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Circumpolar habitat use in the southern elephant seal: implications for foraging success and population trajectories

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Abstract. In the Southern Ocean, wide-ranging predators offer the opportunity to quantify how animals respond to differences in the environment because their behavior and population trends are an integrated signal of prevailing conditions within multiple marine habitats. Southern elephant seals in particular, can provide useful insights due to their circumpolar distribution, their long and distant migrations and their performance of extended bouts of deep diving. Furthermore, across their range, elephant seal populations have very different population trends. In this study, we present a data set from the International Polar Year project; Marine Mammals Exploring the Oceans Pole to Pole for southern elephant seals, in which a large number of instruments ($N = 287$) deployed on animals, encompassing a broad circum-Antarctic geographic extent, collected *in situ* ocean data and at-sea foraging metrics that explicitly link foraging behavior and habitat structure in time and space. Broadly speaking, the seals foraged in two habitats, the relatively shallow waters of the Antarctic continental shelf and the Kerguelen Plateau and deep open water regions. Animals of both sexes were more likely to exhibit area-restricted search (ARS) behavior rather than transit in shelf habitats. While Antarctic shelf waters can be regarded as prime habitat for both sexes, female seals tend to move northwards with the advance of sea ice in the late autumn or early winter. The water masses used by the seals also influenced their behavioral mode, with female ARS behavior being most likely in modified Circumpolar Deepwater or northerly Modified Shelf Water, both of which tend to be associated with the outer reaches of the Antarctic Continental Shelf. The combined effects of (1) the differing habitat quality, (2) differing responses to encroaching ice as the winter progresses among colonies, (3) differing distances between breeding and haul-out sites and high quality habitats, and (4) differing long-term regional trends in sea ice extent can explain the differing population trends observed among elephant seal colonies.

Key words: foraging behavior; *Mirounga leonina*; physical oceanography; population status; sea ice; Southern Ocean water masses.

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Introduction

The Southern Ocean controls the mixing of the world's deep and upper water masses and thereby regulates the capacity of the ocean to store and transport heat and carbon as well as having major influences on global biogeochemical cycles (Rintoul 2011). These processes dictate where primary and secondary production occur (Olonscheck et al. 2013), and consequently where higher trophic level species focus their foraging in order to maximize energy acquisition at minimum cost, thereby maximizing fitness (Murphy et al. 2012). Consequently, monitoring animal behavior and population trends in relation to *in situ* habitat structure provides spatio-temporally explicit information on changes in the distribution of predator aggregations and foraging behavior, which are essential for understanding ecological processes (Block et al. 2011). Moreover, coupling the diving behavior of marine predators with characteristics of their ocean habitats is a particularly powerful way to understand biophysical interactions and enhance our ability to quantify and understand ecological patterns and processes in marine environments (Melbourne-Thomas et al. 2013). The Southern Ocean has a unique predator fauna as a result of its isolation and extreme environmental conditions. To be successful, species have evolved diverse life-history patterns adapted to extensive seasonal and interannual fluctuations in both the physical and biological environment. Quantifying where and when predators concentrate their foraging effort contributes to resolving a number of important ecological issues, such as the distribution and availability of resources along with their spatial and temporal variability.

Variation in prey availability leads predators to shift their foraging locations and modify foraging behavior, which can affect their foraging success, which in turn influences survival, breeding success, and eventually population abundance, all of which are readily measurable (New et al. 2014). An important first step in understanding these complex processes is to quantify patterns of habitat use and foraging ecology of top predators such as seals. Ocean properties are the fundamental determinant of habitat suitability for marine predators, and in many ways are analogous to the way that terrain or vegetation types determine habitats for terrestrial predators. However, in marine systems such data are often incomplete or totally lacking, because animals use areas of ocean that are generally inaccessible or difficult to monitor. Furthermore, the marine environment is highly dynamic. Primary productivity can be transported over vast areas due to advection and predators need to track the shifts. In polar regions seasonally dynamic sea ice cover adds further to the complexity (Charrassin et al. 2008).

