Winter habitat predictions of a key Southern Ocean predator, the Antarctic fur seal (*Arctocephalus gazella*)

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Abstract

Quantification of the physical and biological environmental factors that influence the spatial distribution of higher trophic species is central to inform management and develop ecosystem models, particularly in light of ocean changes. We used tracking data from 184 female Antarctic fur seals (*Arctocephalus gazella*) to develop habitat models for three breeding colonies for the poorly studied Southern Ocean winter period. Models were used to identify and predict the broadly important winter foraging habitat and to elucidate the environmental factors influencing these areas. Model predictions closely matched observations and several core areas of foraging habitat were identified for each colony, with notable areas of inter-colony overlap suggesting shared productive foraging grounds. Seals displayed clear choice of foraging habitat, travelling through areas of presumably poorer quality to access habitats that likely offer an energetic advantage in terms of prey intake. The relationships between environmental predictors and foraging habitat varied between colonies, with the principal predictors being wind speed, sea surface temperature, chlorophyll a concentration, bathymetry and distance to the colony. The availability of core foraging areas was not consistent throughout the winter period. The habitat models developed in this study not only reveal the core foraging habitats of Antarctic fur seals from multiple colonies, but can facilitate the hindcasting of historical foraging habitats as well as novel predictions of important habitat for other major colonies currently lacking information of the at-sea distribution of this major Southern Ocean consumer.

Key-words: Foraging behaviour, geographical distribution, habitat model, pinniped, prediction, tracking.

1. Introduction

Information on the spatial distribution of marine predators is fundamental to understanding the structure and function of their ecosystems and is ultimately driven by the availability of prey resources that are heterogeneously dispersed in space and time (Russell et al., 1992). The abundance of marine prey is intrinsically linked to physical and biological oceanographic properties, allowing us to relate the distribution and responses (such as breeding success) of higher trophic species with the fundamental bio-physical aspects of their environment (e.g. Friedlaender et al., 2006; Reid and Croxall, 2001). Quantifiable understanding of these factors is necessary to inform and appraise management decisions such as defining marine protected areas (Hyrenbach et al., 2000), fisheries management and by-catch mitigation measures (Burger and Shaffer, 2008), as well as for the development of accurate ecosystem models to assess the effects of future environmental changes.

The Antarctic fur seal (*Arctocephalus gazella*, Peters, 1875) is a highly mobile marine predator that inhabits an extremely dynamic environment, the Southern Ocean. Antarctic fur seals are major consumers in the Southern Ocean ecosystem, in particular of krill (Croxall et al., 1985) often competing with other predators such as penguins for this resource (Barlow et al., 2002; Blanchet et al., 2013). Antarctic fur seals breed at 10 major sites in the Southern Ocean across their circumpolar range (Shirihai, 2002), spanning latitudes from the northernmost colony at the Crozet Islands (46°25’S), north of the Polar Front, to the southernmost at the South Shetland Islands (62°27′S), within the zone of winter sea ice. The at-sea habitat use of Antarctic fur seals reflects these geographical differences and the species exhibits a diverse foraging ecology across their range, with highly flexible summer foraging behaviours within and between colonies associated with local environmental conditions (Lea et al., 2006) and differences in prey (Boyd et al., 1994; Lea et al., 2008; Staniland et al., 2010).

During the winter, non-breeding animals are free from the constraints of central place foraging (Orians and Pearson, 1979) associated with provisioning their offspring. Consequently, female Antarctic fur seals can make wide-ranging migrations (Boyd et al., 2002) of up to eight months. Moreover, the Southern Ocean in winter is both physically and biologically distinct from the summer, with the growth of sea ice, decline in primary productivity due to decreased irradiance and temperature (Clarke, 1988; Mitchell et al., 1991) and a deeper mixed-layer depth because of strong winds (Sakshaug et al., 1991), being major distinctions. Consequently, foraging animals, and their prey, can be expected to behave differently during this time. Female Antarctic fur seals are also gestating during winter (Boyd, 1996) requiring them to make judicious foraging choices to maximise their energy intake in the pre-breeding period. Recent studies of the winter migrations of female Antarctic fur seals show they utilise a variety of habitats during this time, occupying all inter-frontal zones from pole-ward of the Antarctic Circumpolar Current, including ice associated waters, to north of the sub-Antarctic Front, incorporating both shelf and pelagic habitats (Boyd et al., 2002; Staniland et al., 2012).

The variety of foraging habitats utilised by Antarctic fur seals during the winter is reflected in their diet, with differences in the trophic position of their prey between the various inter-frontal zones, both within and between individuals (Walters, 2014). Some female fur seals are also highly faithful to winter foraging grounds returning to the same broad foraging area annually, presumably because of an increased energy acquisition associated with these habitats over the long-term (Arthur et al., 2015). The diversity of habitats used by Antarctic fur seals during the winter suggests that breeding colony location is a key factor in determining the suite of habitat types available for foraging (Mary-Anne Lea, unpublished data). However, despite being a major secondary consumer in the Southern Ocean, the at-sea behaviour of Antarctic fur seals outside the breeding season remains poorly understood. In particular, little is understood about the relationships between marine characteristics and foraging behaviour and how animals from different populations respond to these factors.

Habitat models (or Species Distribution Models) can assist with this process and are often used to describe the environmental drivers of species distribution patterns, providing useful ecological insights (Elith and Leathwick, 2009). Ultimately, they may be used to make predictions of species distributions in un-sampled areas or under changing environmental conditions, and have been employed across a variety of taxa, scales and environments using a range of methodologies (Guisan and Zimmermann, 2000). The fundamental information on the distribution of marine predators that is needed to build such models is often provided by telemetry studies. However, these studies are often restricted to a single site or season. For Antarctic fur seals, Guinet et al. (2001) developed a probabilistic model for the distribution of diving activity of lactating seals at Îles Kerguelen, which predicted where animals should concentrate their foraging based on the oceanographic conditions within that year. The authors note that studies conducted over several years will provide further insights into the effects of oceanographic conditions on the foraging ecology and at-sea distribution of this, and other, marine predator species.

Here, we examine the at-sea distribution and foraging habitats of female Antarctic fur seals from three breeding colonies across multiple inter-breeding periods in the Atlantic and Indian sectors of the Southern Ocean. The study aims to: (1) identify important foraging habitats for Antarctic fur seals during the non-breeding, winter season, (2) describe the environmental factors that characterise these areas and compare these relationships between animals from three major breeding populations and (3) develop predictive models for foraging habitat.

