in the SDMs. For each dynamic variable we calculated the Pearson correlation coefficient, *r*, in each pixel across the temporal range of data (Supporting Information Table A1). This quantified the rate of change of each variable as a function of time, permitting an assessment of the long-term environmental trends. This also facilitated a direct comparison of the rate of change across variables measured on considerably different scales, for example a direct comparison could be made between SST measured in ^{o}C and WIND measured in m/s^{-2}.

To determine the historical foraging habitats of fur seals we mapped the spatial distribution of animals from the three colonies for the past 20 years across the observed spatial extent of tracking data. Dynamic variables were extracted as above for the period 1993-2013, spanning the earliest observations for all parameters used in the models (Supporting Information Table A1). CHLa data was not available prior to 1997, so this parameter was excluded. Static variables were extracted once. Data were then averaged to produce a mean parameter value per pixel for the five-yearly periods 1993-97, 1998-2002, 2003-07 and 2008-current observations. A five-year grouping was chosen as intervals shorter than this may be subject to annual extremes, while longer intervals would reduce the number of groupings available for the assessment of long-term trends. We then applied the SDM for each colony to these data to retrospectively predict historical foraging habitats that could be compared to current observations (2008 onwards).

The mean predicted *time spent* and standard error (SE) for each grid cell was used as a measure of quality and stability in predicted habitat during winter. The mean predicted *time spent* summarises the average foraging habitat while the SE represents the variability in foraging habitat during each period. Adapting the approaches of Louzao *et al.* (2013) and Bellier *et al.* (2007) to our study, habitat was classified into three categories: (1) *Regular foraging habitat* was defined as grid cells where the five-yearly mean and SE was higher than the overall mean, and lower than the overall SE, across all grid cells and 20 years. Seals consistently use these areas every year. (2) *Unfavourable foraging habitat* was defined as grid cells where the five-yearly mean and SE was lower than the overall mean, and lower than the overall SE, across all grid cells and 20 years. Seals rarely use these areas. (3) *Variable foraging habitat* encompassed remaining cells, which had a greater SE than the average across all grid cells and 20 years. Seals use these areas in some, but not all, years.

2.4. TEMPORAL VARIABILITY IN WINTER HABITAT USE AND OVERLAP WITH MANAGEMENT AREAS

The availability and use of foraging habitat by Antarctic fur seals is affected by intrinsic factors such as breeding status and extrinsic factors such sea ice cover, both of which contribute to seasonal variation in habitat use across the nine month winter period (Arthur *et al.* 2017). Following the modelling approach outlined in Arthur *et al.* (2017), we developed SDMs for each of the three fur seal colonies in this study during three periods: early winter (March-May), mid winter (June-August) and late winter (September-December). Environmental data were subset by period and climatologies (mean value per cell for that period) were calculated for each parameter.

The SDM for each colony was then applied to these data with the inclusion of a 'period' term (Table 1b).

In the Southern Ocean, the major fisheries management body is the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), which manages the area south of the Antarctic Convergence. The CCAMLR Convention Area is divided into statistical areas (Statistical Area 48: Southern Atlantic, Statistical Area 58: Southern Indian, Statistical Area 88: Southern Pacific), which are further divided into subareas and divisions based on general oceanographic conditions and biological characteristics such as discrete populations of certain species (CCAMLR 2015b) (see Fig. 1a). We overlaid the predictions of foraging habitat for Antarctic fur seals from Marion Island, Bird Island and Cape Shirreff with CCAMLR management areas to determine regions of overlap during the three winter periods. Using data reported to CCAMLR by all fisheries operating inside the Convention Area (CCAMLR 2015a) we calculated the total fishing effort, and therefore potential for fisheries competition and interaction with fur seals, at these times. Fishing effort was expressed in fishing days (CCAMLR 2015a), representing the total number of days during which fishing occurred for all fisheries during fur seal tracking observations (2008-13 winters).

3. Results

3.1. ENVIRONMENTAL CHANGE AND RETROSPECTIVE HABITAT MODELLING

There were clear long-term trends in several environmental parameters across the spatial domain of our study over recent decades, most notably SST, WIND and ICE (Fig. 2, Supporting Information Fig. A1). Around Marion Island, there was an overall warming trend of SST ($r > 0.2$) and decrease in WIND ($r < -0.2$) across
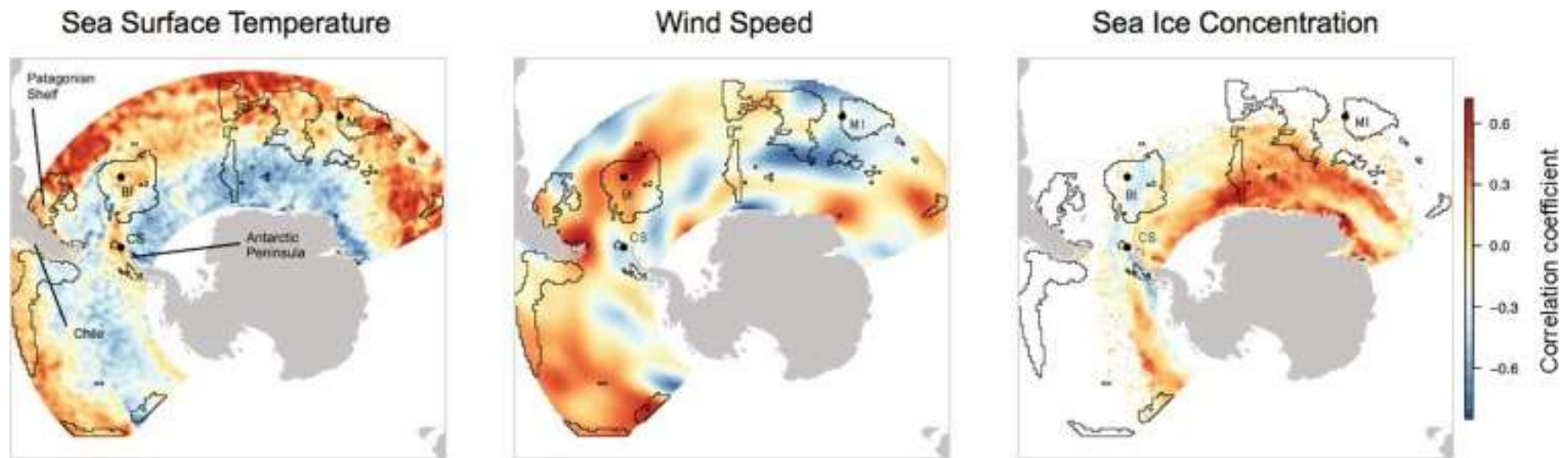
Fig. 2. Pearson correlation coefficients, *r*, for each pixel of a 0.6° × 0.6° grid matching the spatial extent of core Antarctic fur seal habitat (black lines) for sea surface temperature (SST, 1982–2013), wind magnitude (WIND, 1979–2013) and sea ice cover (ICE, 1979–2013). Locations of the Marion Island (MI), Bird Island (BI) and Cape Shirreff (CS) colonies are shown by black circles. The source of environmental data is provided in Table A1.

contemporary core fur seal habitats, while ICE showed an increasing trend in the southern core habitats. Sea surface temperature also had a warming trend in contemporary core areas around Bird Island and the Patagonian Shelf as well as around the Western Antarctic Peninsula and oceanic foraging habitats to the far west of the study area. There was a cooling trend in contemporary core habitat off the south west coast of Chile and in southern regions of the Southern Atlantic Ocean. Generally, WIND showed a strong positive trend ($r > 0.3$) in some core seal habitats for Bird Island and Cape Shirreff, with the exception of waters off the Western Antarctic Peninsula, which had a negative trend. Sea ice concentration decreased in the core habitats around South Georgia and the Western Antarctic Peninsula ($r < -0.3$).