The development of miniaturized logging and satellite-linked monitoring equipment that can be attached to marine animals has revolutionized how we gather information in extreme environments like the Southern Ocean (Aarts et al. 2008). Biologists can now monitor *in situ* oceanographic conditions simultaneously with animal behavior (Biuw et al. 2007, Charrassin et al. 2008), creating a vital link in understanding animals' responses to local changes in food availability and how they use different habitats (Costa et al. 2010).

The world's oceans are heterogeneous and comprise a variety of different water masses. Functionally, these water masses can be regarded as different marine habitats. Water masses are large-scale, three-dimensional features, sharing common water temperature, salinity and density ranges, where unique combinations of these variables define each individual water mass's evolution and physical structure (Herraiz-Borreguero and Rintoul 2011). The geo-chemical and

biological properties of individual water masses can also be described (Constable et al. 2014). For example, cold, saline, and dense waters formed by the production of sea ice, sink to the ocean floor carrying high oxygen concentrations. Here, they become rich in nutrients, but due to their depth, remain biologically inert, at least with respect to primary production by photosynthetic organisms (Moore et al. 2013). However, if such water masses rise to the surface once they are in the eutrophic zone, they readily support diverse biological communities. Thus, features that induce upwelling, such as ocean topography (i.e., the presence of sea-mounts, submarine ridges, or shelves) and the presence of fronts (where different water masses meet) and the presence of sea ice drive high productivity, which can influence patterns of biological diversity and animal abundance (Bost et al. 2009).

In the Southern Ocean, wide-ranging predators, such as albatross, seals, and cetaceans offer a unique opportunity to quantify how animals respond to differences in the environment because their behavior and population trends reflect an integrated signal of prevailing conditions across multiple marine habitats. Southern elephant seals (*Mirounga leonina*) in particular can provide insight into responses to conditions across broad geographic regions due to their circumpolar distribution, and their extensive migrations (they spend more than 10 months of the year at sea undertaking migrations that can extend several thousand kilometers (Hindell and McMahon 2000, Bailleul et al. 2007). Combining data from multiple populations of this species provide integrated *in situ* biophysical information from the entire Southern Ocean (Biuw et al. 2007, Charrassin et al. 2008, Roquet et al. 2013). Elephant seals dive almost continuously while at sea (McIntyre et al. 2010) and therefore provide valuable high-resolution information on the physical attributes of the water column where ever they travel (Costa et al. 2012). This is exactly the information required for determining water mass structure and evolution. Given that elephant seals make very deep dives (up to 2000 m+), three-dimensional ocean habitat structure can be quantified by the data they can collect during their two annual migration phases; postbreeding and postmolting, data very difficult to replicate with conventional sampling from ships or ocean buoys (Roquet et al. 2013). Finally, elephant seals show strong site fidelity, returning reliably to natal breeding grounds twice a year, allowing for both attachment and recovery of instruments.

Across their range, southern elephant seal populations occur in four genetically distinct stocks (Slade et al. 1998). The South Georgia, Peninsula Valdes, and Kerguelen stocks are all either stable or increasing slightly. However, the Macquarie Island stock in the southern Pacific is decreasing, and has been doing so for several decades (van den Hoff et al. 2014). A number of hypotheses have been advanced to explain why this stock shows a different population trend from the others; the prevailing explanation is that food availability is the principal determinant of population growth (McMahon et al. 2005*b*). Tracking studies have indicated that individual seals use different regions of the Southern Ocean, ranging from waters north of the subantarctic Front to the continental shelf of the Antarctic Continent. Biuw et al. (2007) postulated that the differing population trends seen among the stocks may be linked to the quality or quantity of food available in particular regions used by the different populations, noting that seals from the declining Macquarie Island population did not fatten quickly when they returned to the sea after breeding. Without coordinated tracking and accompanying population monitoring studies encompassing all of the major populations, it is not possible to test this hypothesis given the importance of identifying different marine habitats, their relative quality and then linking this to population growth rates. However, the recent International Polar Year program, Marine Mammals Exploring the Oceans Pole to Pole (MEOP), provided a unique opportunity for a global study of elephant seals equipped with oceanographic sensor satellite tags that allow us to explicitly link foraging behavior and habitat structure in time and space.