2. Materials and methods

2.1. Study sites and instrumentation

The study was conducted at three Antarctic fur seal breeding colonies: Marion Island (46°54’S, 37°44’E, Prince Edward Islands), Bird Island (54°00’S, 38°03’W, South Georgia) and Cape Shirreff (62°27′S, 60°47′W, South Shetland Islands) (Fig. 1). At Marion Island, the study was undertaken over five years between 2008 and 2013, at Bird Island for four years between 2008 and 2011 and at Cape Shirreff for three years between 2008 and 2010. Adult females were captured towards the end of lactation between February and April and were instrumented with a global-location sensing (GLS; British Antarctic Survey, Cambridge UK) logger for the duration of their winter migrations. Seals were recaptured and instruments recovered at the start of the following breeding season in November-December when pregnant females return to the colony to pup. Several animals were recaptured in subsequent years. Animal handling, GLS logger architecture, attachment and calibration methods are detailed in Arthur et al. (2015) provided in Supporting Information S1.

2.2. Tracking datasets

Locations were produced from the raw light and temperature data from GLS loggers following the Bayesian approach of Sumner et al. (2009) using the R software (R Core Team, 2014) package ‘tripEstimation’ (Sumner and Wotherspoon, 2010). In summary, two location estimates per day (dawn and dusk) were produced from the posterior mean for each twilight period that were summarised from the accepted Markov Chain Monte Carlo (MCMC) samples. Full details of geo-location model design and implementation are presented in Supporting Information S2. Seals undertook between 1-9 forging trips per winter with the average ± SD being 2.2 ± 1.5 at Marion Island, 2.5 ± 1.6 at Bird Island, while all animals at Cape Shirreff undertook a single trip. For animals making multiple foraging excursions from their colony, tracks were split into individual trips and analysed independently. Individual trips were identified in the raw light data, with haul-outs typified by distinctly messy light curves resulting from the animal periodically shading the light sensor while on land. Winter foraging trips encompassed the first post-weaning excursion (typified by a marked increase in duration from short trips during lactation) to the animal’s return to the colony the following breeding season. Between 2008-13, 184 GLS tags were recovered from post winter migrations across the three colonies (Table 1). Unprocessed GLS data are publicly available from the Australian Antarctic Data Centre (http://data.aad.gov.au) for each site: Marion Island (Lea et al., 2014a), Bird Island (Lea et al., 2014c) and Cape Shirreff (Lea et al., 2014b).

2.3. Habitat models

Models were constructed to explain the spatial distribution of Antarctic fur seal habitat use during the winter. The mean time spent in each cell (total time spent divided by the number of seals visiting each cell) of a 60 km x 60 km grid consistent across the spatial extent of locations (Table 1) was calculated for the period of study to quantify habitat use, hereto referred to as *time spent*. A grid of this resolution was chosen to match the error uncertainty surrounding geo-location estimates, which is shown to be 70 ± 35 km for an Antarctic fur seal carrying GLS and Argos tags simultaneously (Mary-Anne Lea, unpublished data). Time spent is a proxy for foraging effort as animals are likely to spend more time in an area which they are actively exploiting than when travelling between foraging areas (Barraquand and Benhamou, 2008; Kareiva and Odell, 1987). Time spent was a continuum from low to high use and can be considered a “usage” approach, being similar to kernel density analysis often applied to tracking data, rather than as a binary presence-absence response contrasting areas where animals did go with areas that they didn’t go. Three winter habitat models were generated: one for each colony with data pooled across all available years. Prior to developing these models, an assessment of the adequacy of the sample size at each colony was undertaken. We assessed the amount of new information (i.e. grid cells) arising from the inclusion of each additional individual seal (averaged over 100 permutations), providing an estimate of the minimum number of individuals needed to adequately represent the spatial distribution patterns of animals from each colony.

2.3.1. Environmental parameters

A suite of environmental variables that potentially influenced time spent was included in models to characterise fur seal habitat. Variables were chosen for a priori reasons based on our understanding of the nature of the variables and how they relate to the biology of the seals. Variables included static parameters: bathymetry (BATHY) and distance to colony (d2col) and dynamic parameters: sea surface temperature (SST), sea surface height anomaly (SSHa), chlorophyll a concentration (CHLa), wind speed, surface current magnitude (CURR) and eddy kinetic energy (EKE). Variability of sea surface height anomaly (SSHV) and the gradient of sea surface temperature (SSTG) were also included (Fig. 1). The source, spatial resolution and oceanographic significance of environmental variables are provided in Table A1. Environmental data were extracted for each pixel of the spatial domain at weekly intervals spanning the temporal range of location data at each colony. The grid based approach aggregated tracking data over multiple years, so weekly maps were averaged to produce one mean parameter value per cell for the period of study (in the case of SSHV variance was calculated) to create a temporal climatology (Sumner et al., 2003). These climatologies allow investigation of the influence of environmental factors on seal habitat use across broad spatial and temporal scales. All variables were re-interpolated across a 60 km x 60 km grid to match the time spent response data. All data, including environmental predictors and time-spent response, were then re-projected to Lambert azimuthal equal-area projection. Environmental data were available from the Australian Antarctic Data Centre and extracted using the R package ‘raadtools’ (Sumner, 2015).

2.3.2. Model design and predictions

Generalized additive models (GAMs) were fitted to the relationship between time spent and environmental predictors. To determine the most appropriate error structure, a comparison was made between Gaussian models with an identity link, log-transformed Gaussian with identity link, and Gamma with a log link models. Log-likelihood and Akaike’s Information Criterion (AIC) scores adjusted to account for transformation were used for model comparison and to determine the most appropriate error structure. The distribution of environmental predictors was examined and data were log-transformed where appropriate to meet the assumptions of normality. For numerical stability, predictors were scaled and centred to account for the considerably different scales of measurement. Highly correlated predictor variables (Pearson's $r > 0.9$) were excluded from the models. Model selection was undertaken using the maximum-likelihood approach to minimise the AIC. Models including all combination of variables were compared and ranked by their Akaike weight (*w*AIC) to represent the relative likelihood of each model.

To account for individual variability in the response term, it is possible to include a random term in the GAM framework (Wood, 2006). However, such models are computationally demanding and potentially problematic for smaller relative sample sizes (Raymond et al., 2014), so standard GAMs were utilised. The influence of individual variability was instead reduced by using the average value of time spent across individuals in each cell. A further problem arises with tracking data that are often spatially auto-correlated, which can lead to violations of the assumption of independence of residuals. We therefore included a spatial autocorrelation structure in all models (Dormann et al., 2007).

Model performance was evaluated by assessing model fit and predictive performance. Model fit was indicated by the percent deviance explained and by checking model residuals. The predictive performance of models was assessed by calculating the root mean-squared error (RMSE) using a k-fold cross-validation procedure. Grid cells were randomly assigned to one of 10 folds where models were trained on nine folds and tested on the remaining one, with each fold withheld in turn. The RMSE (expressed in the same units as the response) was aggregated across the 10 sets of results. The best model for each population was then fit on the unscaled and uncentred environmental predictor variables with the sole purpose of aiding the interpretability of the smoothed relationships on meaningful scales. Lastly, validated models were used to predict winter habitat use of fur seals by interpolating across the entire spatial domain of the locations observed for each colony. All analyses were conducted in R 3.2.0 (R Development Core Team).