The SDMs for each colony were used to hindcast foraging habitat from 1993 to 2007, immediately before current observations commenced. At Marion Island, the hindcast *time spent* indicated little change in the location of core habitat and was consistently in close proximity to the east of the colony, as well as areas further to the west and south, matching our 2008-13 observations (Fig. 3a). The SE of predictions was low across the spatial domain excepting the far northwest corner. Regular and unfavourable habitat increased by, on average, 4.1% (SD: ± 7.7) and 1.8% (SD: ± 4.4) each 5-years between 1993-2013. However, these increases were probably a product of a change in variable foraging habitat, which decreased by an average of 6.0% (SD: ± 11.1) over the same period as there was no consistent overall change to either regular or unfavourable habitat (Table 2).
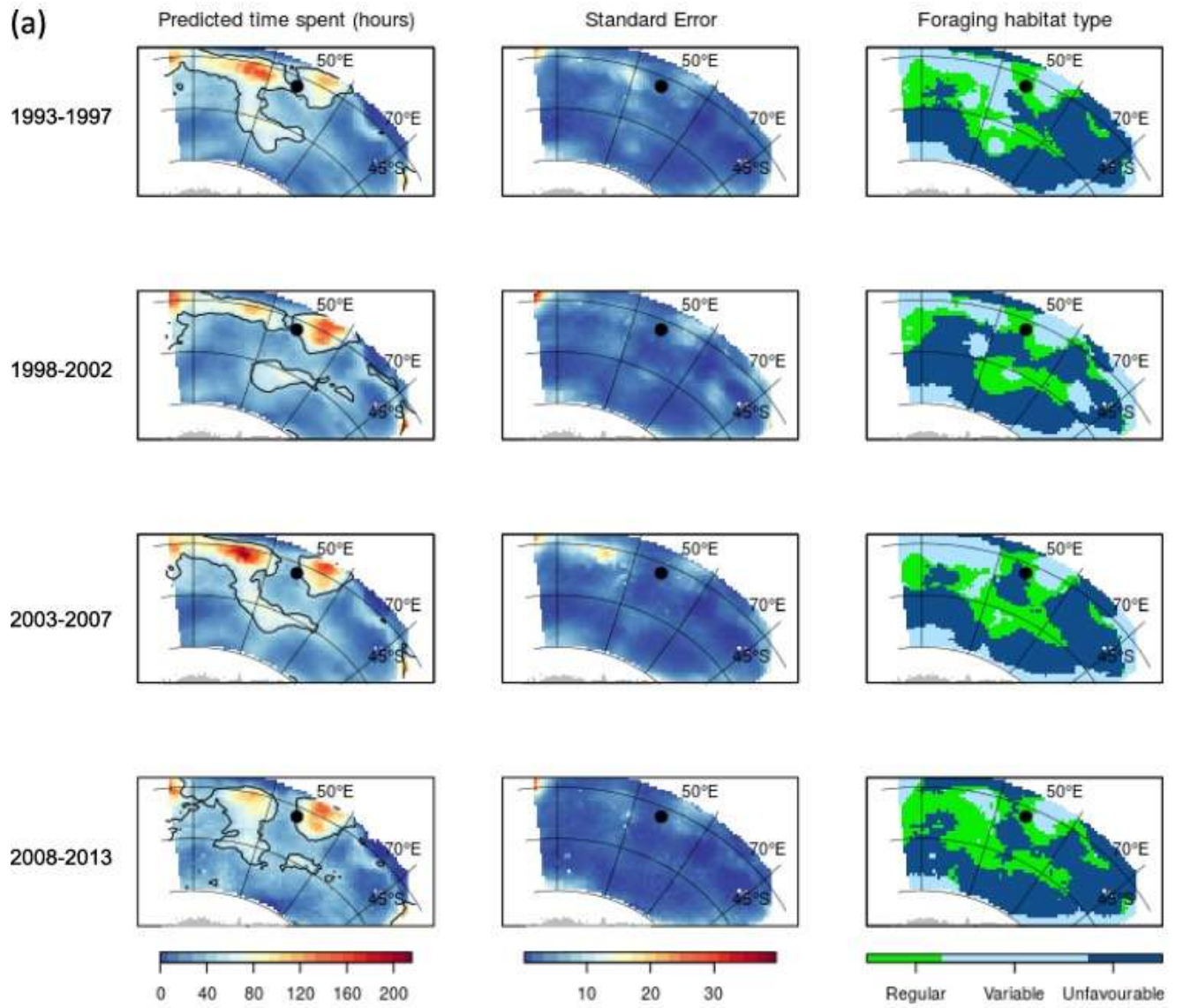
At Bird Island, the distribution of predicted *time spent* for five-yearly periods between 1993-2007 was consistent and closely matched our 2008-11 observations (Fig. 3b). Core foraging habitat for this entire period included waters around South Georgia and the Patagonian Shelf. Core habitat was also identified for each period at