3. Results

3.1. Distribution of time spent in area

Between 2008-13, a total of 320 foraging trips and 83,796 location estimates were observed for 184 female Antarctic fur seals during the austral winter. At Marion Island, 54,051 locations from 227 trips were available for 119 female seals with 12,328 locations from 56 trips and 28 seals at Bird Island, and 17,417 locations across 37 trips collected for 37 animals from Cape Shirreff (Table 1, Fig. A1). For Marion Island, the cumulative information curve showed that the number of newly visited grid cells arising from the inclusion of each additional animal asymptotes at approximately 50 individuals (Fig. 2c), indicating we had an adequate sample to accurately represent the spatial use patterns of the population. The curve for Bird Island closely matched that of Marion Island, however it failed to level out completely, suggesting that additional animals would better represent the distribution patterns of this population. Similarly, at Cape Shirreff, 37 individuals were observed and although the curve is beginning to asymptote, it failed to level out entirely (Fig. 2c), indicating a greater number of animals are needed to more fully characterise the variability in habitat use.

The distribution of time spent for Marion Island fur seals indicated that animals utilised a diversity of areas during their winter migrations (Fig. 3). Of prominent use were areas located approximately 100-800 km to the north and east of Marion Island associated with the Del Cano Rise, and pelagic waters to the west of the island between 20-30°E. Time spent values were also high in several areas to the south of the colony at approximately 55°S as well as other locations at the extreme east and west of the population’s range, notably around Bouvet Island and east of Iles Kerguelen. Seals spent relatively little time in local waters within several hundred kilometres to the west and south of Marion Island, suggesting animals transited through these areas to reach distant foraging grounds.

For the Bird Island population, time spent was concentrated mostly in local waters within approximately 300 km of South Georgia, particularly to the northwest of the colony (Fig. 3). There was a further area of high usage to the south of South Georgia. Additional high-use areas were off the Patagonian coast of South America, east of South Georgia towards the Scotia Arc and South Sandwich Islands and on the continental shelf along the western Antarctic Peninsula.

At Cape Shirreff, the areas of high usage were along the southern coast of Chile associated with the shelf-break and pelagic waters further west of this region (Fig. 3), and waters to the west of South Georgia. Time spent values were high along the Patagonian shelf-break and several distant pelagic areas at the western extent of the population's range (westward of 110°W longitude) resulting from individual animals concentrating their efforts in these regions for extended periods.

3.2. Environmental characteristics of high-use areas

Across the spatial distribution of all three populations, EKE and CURR oceanographic variables were highly correlated ($r > 0.95$). CURR was subsequently excluded from analyses, leaving nine predictor variables available for model build. For the Marion Island population, the best model explaining mean time spent in a grid cell included all variables but SSTG (wAIC = 0.691; Table 2) fit to a Gamma error structure. Model residuals were normally distributed and the model explained 73.3% of the deviance in the data and had good predictive performance (r^2 = 0.704, RMSE = 14.30). Omitting the spatial autocorrelation term from the model still produced good model fit (r^2 = 0.413, RMSE = 19.93), suggesting the broad relationships between time spent and environmental variables were robust. The strongest relationships between foraging effort and the seals' environment were observed with Wind, SST, SSHV and d2col. Antarctic fur seals from Marion Island spent more time, on average, in areas of higher wind speeds (>12 $m.s^{-1}$) with greater

SSHV. Seals were found in water temperatures that were either colder (~0^{o}C) or warmer (between 6^{o}C and 10^{o}C) than average and areas that were further (>1500 km) from the colony (Fig. 4a).

The best model for the Bird Island population was a reduced Gamma model excluding CHLa and SSHV (*w*AIC = 0.355; Table 2). Model assessment suggested a good fit to the observed data with the model explaining 85.3% of the deviance in the data and having good predictive performance (r^2 = 0.828, RMSE = 13.24). Model performance was good when the spatial autocorrelation term was excluded (r^2 = 0.591, RMSE = 19.76). The clearest relationships with time spent were with Wind, BATHY and d2col. These indicated that cells close to the colony (<500 km), with shallow relative water depths (<2000 m) and with lower wind speeds (<10 $m.s^{-1}$) had high mean time spent values (Fig. 4b).

At Cape Shirreff, the best model explaining time spent was a Gamma model excluding SSTG and BATHY predictor terms (*w*AIC = 0.594; Table 2). Model residuals and cross validation indicated the model was a good fit to the observations, explaining 72.5% of the deviance in the data (r^2 = 0.701, RMSE = 15.63). Model performance was good when the spatial autocorrelation structure was omitted (r^2 = 0.461, RMSE = 20.55). The strongest relationships between mean time spent and environmental predictors were for d2col, Wind and SST. The smoothed relationships indicated that seals from Cape Shirreff spent more time in areas of colder (between -1^{o}C and 5^{o}C) or warmer (>10^{o}C) than average waters and with high relative wind speeds (>10 $m.s^{-1}$) when closer to the colony (Fig 4c).

3.3. Predicting important winter foraging habitat

The habitat models were interpolated across the entire spatial domain of observations from each population. The resultant distribution maps of winter foraging habitat are shown in Figure 3. For all three populations these predictions closely matched the time-spent observations recorded in this study, giving us further confidence in the ability of the models to make realistic predictions of important foraging habitat for Antarctic fur seals in the different oceanic basins. For seals from the Marion Island colony, the model successfully predicted the major areas of observed time spent, being those regions to the east, west and far south of the colony. At Bird Island, likely important foraging habitat was identified in waters local to South Georgia and extending south, as well as on the Patagonian Shelf, north of the Scotia Arc and the West Antarctic Peninsula, closely matching observations. Newly predicated habitat was located north of Tierra del Fuego (southern tip of South America) and at the extreme eastern edge of the range of tracked animals, however, we note this is driven by observations from a single animal only. The Cape Shirreff model predictions also closely matched the observations, with the model identifying the three major focal areas for animals from this population: the southern Chilean coast, the Patagonian Shelf break and around South Georgia. Notably, additional important foraging habitats were predicted for coastal waters on the Patagonian Shelf and oceanic waters around 100°W longitude at the northern extent of the population's range, which were areas with no previous observations.

Predicted important foraging habitats were not wholly distinct between the three populations, with clear overlap of some areas (Fig. 3). Seals from Cape Shirreff and Bird Island in particular, have considerable overlap in their predicted use of habitats around South Georgia, along the Patagonian Shelf and, to a lesser degree, waters of the western Antarctic Peninsula. Important foraging habitat around Bouvet Island in the Southern Atlantic sector is also likely to be shared by the Bird and Marion Island populations.

4. Discussion

Our study considers time spent as a proxy for foraging effort in Antarctic fur seals. Residence time is a suitable proxy as an animal is likely to spend more time in an area that it is actively exploiting (area-restricted search) than when travelling between foraging areas (Barraquand and Benhamou, 2008) and several studies have shown high relative residence times to be associated with increased dive effort and food intake in marine predators (Cotté et al., 2007; Thums et al., 2008), including Antarctic fur seals (Arthur et al., 2016). We therefore refer to foraging habitat and effort henceforth.