Table 2. The number of cells (ncells) and percentage change (% change) in winter foraging habitat type between five-yearly periods from 1993 to current observations (2013 Marion Island, 2011 Bird Island, 2010 Cape Shirreff). Regular habitat = grid cells where the five-yearly mean and SE was higher than the overall mean, and lower than the overall SE, across all grid cells and 20 years, Unfavourable habitat = grid cells where the five-yearly mean and SE was lower than the overall mean, and lower than the overall SE, across all grid cells and 20 years, Variable habitat = grid cells which had a greater SE than the average across all grid cells and 20 years.
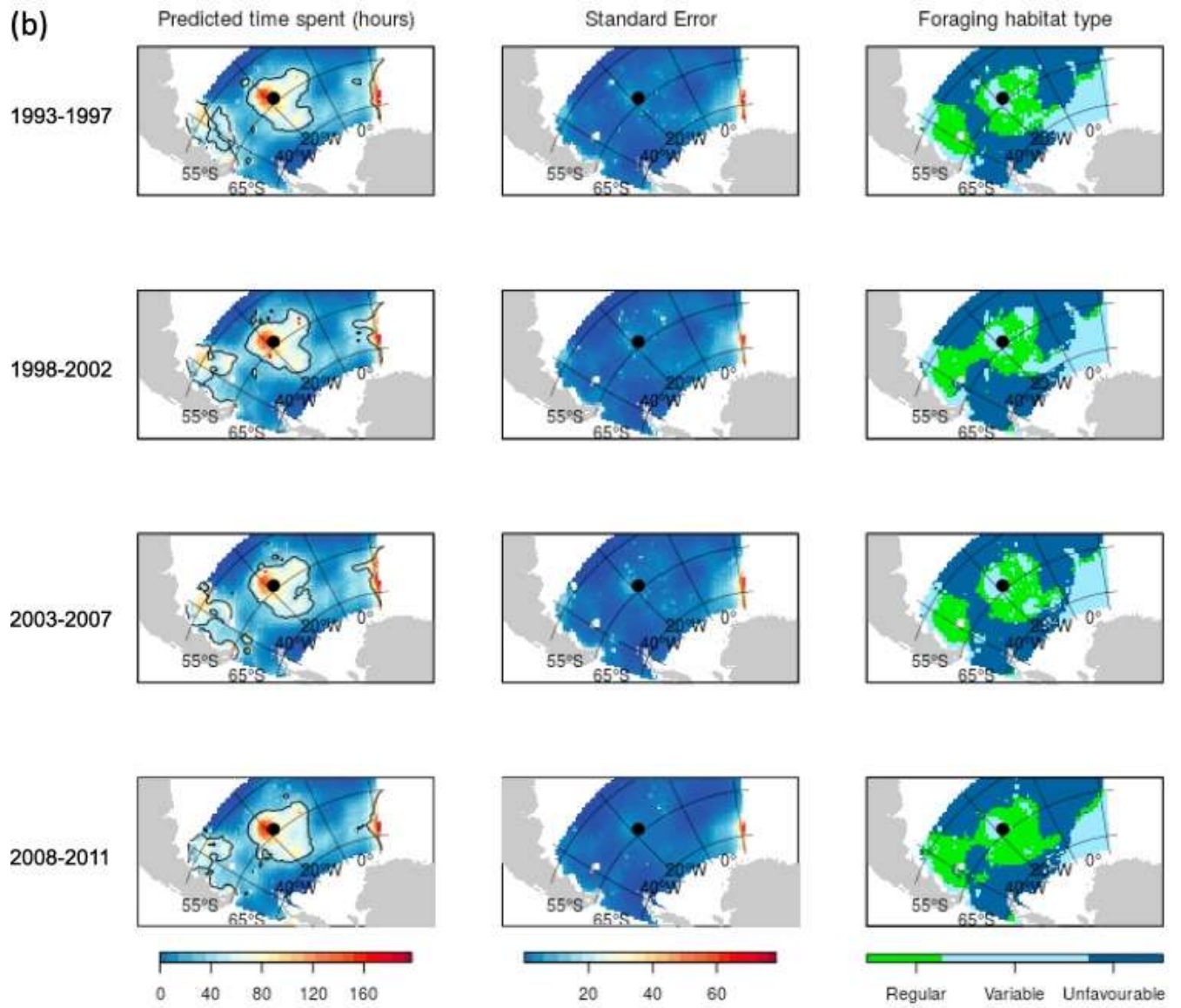
Colony	Time period	Regular habitat		Unfavourable habitat		Variable habitat	
		ncells	% change	ncells	% change	ncells	% change
Marion Is.	1993-97	2034		2948		2229	
	1998-2002	1959	-3.7	2995	1.6	2257	1.2
	2003-07	2041	4.2	2920	-2.5	2250	-0.3
	2008-13	2281	11.8	3105	6.3	1825	-18.9
	Mean		**4.1 ± 7.7**		**1.8 ± 4.4**		**-6.0 ± 11.1**
Bird Is.	1993-97	2323		3245		2500	
	1998-2002	2271	-2.2	3288	1.3	2501	<0.0
	2003-07	2329	2.5	3279	-0.3	2452	-1.9
	2008-11	2541	9.0	3358	2.4	2217	-9.6
	Mean		**3.1 ± 5.6**		**1.1 ± 1.3**		**-3.8 ± 5.0**
Cape Shirreff	1993-97	1832		4338		2736	
	1998-2002	1993	8.8	4300	-0.8	2575	-5.9
	2003-07	1965	-1.4	4303	<0.0	2610	1.4

2008-10	2093	6.5		4542	5.5		2365	-9.4
Mean		**4.6 ± 5.3**			**1.5 ± 3.4**			**-4.6 ± 5.5**

(a)

	Predicted time spent (hours)	Standard Error	Foraging habitat type
1993-1997			
1998-2002			
2003-2007			
2008-2013			

0   40   80   120 160 200

10   20   30

Regular   Variable   Unfavourable

(b)

Predicted time spent (hours)   Standard Error   Foraging habitat type

1993-1997

1998-2002

2003-2007

2008-2011

0 40 80 120 160

20 40 60

Regular   Variable   Unfavourable
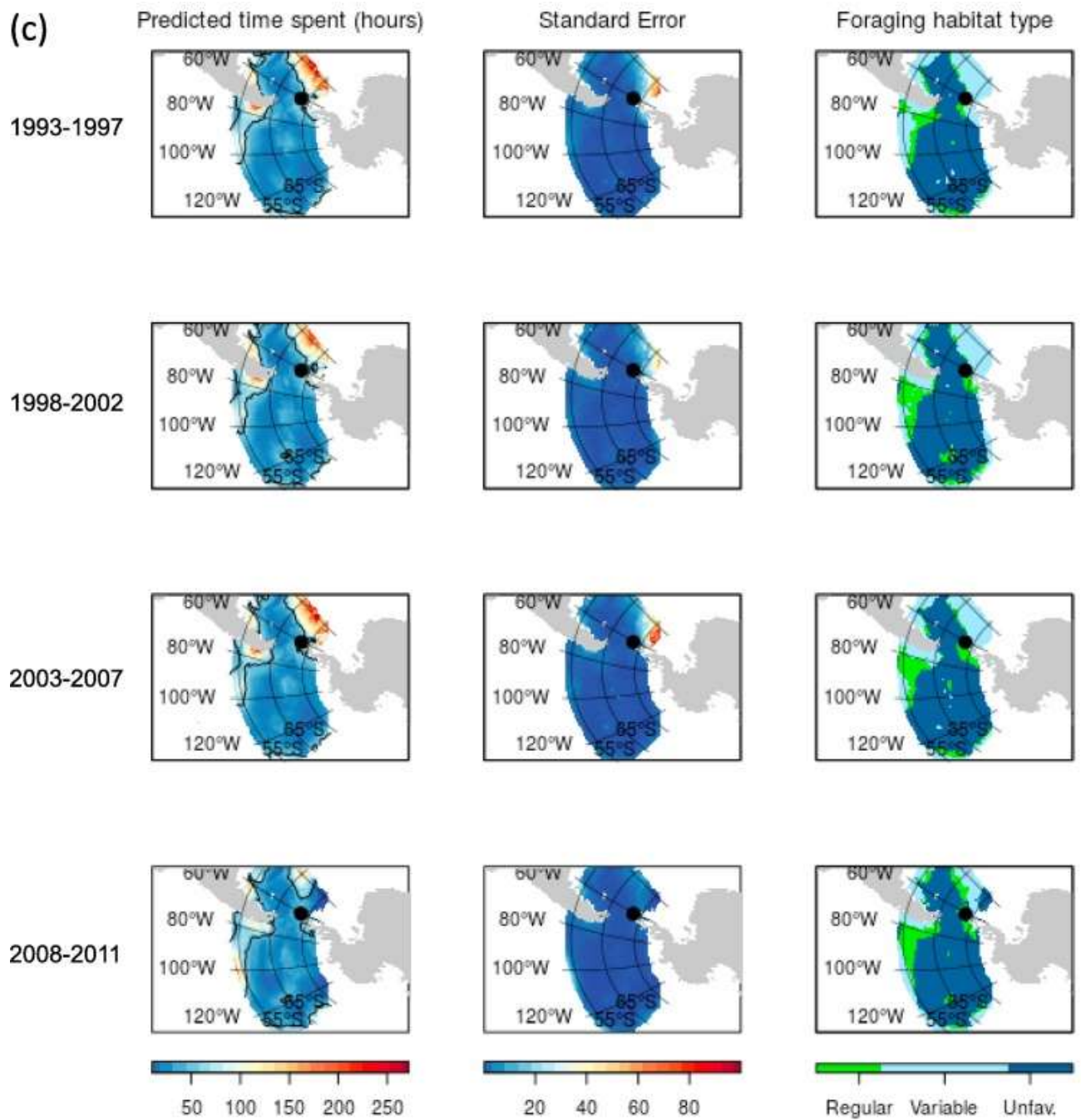
Fig. 3. Mean predicted time spent (hours), standard error (SE) and habitat suitability (foraging habitat type) for five-yearly periods between 1993 to current observations for female Antarctic fur seals from (a) Marion Island, (b) Bird Island and (c) Cape Shirreff during the non-breeding winter. Core foraging habitats (75% distribution areas) are shown in black lines. Black circles represent colony locations. Regular foraging habitat is observed annually (higher than 20 year average mean and low SE); variable foraging habitat is used by animals in some years (higher than 20 year average SE); Unfavourable foraging habitat is rarely used by animals (lower than 20 year average mean and SE).

the extreme east of the population's range, however the high associated SE suggests these predictions are not robust. The broad distribution of regular foraging habitat was consistent between 1993-2011 (Fig. 3b), with regular and unfavourable habitat changing by, on average, 3.1% (SD: ± 5.6) and 1.1% (SD: ± 1.3) per five years. Variable habitat displayed a constant decrease across the 20 years (Table 2).

Hindcasted *time spent* values at Cape Shirreff between 1993-2008 also revealed core foraging areas were broadly consistent across each five-year period and closely matched the observations from 2008-10 (Fig. 3c). Core areas included waters off the southwest of Chile extending west, the Patagonian shelf and waters around South Georgia. The SE of predictions was low across the spatial domain except for in the far southeast in the northern Weddell Sea. The distribution of regular foraging habitat around the Western Antarctic Peninsula and South Georgia shifted between 1993-2010. Overall, regular foraging habitat increased by 4.6% (SD: ± 5.3) every five years, while variable habitat decreased by 4.6% (SD: ± 5.4).

3.2. TEMPORAL VARIABILITY IN WINTER HABITAT USE

To assess temporal variability of core seal habitat we split the non-breeding winter into three periods: early, mid and late. At Marion Island, the spatial distribution of observed *time spent* showed clear variations in both latitude and longitude across the winter (Fig. 4, Supporting Information Fig. A2). Regions of relatively high use were located further south (south of 55°S) in early and mid winter than in late winter, following the expansion of sea ice (Fig. 4). Longitudinally distant areas, particularly to the far west of Marion Island (west of 20°E), were used more in mid and late winter. *Time spent* was consistently high to the east and west of the colony in relative close proximity throughout the winter. The Marion Island SDM with 'period' term
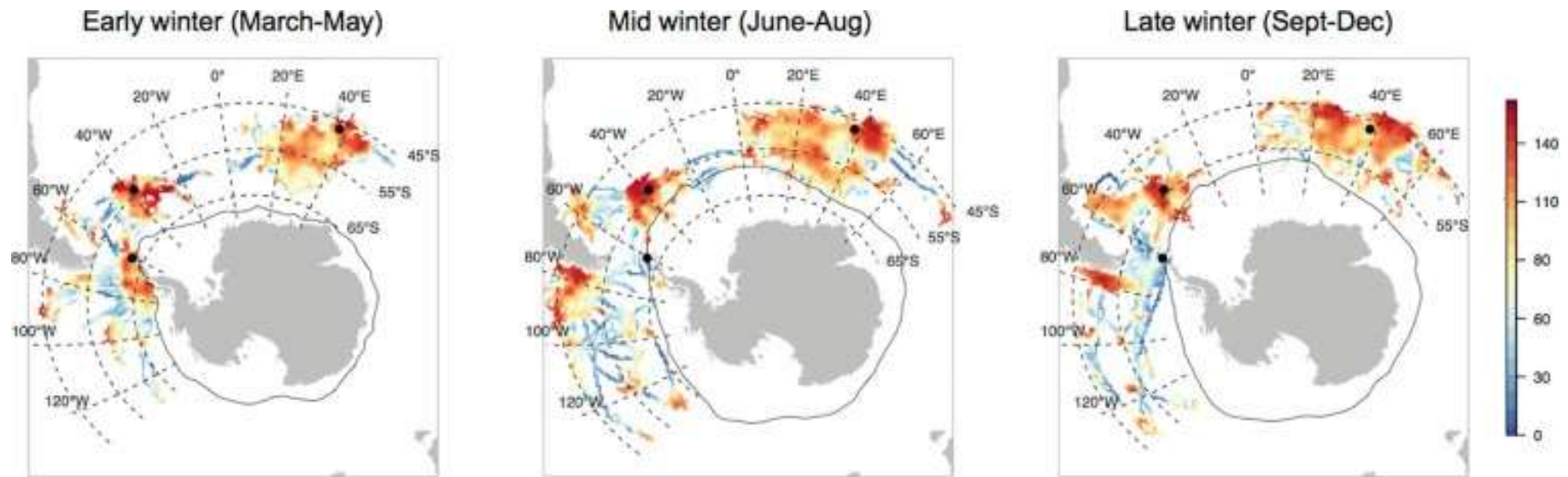
Fig. 4. Observed habitat use (time spent in hours per cell of a 0.6° × 0.6° grid) for 184 female Antarctic fur seals from Marion Island (2008–2013), Bird Island (2008–2011) and Cape Shirreff (2008–2010) (black circles) across three non-breeding periods: early (March–May), mid (June–August) and late (September–December). The average position of the sea ice edge for each period is shown by black lines.

had normally distributed model residuals and explained 65.4% of the deviance in the data. The model also had good predictive performance in cross-validation ($r^2 = 0.653$, RMSE = 17.71).

The spatial distribution of *time spent* for the Bird Island population was mostly concentrated in local waters around South Georgia and showed little temporal variability over the winter (Fig. 4, Supporting Information Fig. A2). There were, however, seasonal differences in the use of the Patagonian Shelf and associated shelf break, with *time spent* in this area increasing across the winter. The residuals of the SDM with 'period' term were normally distributed and model assessment suggested a good fit to the observations, explaining 57.5% of the deviance and having reasonable cross-validation predictive ability ($r^2 = 0.43$, RMSE = 30.32).

At Cape Shirreff, there was clear temporal variability in *time spent* values across the winter (Fig. 4, Supporting Information Fig. A2). In early winter, *time spent* was high close to the colony and south along the Western Antarctic Peninsula. Seals spent very little time in these areas as the winter progressed and sea ice formed (Fig. 4). Concurrently, *time spent* in waters off the southwest coast of Chile was low in early winter and increased in mid and late winter. Seals from Cape Shirreff also increased their longitudinal range further into the Southern Pacific Ocean throughout winter. The SDM with 'period' term had normally distributed residuals and explained 53.1% of the deviance in the data. The model had good predictive performance ($r^2 = 0.525$, RMSE = 22.9).

The models for each colony were interpolated across the spatial domain for each period of the winter. The predicted core habitat for all three colonies combined is presented in Fig. 1b-d.