By using tracking data from multiple sites in the Southern Ocean across several years this study has revealed the broadly important foraging habitats, and the environmental conditions that characterise these, for female Antarctic fur seals during the poorly studied winter period. During that time, when animals are free to range widely, there are several habitats that are important for seals. The performance of habitat models was good, with predictions interpolated across the spatial domain of each population closely matching the observed data. The models also identified several novel areas of importance where no animals had been observed, particularly for the Cape Shirreff population. The cumulative information analysis suggested the minimum number of animals needed to adequately characterise the spatial use patterns of this population was not achieved, unlike at Marion Island where little novel habitat was predicted. We are therefore confident in the ability of the habitat models to make realistic predictions of the foraging habitat for this species.

Habitat models can perform well in characterizing the distribution of species within their current range and interpolation is generally reliable providing data and model design are reasonable (Elith and Leathwick, 2009). Habitat modelling has been used to quantify species-environment relationships and predict the distributions of a variety of taxa including terrestrial and aquatic plant species, terrestrial animal species, fish, plant communities, vegetation types and biodiversity (For reviews see Guisan and Thuiller, 2005; Guisan and Zimmermann, 2000). More recently, habitat models have been applied to marine species, including highly mobile top predators in an effort to identify critical oceanic habitats (e.g. Block et al., 2011) including for the Southern Ocean (Hindell et al., 2011; Raymond et al., 2014).

For the three Antarctic fur seal populations in this study, distinct foraging areas were identified for the winter period. At Marion Island, core foraging areas were contiguous with the Del

Cano Rise, a prominent bathymetric feature associated with the development of eddies and spring/summer phytoplankton blooms (Pollard et al., 2007; Venables et al., 2007) known to be utilised by foraging predators from Marion Island (de Bruyn et al., 2009). Further core habitat was to the west of the colony and south towards the Polar Front, a region of focus for several apex predator species because of the predictable distribution of prey such as mesopelagic fish (Bost et al., 2009). At Bird Island, core habitat was located in the productive waters around South Georgia and downstream, where zooplankton biomass is approximately four to five times higher than in other typical Southern Ocean areas (Atkinson et al., 2001), as well as on the Patagonian Shelf which is an important winter foraging region for other predators from South Georgia such as white-chinned petrels (*Procellaria aequinoctialis*, Linnaeus, 1758) (Phillips et al., 2006). These results broadly match those of the only other studies of the winter movements of Antarctic fur seals from South Georgia (Boyd et al., 2002; Staniland et al., 2012). For Antarctic fur seals from the South Shetland Islands, important habitat was located off the Chilean coast proximate to the high-primary productivity, cold Humboldt Current system and associated upwelling (Daneri et al., 2000) as well as the Patagonian Shelf break and around South Georgia.

The use of core foraging areas is ultimately driven by prey availability. Unfortunately, direct measurements of prey distribution have poor spatial and temporal coverage in the Southern Ocean and regional-scale models therefore rely on environmental proxies that characterise ocean processes related to prey distribution (Bost et al., 2009). Nonetheless, investigation of proximate drivers can aid in understanding the bio-physical properties of habitats. The environmental parameters in this study provide indices, effectively summarising the environment across years. Consequently, this limits the inferences that can be made, precluding the investigation of fine-scale spatial or temporal regional relationships. Any relationships that are identified, however, are likely to be broad and generally robust. Although the relationships between foraging effort and environmental parameters differed between populations, the principal predictors in habitat models were wind speed, sea surface temperature, distance to colony, bathymetry and sea surface height variability.

Wind speed contributed strongly to all three models. Antarctic fur seals from Marion Island and Cape Shirreff foraged more in windier areas, while seals from Bird Island foraged in areas with low to moderate wind speeds, as was observed for female northern fur seals (*Callorhinus ursinus*, Linnaeus, 1758) (Sterling et al., 2014), a northern hemisphere analogue for Antarctic fur seals. Wind strength and associated winter storms can impact the dispersal routes of predators (Lea et al., 2009) and the vertical distribution of biomass, with prey driven deeper by the increased mixing and turbulence resulting from higher wind stress (Incze et al., 2001). Seals from Bird Island, which feed largely on lower trophic level prey such as krill (Reid and Arnould, 1996), foraged more in areas of reduced wind speeds where prey fields may be higher in the water column and therefore more accessible. Conversely, at Marion Island and Cape Shirreff, seals preferred windier areas. Marion Island animals, which feed mainly on mesopelagic fish and squid in winter (Walters, 2014) also foraged more in areas with higher eddy kinetic energy. Wind is important to the vertical distribution of biomass in mesoscale eddies, with zooplankton distribution typically deeper under high wind events (Mackas et al., 2005). Despite high winds impacting the vertical distribution of biomass the aggregation of prey in eddy features such as those along the South West Indian Ridge around Marion Island (Ansorge and Lutjeharms, 2005) makes them important areas to foraging predators (Nel et al., 2001).

Habitat accessibility was also an important determinant of foraging habitat, with animals typically foraging less in areas that were relatively distant from breeding colonies, likely because of the energetic costs associated with travel. The exception was at Marion Island, were animals foraged more in distant areas. Sea surface temperature contributed highly to habitat models for Marion Island and Cape Shirreff, with animals decreasing their foraging effort in areas of average temperatures and preferring relatively cold or warmer waters. Although the use of water masses with certain temperatures by foraging predators can indicate preferences for productive oceanic features such as fronts (e.g. King penguins and the Polar Front; Péron et al., 2012), temperature is inherently coupled with latitude in the Southern Ocean and may simply be a product of how far north or south seals travelled during their wide-ranging migrations. Seals from Marion Island foraged more in areas of elevated average chlorophyll-a concentration, supporting observations for this species during the summer season at Kerguelen Island (Guinet et al., 2001). The habitat model for Bird Island showed a strong positive relationship with bathymetry, indicating seals preferred to forage in the shallower waters (<2000 m) of South Georgia and the Patagonian Shelf (Fig 1) where they feed on neritic prey (Walters, 2014).

The availability of important foraging habitats to Antarctic fur seals varies throughout the winter and usage of the major habitats identified here will not be consistent throughout the winter. If the non-breeding winter season is divided into three periods: early winter (March-May), mid-winter (June-August) and late winter (September-December), there are obvious differences in habitat availability. At Marion Island, seals had a reduced longitudinal range in early winter relative to mid or late winter (Fig. 2a) due to their recent departure from the colony. Seals utilised more southerly regions in early and mid-winter, shifting their distribution north in late winter (Fig. 2b), where foraging habitats east and west of the colony are likely to be exploited. At Bird Island, there were no significant variations in latitudinal range across the season (Fig. 2b). Fur seals from Cape Shirreff displayed a notable latitudinal shift in distribution across the winter, utilising areas between 60-65°S in early winter and more northerly habitats around 45-55°S as winter progressed (Fig. 2b).

The accessibility and use of foraging habitat can vary in response to factors including environmental conditions, prey availability, competition, predation risk, breeding status and age (Field et al., 2005; Heithaus and Dill, 2006; Nakano, 1995; Nordstrom et al., 2013; Weimerskirch et al., 1993). Of particular importance, is the reproductive cycle, with the early post-breeding period a critical time for recovering body condition after the extended lactation of otariid seals, which is energetically costly (Pitcher et al., 1998). Although animals are released from the constraints of parental care and free to travel farther during this time (Lowther et al., 2014), predictable and profitable habitat in close proximity to breeding colonies, such as those to the east of Marion Island, around South Georgia and the Antarctic Peninsula, will be critical for fast energy acquisition. For marine predators lacking specialised adaptations, the growth of winter sea ice can represent a barrier excluding them from an area (Ainley et al., 2003). Although some Antarctic fur seal females are known to utilise sea-ice habitats during winter (Mary-Anne Lea, unpublished data), they are not considered an ice-obligate species and are mostly absent from areas of significant ice cover. Consequently, the availability of southerly habitats to fur seals, particularly around the Western Antarctic Peninsula and south of South Georgia, where krill is a significant dietary component (Walters, 2014), is restricted to the early winter prior to the growth of sea ice (Fig. 2a). As ice cover excludes seals from southern regions in mid to late winter, more northerly habitats are increasingly utilised, especially for animals from Cape Shirreff where areas off the Chilean coast and around South Georgia and the Patagonian Shelf are important. We suggest that habitats close to breeding colonies and those that will be covered by winter sea ice are critical immediately after seals depart the colony in April-May, whereas regions farther north will be increasingly utilised throughout mid to late winter during which time the availability and quality of food resources can strongly effect the risk of abortion (Soto et al., 2004) and reproductive success the following breeding season (Boyd et al., 1995).

The important Antarctic fur seal foraging areas identified in this study were not unique to colonies, with some areas used by seals from multiple populations. Animals from Bird Island and Cape Shirreff in particular had considerable overlap of foraging areas, as do the Bird and Marion Island populations although to a lesser degree. Furthermore, there will likely be inter-population overlap with seals from the study populations and other colonies in the Southern Atlantic and Indian Oceans including Crozet, Kerguelen, Heard, Bouvet, the South Sandwich and the South Orkney

Islands. Although Antarctic fur seals are generally regarded as philopatric in respect of breeding sites (Lunn and Boyd, 1991), tracking studies demonstrate the species' capacity for widespread dispersal (e.g. Boyd et al., 2002). It is not unexpected, therefore, that animals from multiple breeding sites will migrate to shared productive areas. Some Antarctic fur seals are highly faithful to winter foraging grounds and return to the same broad area annually (Arthur et al., 2015) and the pattern of inter-colony overlap may, in part, be a product of colony memory of major foraging habitats (Bonadonna et al., 2001).

5. Conclusions

When considered together, the areas identified in this study constitute the important foraging habitats that are exploited by a key Southern Ocean predator throughout the poorly studied non-breeding winter period. The broad spatial and temporal approach of this study has produced realistic estimates of the foraging habitat of Antarctic fur seals from three populations in the Southern Atlantic and Indian Oceans. Seals display clear choice of foraging habitat, travelling through regions of seemingly poorer quality habitat to access areas with probable elevated prey availability. Such areas can be several thousand kilometres from breeding colonies and consequently the seals balance energy intake with the costs of travel and prey searching (Charnov, 1976).

Appreciation of the temporal shifts in availability and use of foraging habitats during this ~9-month period is important not only biologically, but also from a management context. Antarctic fur seals are currently the only pinniped indicator species contributing to the Commission for the Conservation of Antarctic Marine Living Resources' (CCAMLR) Ecosystem Monitoring Program (CEMP), which aims to manage the ecological impacts of commercial harvests in the Southern Ocean. An increased understanding of the habitat use of this species is therefore critical to inform conservation management and will facilitate future investigation of the potential effects of short (i.e.

El Niño Southern Oscillation and Southern Annular Mode) and long-term oceanographic changes (i.e. climate change) on the habitat use and foraging efficiency of this species.

Recently, the objective of habitat models has shifted towards documenting habitat change and extrapolating model predictions to novel areas (Elith and Leathwick, 2009). The habitat models developed in this study can be used to hindcast foraging habitat, establishing historical distribution ranges that can be compared to current observations to indicate past habitat changes and improve our understanding of future distribution shifts. The development of seasonal habitat models to better elucidate the temporal variation in habitat importance over the winter will also help quantify when key foraging habitats are used by fur seals and to what degree any potential overlap with human activities such as fishing may occur. For marine predators, habitat models are a useful conservation tool to identify critical habitats of understudied populations without the need to undertake time-consuming and expensive tracking programs. Subsequently, habitat models for the three Antarctic fur seal colonies from this study can be used to predict critical foraging habitat for seals from other key Southern Ocean colonies where information on the winter at-sea distribution is currently not available. Among other considerations, information on local habitat availability and preferences will be necessary for accurate extrapolation (Torres et al., 2015) and careful consideration of the environmental and oceanographic similarities of model and prediction populations will be important.

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Figure legends

Figure 1. Maps of eight environmental climatology variables likely to influence fur seal foraging effort during the Southern Ocean winter (April-December). Variables were averaged across all winters in the study period (2008-13), except for SSHa Variance, for which variance was calculated. The locations of the three study colonies are shown on the map in the bottom right panel.

Figure 2. (a) Winter tracks for female Antarctic fur seals (n=184) split into three periods: early (March-May), mid (June-August) and late (September-December) winter. The mean sea-ice extent for each period over the five years (2008-13) is represented by the dashed lines. (b) Density distribution of locations by latitude of fur seals from Marion Island (n=119), Bird Island (n=28) and

Cape Shirreff (n=37) during early (red), mid (blue) and late winter (green). Triangles show the latitude of each colony. (c) The average number of new grid cells visited with the inclusion of additional animals for the Marion Island (black), Bird Island (light grey) and Cape Shirreff (dark grey) colonies.

Figure 3. Observed and predicted winter habitat use (time spent in hours per cell of a 60 km x 60 km grid) for female Antarctic fur seals from Marion Island, Bird Island and Cape Shirreff. 75% distribution areas are shown by solid black lines. Dashed lines show the average position of the sea-ice edge for early, mid and late winter. Black triangles show the location of each colony.

Figure 4. Predicted time spent per grid cell in relation to key environmental parameters (unscaled and uncentred) for the winter foraging effort of female Antarctic fur seals. Lines show the prediction of a GAM fit to a Gamma error structure for (a) Marion Island, (b) Bird Island and (c) Cape Shirreff. Shading represents the 95% confidence interval for predictions. Black bars show the distribution of observations. SST = sea surface temperature, 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.