3.3. OVERLAP WITH MANAGEMENT AREAS AND FISHING EFFORT

In early winter fur seal habitat overlapped significantly with CCAMLR subareas 88.3 and 48.1 along the Western Antarctic Peninsula, and subareas 48.2 and 48.3 around the South Orkney Islands and South Georgia respectively (Fig. 1b). Significant overlap was also observed in subarea 48.6 and divisions 58.7 and 58.6 around Marion and Crozet Islands respectively, and 58.4.4b south of Crozet Islands. In mid winter (Fig. 1c), core fur seal habitat in the South Atlantic sector was congruent with subareas 48.2 and 48.3. Substantial core habitat overlapped with subarea 48.6. In the Southern Indian sector, mid winter habitat was observed in divisions 58.7 and 58.6, and 58.5.1 and 58.5.2 around Iles Kerguelen and Heard Island. Significant overlap also occurred with divisions 58.4.4b and 58.4.3a south west of Kerguelen Island. In late winter (Fig. 1d), core habitat overlapped with subareas 48.2, 48.3 and 48.4 (around the South Sandwich Islands) in the Southern Atlantic sector. In the Southern Indian sector, core foraging habitat in late winter overlapped with division 58.6 and south to divisions 58.4.4a and 58.4.4b. During all three seasons substantial areas of core habitat occurred outside of the CCAMLR convention area, notably the Patagonian Shelf, the southern coast of Chile and pelagic waters extending west, and areas to the west of Marion Island.

The fishing effort in CCAMLR areas of significant spatio-temporal overlap with core seal habitat is presented in Fig. 1 and Table 3. In early winter (Fig. 1b), high fishing effort occurred in subareas 48.2 around the South Orkney Islands and 48.1 along the Western Antarctic Peninsula, at 1320 and 1125 fishing days respectively (Table 3). Fishing effort was also high, 858 days, in division 58.6 around the Crozet Islands. Fishing effort during mid winter (Fig. 1c) congruent to seal habitat was particularly high in subarea 48.3 around South Georgia at 4334 fishing days, and was

Table 3. The winter fishing effort of all fisheries operating in the CCAMLR Convention Area. Fishing effort is expressed as total fishing days during the winters of 2008-13 inclusive for each of the 19 CCAMLR subareas/divisions. Early winter = March-May, Mid winter = June-August, Late winter = September-December, Use by AFS = subareas/divisions that incorporated core Antarctic fur seal habitat at some period during winter.

Subarea/Division	Fishing effort			Use by AFS
	Early winter	Mid winter	Late winter	
Southern Atlantic (Area 48)				
48.1	1125	1053	237	early, mid
48.2	1320	798	22	early, mid, late
48.3	305	4334	1679	early, mid, late
48.4	264	50	0	early, mid, late
48.5	5	0	0	early, mid
48.6	297	40	110	early, mid, late
Southern Indian (Area 58)				
58.4.1	223	0	0	-
58.4.2	123	0	0	mid
58.4.3a	27	47	11	mid, late
58.4.3b	44	32	0	-
58.4.4a	0	8	10	early, mid, late
58.4.4b	49	93	46	early, mid, late
58.5.1	938	925	2389	mid
58.5.2	398	956	885	mid

58.6	858	396	420	early, mid, late
58.7	91	98	175	early, mid, late
Southern Pacific (Area 88)				
88.1	323	0	0	-
88.2	337	0	0	early, mid
88.3	25	0	0	early, mid

also high in subarea 48.2 (798 days, Table 3). In the Southern Indian sector, high mid winter fishing effort overlapped with seal habitat in subarea 58.5.1 (925 days) east of Iles Kerguelen (Table 3). During late winter (Fig. 1d), core fur seal habitat was congruent with high fishing effort in subareas 48.3 (1679 days) and division 58.6 (420 days, Table 3).

4. Discussion

4.1. BASELINE FORAGING HABITATS OF ANTARCTIC FUR SEALS

By hindcasting pre-existing SDMs we have provided estimates of the historical foraging habitats for three Antarctic fur seal populations in the Southern Ocean. This necessitated extrapolating in environmental space, which is inherently risky as, in this instance, there are no past observations to support predictions (Elith & Leathwick 2009). However, such extrapolation is necessary if we are to explore how currently used winter habitats might have changed over the past 25 years, a vital step if we are to consider how future change might further impact these populations; similar temporal transferability of SDMs has successfully being shown for albatross in the Southern Ocean (Louzao *et al.* 2013). There has been notable change over the last ~30 years to the winter physical ocean environment in the regions which today have relatively high time spent by female Antarctic fur seals. In particular, there were long term trends in SST, WIND and ICE during winter. The direction of trends varied regionally, signifying environmental change pressures are colony specific. In the Southern Indian sector, habitats used by Marion Island animals have undergone warming of surface waters and an overall weakening in wind speeds, while southern habitats have shown an increasing trend in sea ice concentration. In contrast, foraging habitats for the Bird Island and Cape Shirreff populations in the Southern Atlantic

sector have experienced an overall increase in wind speeds and a loss of sea ice concentration. Changes to SST varied, with some habitats warming while others have cooled. These observations are in broad agreement with more comprehensive studies of the wider Southern Ocean climate system (For a review see Mayewski *et al.* 2009).

It remains poorly understood how the biological component of Southern Ocean ecosystems will be affected by climate change. However, several studies have shown links between the physical effects of climate change and biological responses. For example, warming of waters and a shift towards positive phases of the Southern Annular Mode, the dominant mode of atmospheric variability in the Southern Ocean, is expected to lead to a deepening of the mixed layer depth and associated negative impacts for biological productivity (Sallée *et al.* 2010). Changes to water temperature and declines in sea ice are affecting the abundance, distribution and life cycle of prey species, such as Antarctic krill (*Euphausia superba*, Smetacek & Nicol 2005; Flores *et al.* 2012). Wind speed can also impact the distribution of prey (Pelland *et al.* 2014; Sterling *et al.* 2014), with stronger winds leading to increased turbulence and mixing which can drive prey deeper in the water column (Incze *et al.* 2001). Such changes could lead to an overall shift in the vertical distribution of prey, forcing seals to dive deeper and less frequently.

Despite obvious environmental changes, the hindcasting of likely historical distributions of foraging habitats revealed these to be relatively stable since 1993, particularly at Marion and Bird Islands. The population of Antarctic fur seals at both Marion Island and South Georgia has grown rapidly since harvesting in the 18th and 19th centuries (Payne 1977; Hofmeyr *et al.* 2006), although population growth has slowed or plateaued in recent years (Boyd 1993; Wege *et al.* 2016). Such rapid population recovery was probably facilitated by favourable conditions, namely

reduced competition for prey (Croxall *et al.* 1988), which in the case of the South Georgia population comprises the largest concentrations of krill in the Southern Ocean (Atkinson *et al.* 2008). However, we note that population growth has slowed in concert with environmental changes, particularly at South Georgia, suggesting that changes to the physical environment may, in part, be playing a role. Although this is difficult to disentangle from the population reaching carrying capacity, the carrying capacity of any population is not a fixed point and varies as the environment changes (Begon *et al.* 2006). At South Georgia, increases in ecosystem variability (driven by positive El Niño Southern Oscillation anomalies) and lower krill availability during the breeding season since 1990, have increased the fitness costs associated with breeding for females and resulted in significant changes to population structure and phenotypic and genetic variation (Forcada *et al.* 2008; Forcada & Hoffman 2014). Population-level changes such as these may affect the use of winter foraging habitat by animals in the future.