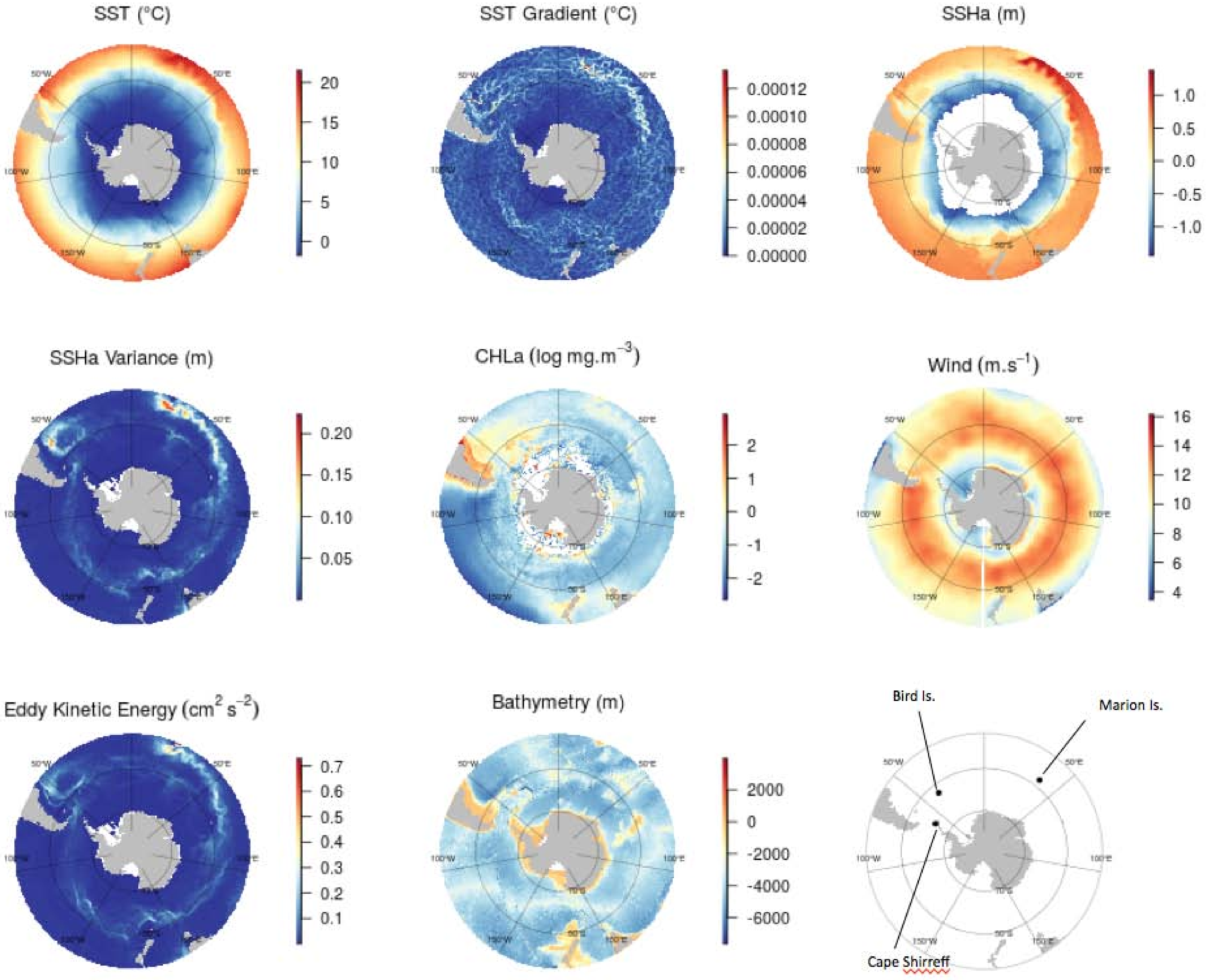
Table 1. Summary of data: Number of tags deployed, recovered, trips recorded and locations estimated by site and year collected for the winter foraging trips of female Antarctic fur seals.

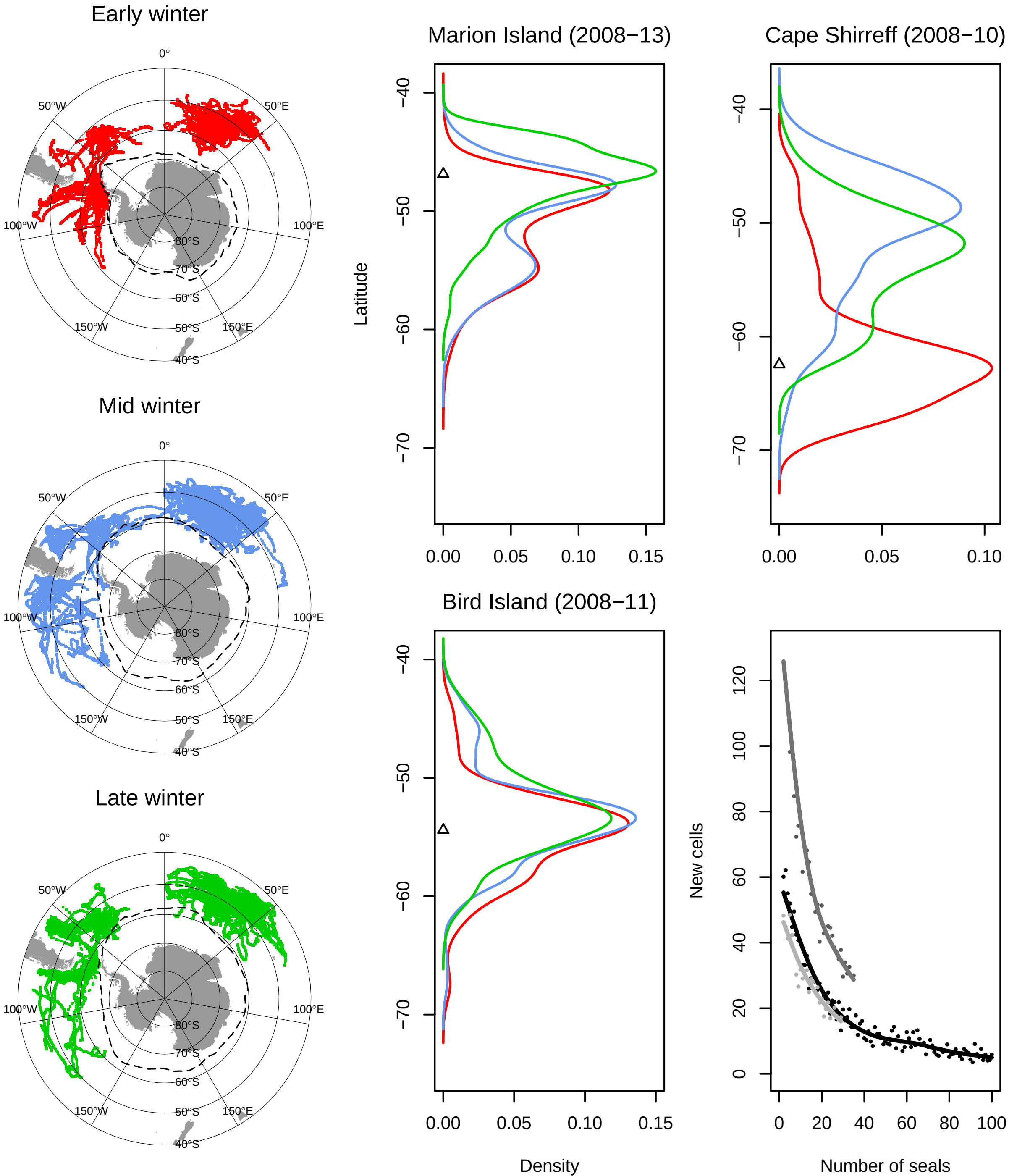
Site	Year	GLS deployed	GLS recovered	N trips	N locations	
						Latitud
Marion Island	2008	30	20	42	9035	
	2009	31	10	27	6509	
	2010	16	8	17	3148	
	2011	42	32	71	13 588	
	2012	30	26	41	16 709	
	2013	30	23	28	5062	
	All years	*179*	*119*	*227*	*54 051*	*41.4°S*
Bird Island	2008	29	3	6	1407	
	2009	30	9	18	4665	
	2010	30	10	21	4186	
	2011	30	6	11	2070	
	All years	*119*	*28*	*56*	*12 328*	*41.7°S*
Cape Shirreff	2008	18	14	14	6562	
	2009	19	11	11	5309	
	2010	19	12	12	5546	
	All years	*56*	*37*	*37*	*17 417*	*41.3°S*
Total		**354**	**184**	**320**	**83 796**	