At Cape Shirreff, hindcasting showed that foraging habitats may have changed in recent decades, with a persistent expansion of regular regions with high time spent between 1993 and 2010. Increases were clearest around the Western Antarctic Peninsula and the South Orkney Islands towards South Georgia. These regions of the Southern Ocean have experienced some of the strongest warming on Earth, with increases in both air and ocean temperatures (Vaughan *et al.* 2003; Meredith & King 2005) concomitant with a reduction in sea ice (Stammerjohn *et al.* 2008). Indeed our results can link improved foraging habitat quality for Cape Shirreff animals to areas that have experienced ocean warming and a reduction of winter sea ice. Antarctic sea ice can present a barrier to marine predators lacking suitable adaptations, excluding them from an area (Ainley *et al.* 2003). Unlike other Antarctic pinnipeds, Antarctic

fur seals are not considered an ice obligate species and typically avoid areas of significant ice cover (see Fig. 4). The reduction of winter sea ice on the Western Antarctic Peninsula and waters south of South Georgia has therefore allowed foraging animals to access this previously unfavourable habitat. Similar climate-driven improvements in Southern Ocean habitat quality have been reported for wandering albatross (*Diomedea exulans*), with changes to wind patterns (Weimerskirch *et al.* 2012) and southern elephant seals (*Mirounga leonina*), whose population at Macquarie Island responds positively to reduced sea ice cover (van den Hoff *et al.* 2014).

The increase in habitat availability at Cape Shirreff is not reflected in recent population trends of the colony. Although the population has grown rapidly since re-colonisation in the late 1950's, pup production slowed by the early 2000's (Hucke-Gaete *et al.* 2004), with evidence of a population decline since (Schwarz *et al.* 2013). However, this is probably the result of top-down control by leopard seal (*Hydrurga leptonyx*) predation on pups, rather than bottom-up processes, and it is predicted that the population would increase in size if this pressure were removed (Schwarz *et al.* 2013). The expansion of winter foraging habitat reported here may, therefore, facilitate any potential expansion of this population.

4.2. TEMPORAL HABITAT USE AND IMPLICATIONS FOR MANAGEMENT

Spatio-temporally explicit SDMs were developed for the three Antarctic fur seal study populations which identified important habitat at several stages of the Southern Ocean winter, with core areas differing between early, mid and late winter, particularly at Marion Island and Cape Shirreff. Use of these habitats will ultimately be driven by prey availability and the temporal changes in diet reported for female

Antarctic fur seals during winter (Walters 2014) reflect this. The distribution of fur seals during winter is also influenced by the extent of sea ice, with animals being excluded from more southerly areas with the expansion of winter sea ice (see Fig. 4).

Appreciation of the changes in habitat use of marine animals throughout their annual cycle is necessary to inform a range of management measures such as the development of realistic ecosystem models, the design of marine protected areas and assessment of fisheries interactions. In the Southern Ocean, CCAMLR seeks to manage the ecological impacts of commercial harvests. A key component is monitoring the life-history parameters of select dependant predator species, one of which is the Antarctic fur seal, in the CCAMLR Ecosystem Monitoring Program (CEMP) (CCAMLR 2013a). The parameters measured in CEMP operate at various spatial and temporal scales (Kock *et al.* 2007) and may reflect changes in the ecosystem over days to months (Agnew 1997). Ultimately, demographic measures such as pup production in Antarctic fur seal is, in part, determined by environmental conditions and prey availability during the preceding winter/spring (Boyd *et al.* 1995). In order to effectively interpret the response of Antarctic fur seals in the CCAMLR context it is important to quantify habitat use and potential overlap with fisheries outside of the breeding season, when the majority of population monitoring currently occurs. The spatio-temporally explicit winter SDMs developed here are directly relevant to this management framework.

Female Antarctic fur seals from the three study populations foraged in 16 of the 19 CCAMLR subareas and divisions throughout the winter (Table 3). Core fur seal habitat coincided with high fishing effort in a number of these areas, suggesting there is a potential for operational interaction with some of the fisheries managed by CCAMLR. Toothfish (*Dissostichus* spp.) fisheries probably have minimal impact on

fur seals as toothfish are not a prey item and entanglement and by-catch of seals in long-lines is very rare. In contrast fisheries for icefish (*Champsocephalus* spp.) and krill do have the potential to have an impact if they are not well regulated as both fisheries target resources that are prey items for fur seals. Further, there has been incidental by-catch of Antarctic fur seals in CCAMLR managed fisheries (AFMA 2003; Hooper *et al.* 2005), but all krill fishing nets now have a mandatory seal exclusion device and there have been no reports of seal by-catch since their introduction (CCAMLR 2015c). Therefore, competition is the most likely interaction that Antarctic fur seals will have with some Southern Ocean fisheries.

Foraging habitat was relatively stable throughout the winter for Bird Island animals, with waters around South Georgia and the South Orkney Islands important habitat. Fishing effort was also consistently high in this area across the winter. Bottom-up forces have a substantial influence on the population of Antarctic fur seals at South Georgia, with the availability and predictability of a major prey source, Antarctic krill, a key factor (Reid & Croxall 2001). Indeed offspring production is strongly associated with krill size and abundance in a suite of predators from South Georgia including Antarctic fur seals, albatross and penguins (Croxall *et al.* 1999; Murphy *et al.* 2007). The Southern Ocean krill harvest is focussed around South Georgia, the South Orkney and South Shetland Islands in winter (see Croxall & Nicol 2004). The majority of female Antarctic fur seals from South Georgia in this study overlapped significantly with some areas of high fishing effort and our study animals did not migrate away from the region in winter, unlike some other species (Trathan *et al.* 2012). Our results suggest the potential for competition with fisheries during winter, which further strengthens the importance of on-going monitoring of the South Georgia fur seal population under CEMP and other science initiatives. Currently, the

total catch taken by the winter krill fishery at South Georgia is small at about 43,500 tonnes per annum (Trathan *et al.* 2014) thus, though the competitive effects of the fishery are generally low, our results highlight that there is the potential for this to increase should the regional climate continue to warm, or the winter krill fishery increase.

In the Southern Indian Ocean, core foraging habitats of the Marion Island population coincided with periods of high fishing effort in several regions, most notably between Marion and Crozet Islands and extending south. The productivity of this area is used by foraging predators from Marion Island (de Bruyn *et al.* 2009; Arthur *et al.* 2017). This region of the Southern Ocean is also the focus of finfish fisheries particularly for Patagonian toothfish (*Dissostichus eleginoides*), mackerel icefish (*Champsocephalus gunnari*) and grey rockcod (*Lepidonotothen squamifrons*) (CCAMLR 2013b), the latter two of which are potentially important prey in the diet of Antarctic fur seals in the Southern Indian Ocean (Lea *et al.* 2002; Walters 2014). Fishing effort was particularly high in early winter (March-May). The potential for competition with Marion Island fur seals is greatest in this post-breeding period. Female Antarctic fur seals invest resources in lactation at a greater rate than other otariid seals and can incur high fitness costs (Forcada *et al.* 2008). Subareas 58.6 and 58.7 concurrent with high fishing effort are important for females targeting a reliable foraging habitat in close proximity to the colony in order to recover body condition after the breeding season (Arthur *et al.* 2017). The current catch in these areas, however, consist mostly of Patagonian toothfish, which is not a species readily consumed by Antarctic fur seals. Although competition appears not to be an issue at present, any expansion of fisheries for other species into these areas warrants consideration of the importance of this habitat to fur seals at this time of year.