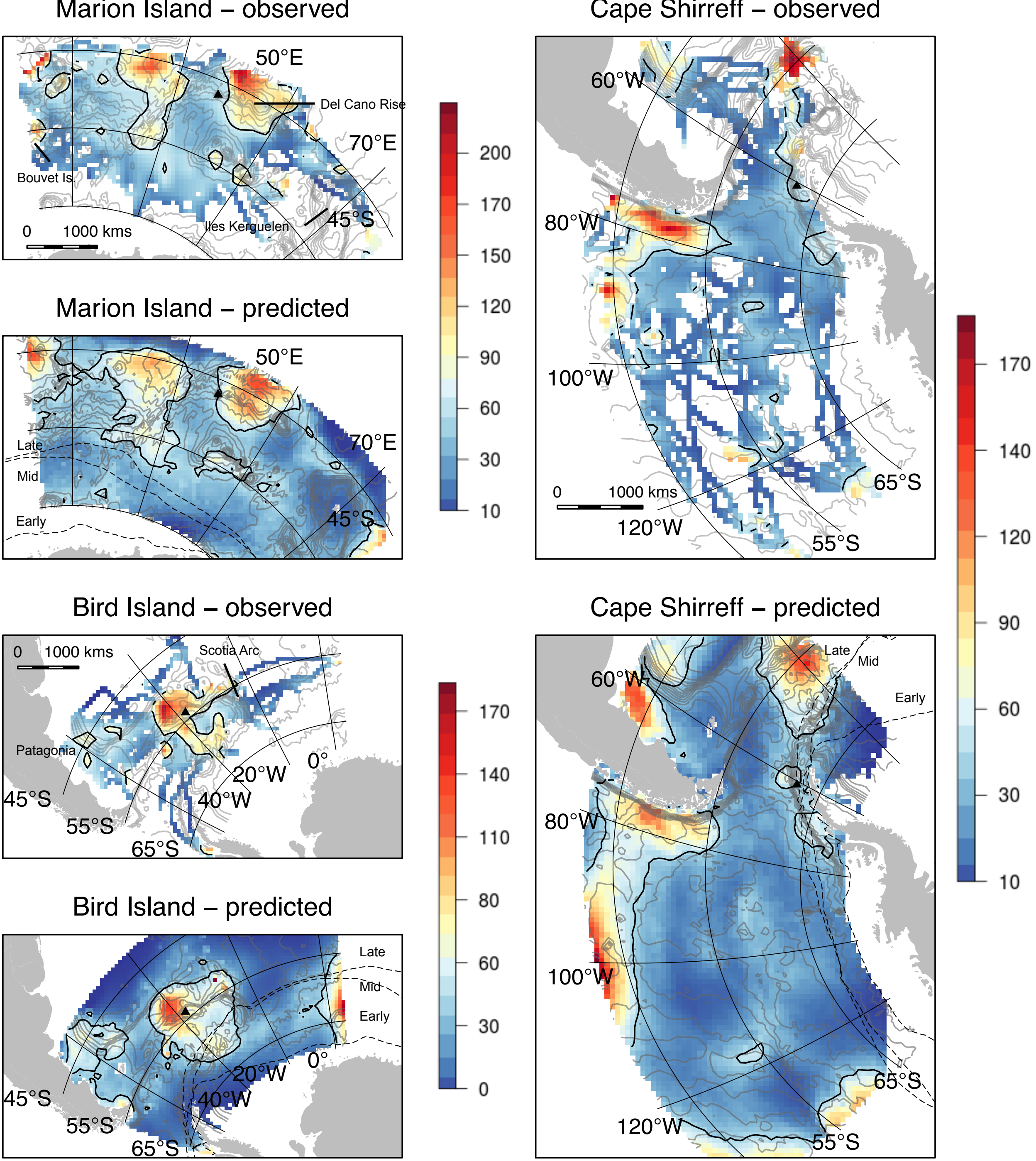
Table 2. Summary of generalised additive model (GAM) comparisons examining the relationship between foraging effort (time spent per grid cell) and environmental variables for: (a) Marion Island, (b) Bird Island and (c) Cape Shirreff colonies. TS = time spent, SST = sea surface temperature, SSTG = sea 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. Only models with a **Δ**AIC <10 are shown and the accepted model is presented in bold.

Candidate models	*k*	LL	AIC	ΔAIC	*w*AIC
(a) Marion Island					
1. **TS ~ SST + SSHa + SSHV + Wind + CHLa + BATHY + EKE + d2col + (lon,lat)**	**10**	**-24833.0**	**49851.2**	**0.0**	**0.691**
2. TS ~ SST + SSTG + SSHa + SSHV + Wind + CHLa + BATHY + EKE + d2col + (lon,lat)	11	-24832.5	49852.9	1.7	0.295
3. TS ~ SST + SSHa + SSHV + Wind + CHLa + EKE + d2col + (lon,lat)	9	-24843.5	49859.1	7.9	0.013
(b) Bird Island					
1. **TS ~ SST + SSTG + SSHa + Wind + BATHY + EKE + d2col + (lon,lat)**	**9**	**-13702.8**	**27563.4**	**0.0**	**0.355**
2. TS ~ SST + SSTG + SSHa + SSHV + Wind + CHLa + BATHY + EKE + d2col + (lon,lat)	11	-13695.9	27563.5	0.1	0.334
3. TS ~ SST + SSTG + SSHa + Wind + CHLa + BATHY + EKE + d2col + (lon,lat)	10	-13702.1	27563.8	0.4	0.291
4. TS ~ SST + SSTG + SSHa + Wind + EKE + d2col + (lon,lat)	8	-13706.8	27569.3	5.9	0.017
(c) Cape Shirreff					
1. **TS ~ SST + SSHa + SSHV + Wind + CHLa + EKE + d2col + (lon,lat)**	**9**	**-27232.9**	**54637.4**	**0.0**	**0.594**
2. TS ~ SST + SSHa + SSHV + Wind + CHLa + BATHY + EKE + d2col + (lon,lat)	10	-27232.9	54638.9	1.5	0.287
3. TS ~ SST + SSTG + SSHA + SSHV + Wind + CHLa + BATHY + EKE + d2col + (lon,lat)	11	-27232.8	54640.7	3.3	0.115