In late winter there is also the potential for competition with finfish fisheries east of Iles Kerguelen. The austral spring is an important period for females as it coincides with the increasing energetic demands of gestation after delayed implantation (Boyd 1996) and reproductive success in the coming summer can be linked to prey availability at this time of year (Boyd *et al.* 1995). It is, therefore, a critical time for the monitoring of potential fisheries competition. Although the use of this area by females from Marion Island appears minimal, the identification of this region as valuable foraging habitat by our models suggest that animals from geographically closer populations, such as Iles Kerguelen and Heard Island, where no non-breeding habitat information currently exist, may be more affected by any potential fisheries competition in this region. Our results are in broad agreement with Guinet *et al.* (2001), who used a similar probabilistic modelling approach and identified these areas as important foraging habitat for female Antarctic fur seals from Iles Kerguelen during the breeding season. Our findings extend this to suggest that areas east of Iles Kerguelen are also likely to be important habitat for animals from this population during the non-breeding season.

Our study of habitat use by Antarctic fur seals is based upon adult female dispersal and distribution. Fur seals, however, are highly dimorphic and male distribution during non-breeding periods is different from female distribution (Boyd *et al.* 1998; Sterling *et al.* 2014). Though less data exist on male over-winter distribution, they are more likely to spend their entire annual cycle within the CCAMLR convention area providing greater potential for overlap with the krill fishery. The differences in distribution of males and females may begin as early as the first year at sea (Kernaléguen *et al.* 2016). Given the differences in foraging ability observed between juvenile and adult Otariids (e.g. Lea *et al.* 2010) and the role that

juvenile survivorship has on population demographics (Baker & Fowler 1992; Fowler *et al.* 2006) the habitat use and ultimate survival of weaned Antarctic fur seal pups is likely to be particularly important for the species.

The core foraging habitats of all three populations in this study coincided with high fishing effort in certain management areas at different periods of the year, suggesting the potential exists for competition for prey resources between this species and Southern Ocean fisheries during the non-breeding season. Given recent proposals for a system of marine protected areas (MPAs) in the Southern Ocean (Delegations of Australia and France 2011; Delegations of Australia 2013; Delegations of New Zealand and the USA 2013) this information could be used in the design and evaluation of MPAs (see Halpern 2014). These may be static in nature (e.g. movements of Adelie penguins were used to justify, in part, the establishment of a high-seas MPACCAMLR 2009), or dynamic closures better suited to protecting shifting habitats (Hobday *et al.* 2013; Lewison *et al.* 2015) like those shown here for Antarctic fur seals.

Although CCAMLR adopts a precautionary and ecosystem-based approach to fisheries management, changes to the physical environment and developments in the fishing industry, such as the recent expansion of the krill fishery into more southern waters in winter due to a lack of sea ice (Nicol *et al.* 2012) have the potential to affect how dependant species, such as Antarctic fur seals, are impacted. The results of our study also show that substantial amounts of the foraging habitat of Antarctic fur seals does not fall within the CCAMLR Convention Area at all stages of the non/pre-breeding season. In particular the southern coast of Chile and associated pelagic waters extending west, the Patagonian Shelf and areas west of Marion Island were consistently important habitats throughout April to November. These areas have large

active fisheries (UN Food and Agriculture Organization 1997), in some cases bigger than those in the Southern Ocean, and are likely to be less well managed with respect to the impacts of commercial harvesting on predator populations compared with the ecosystem-based approach of CCAMLR. As animals from all three populations in this study consistently foraged outside the CCAMLR Convention Area during the non/pre-breeding period, it is worth noting that events or impacts occurring in these regions will be reflected in populations within the Convention Area, providing an important context for the interpretation of the CCAMLR Ecosystem Monitoring Program. Though substantial amounts of the foraging habitat for female Antarctic fur seals falls outside the CCAMLR Convention Area, both males and females remain highly dependent on habitat within the convention area pre- and post-breeding and will remain an important species for understanding how the marine ecosystem is changing.

Author contributions

BA, MAL, MH, PT and MG conceived the ideas and designed the study. BA, MB, NDB undertook fieldwork and data collection. BA, MH and MAL analysed the data. BA, MAL, MH and MG wrote the paper. All authors contributed critically to the drafts and gave final approval for publication.

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Data accessibility

GLS data are housed at Australian Antarctic Data Centre (http://data.aad.gov.au) for each colony: Marion Island (Lea *et al.* 2014a), Cape Shirreff (Lea *et al.* 2014b) and Bird Island (Lea *et al.* 2014c).

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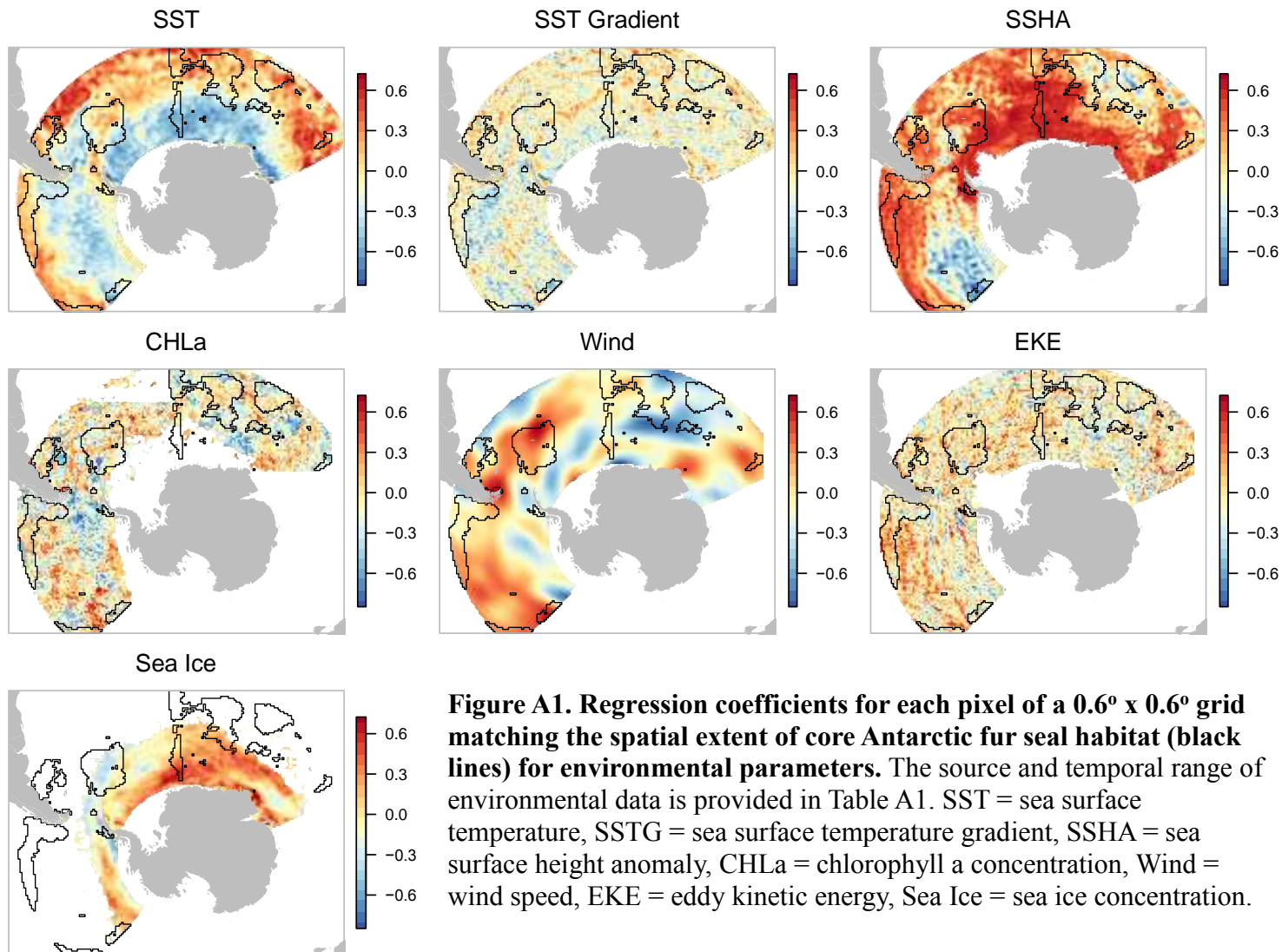Wood, S. (2006) *Generalized additive models: an introduction with R*. CRC press, Boca Raton, Florida, USA.

Supporting Information

Appendix A

Table A1. The source and temporal range of environmental predictor variables used in habitat models. Data are from the Australian Antarctic Data Centre (http://data.aad.gov.au)

Variable	Source	Available temporal range
Sea surface temperature (SST)	OISST	1982-2013
Sea surface temperature gradient (SSTG)	OISST	1982-2013
Sea surface height anomaly (SSHA)	AVISO	1993-2013
Sea surface height anomaly variance (SSHV)	AVISO	1993-2013
Chlorophyll a concentration (CHLa)	SeaWiFS	1997-2013
Wind speed (WIND)	NCEP/DOE AMIP-II	1979-2013
Surface currents (CURR*u* and CURR*v*)	AVISO	1993-2013
Eddy kinetic energy (EKE)	Derived from u and v current components*	1993-2013
Sea ice concentration (ICE)	NSIDC	1979-2013
Bathymetry (BATHY)	gebco_08	static

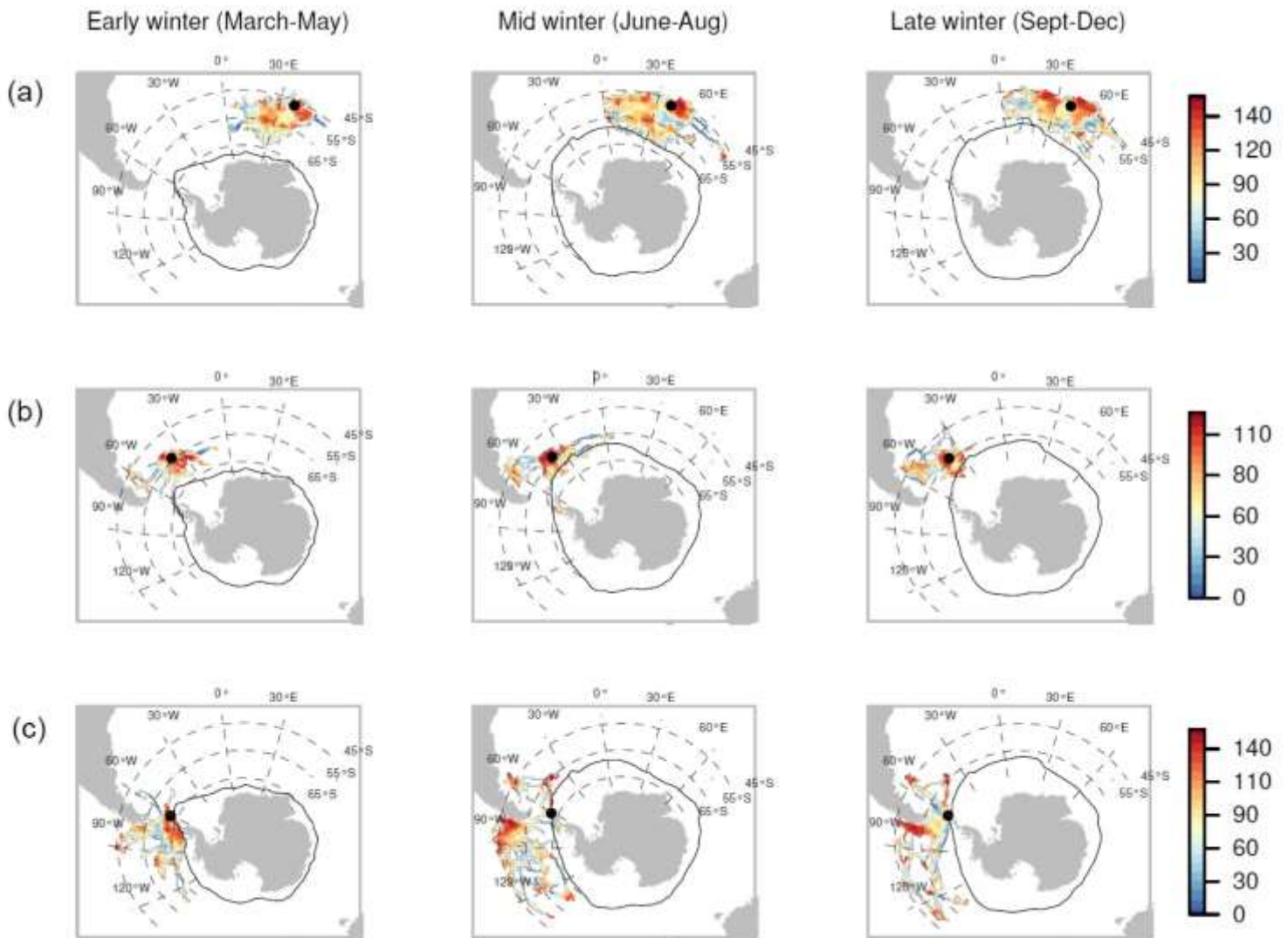*Eddy kinetic energy calculation: $EKE = \frac{1}{2} (CURRu^2 + CURRv^2)$

Figure A1. Regression coefficients for each pixel of a 0.6º x 0.6º grid matching the spatial extent of core Antarctic fur seal habitat (black lines) for environmental parameters. The source and temporal range of environmental data is provided in Table A1. SST = sea surface temperature, SSTG = sea surface temperature gradient, SSHA = sea surface height anomaly, CHLa = chlorophyll a concentration, Wind = wind speed, EKE = eddy kinetic energy, Sea Ice = sea ice concentration.

Figure A2. Observed habitat use (time spent in hours per cell of a 0.6° x 0.6° grid) for female Antarctic fur seals from **(a)** Marion Island (2008-2013), **(b)** Bird Island (2008-2011) and **(c)** Cape Shirreff (2008-2010) across three non-breeding periods: early (March-May), mid (June-August) and late (September-December). Respective colony locations are indicated by black circles and the average position of the sea ice edge for each period is shown by black lines.