k, number of parameters; LL, log-likelihood; AIC, Akaike's Information Criterion; **Δ**AIC, difference in AIC from that of the best fitting model; *w*AIC, AIC weight; prop dive vARS, proportion of the dive in vertical area-restricted search behaviour.


SST (°C)
20
15
10
5
0
SST Gradient (°C)
0.00012
0.00010
0.00008
0.00006
0.00004
0.00002
0.00000
SSHa (m)
1.0
0.5
0.0
-0.5
-1.0
SSHa Variance (m)
0.20
0.15
0.10
0.05
CHLa (log mg.m^{-3})
2
1
0
-1
-2
Wind (m.s^{-1})
16
14
12
10
8
6
4
Eddy Kinetic Energy (cm^2 s^{-2})
0.7
0.6
0.5
0.4
0.3
0.2
0.1
Bathymetry (m)
2000
0
-2000
-4000
-6000
50°W
50°E
100°W
100°E
150°W
150°E
50°S
70°S
Bird Is.
Marion Is.
Cape Shirreff


Early winter
Mid winter
Late winter
0°
50°W
50°E
100°W
100°E
150°W
150°E
80°S
70°S
60°S
50°S
40°S
Marion Island (2008−13)
Cape Shirreff (2008−10)
Bird Island (2008−11)
Latitude
−40
−50
−60
−70
0.00
0.05
0.10
0.15
Density
New cells
0
20
40
60
80
100
120
Number of seals



Marion Island – observed

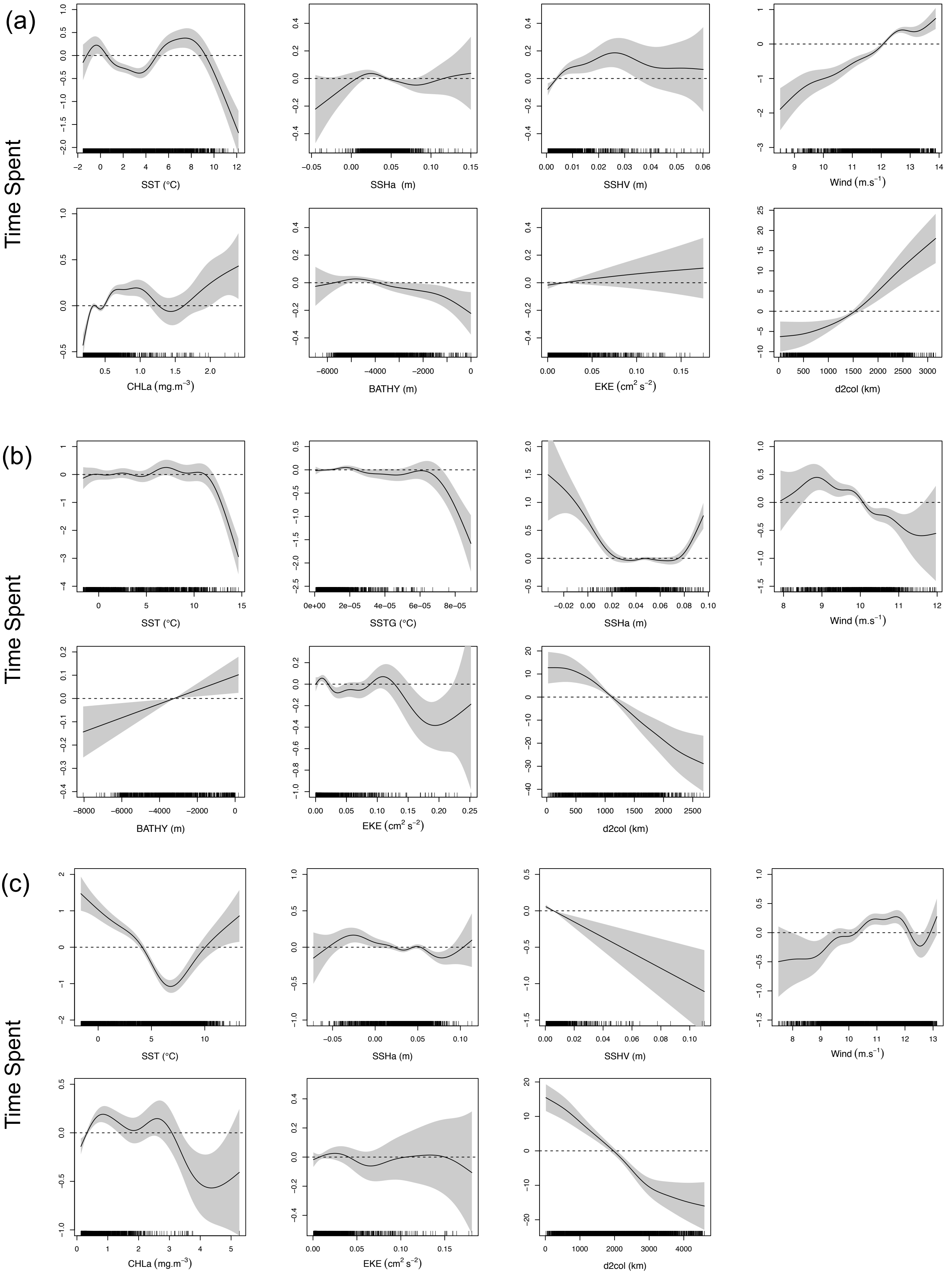
Marion Island – predicted

Bird Island – observed

Bird Island – predicted

Cape Shirreff – observed

Cape Shirreff – predicted


(a)
Time Spent
SST (°C)
SSHa (m)
SSHV (m)
Wind (m.s^{-1})
CHLa (mg.m^{-3})
BATHY (m)
EKE (cm^2 s^{-2})
d2col (km)
(b)
Time Spent
SST (°C)
SSTG (°C)
SSHa (m)
Wind (m.s^{-1})
BATHY (m)
EKE (cm^2 s^{-2})
d2col (km)
(c)
Time Spent
SST (°C)
SSHa (m)
SSHV (m)
Wind (m.s^{-1})
CHLa (mg.m^{-3})
EKE (cm^2 s^{-2})
d2col (km)