In this study, we quantified the habitats used by southern elephant seals across the Southern Ocean. Specifically, we aimed to: (1) describe the at-sea distribution of elephant seals throughout the entire Southern Ocean and identify important foraging areas (2) describe their broad-scale habitat use in terms of Shelf and Deep Ocean, as well as their use of the sea ice zone with respect to time of year and geographic region, (3) use *in situ* Conductivity–Temperature–Depth (CTD)

data to identify the different water masses used by the seals at their foraging depths, (4) assess the regional importance of these water masses to the seals, (5) compare how male and female seals use the most important habitats throughout the annual cycle in response to the seasonal expansion of the ice edge, and (6) finally, compare elephant seal population trends in relation to habitat use among the different stocks.

Methods

Global distribution of southern elephant seal instrument deployments

Two hundred and eighty-seven southern elephant seals were captured at eight deployment sites around the Southern Ocean each year between 2004 and 2010 (with an average of 41 seals per year) at the end of their annual breeding haul-out (prior to the postbreeding migration) or at the end of their annual molt haul-out (prior to the postmolt migration). The seals were chemically sedated (McMahon et al. 2000*b*), weighed, and measured (Field et al. 2002), and a CTD-SRDL-9000 (Conductivity-Temperature-Depth Satellite Relay Data Logger – Sea Mammal Research Unit, St Andrews, UK) was attached to the hair on the seal's head (Field et al. 2012). The combined weight of the tag and glue was approximately 0.5 kg i.e., 0.15% and 0.10% of the mean departure weight of adult female southern elephant seals (338 ± 65 kg) and subadult males (469 ± 202 kg), respectively. We are confident that the instruments did not affect their at-sea behavior given that the smallest instrumented seal weighed 169 kg, making the tag < 0.3% of the seal's weight. Previous studies have demonstrated that seals carrying twice this load (instruments of up to 0.6% of their mass) were unaffected in either the short term (growth rates) or the long term (survival) by carrying these instruments (McMahon et al. 2008).

At-sea seal movements were determined using the ARGOS satellite tracking system. ARGOS uses the Doppler shift in transmitted frequencies to estimate animal location. Positions are subsequently classified into one of the seven location classes (LC 3, 2, 1, 0, A, B, and Z), which have a 68th percentile spatial error ranging from 0.5 km (LC 3) to 10 km (LC B) (Vincent et al. 2002). Location and location quality are provided for each uplink. The CTD-SRDLs remained on the seals until they either fell off or were shed with the hair during the next annual molt.

State-space models (Jonsen et al. 2013) were used (1) to minimize positional errors (2) to estimate location points along movement paths at regular time steps, and (3) to infer whether the movements fell into one of two stochastic movement modes; an area-restricted search (ARS) mode characterized by slow movements with highly variable turning angles indicative of feeding or a contrasting transit mode characterized by high speeds and low turning angles. The positional error correction was carried out using combined speed and Kalman filtering (Patterson et al. 2010). Kalman smoothing was also used to estimate the most likely position every 2 h. The behavioral classification was then derived using Hidden Markov Models (Patterson et al. 2009) using the maximum likelihood approach (Patterson et al. 2009, Sharples et al. 2012, Langrock et al. 2014). Under these models, speeds between positions are modeled using a Gamma distribution and turning angle is characterized using a wrapped-Cauchy distribution. Hidden Markov Model characterization of foraging state correlated well with bouts of positive rates of change in condition (i.e., fattening) (Dragon et al. 2010) inferred from drift rate data (Biuw et al. 2003).

Once the most likely path had been determined for each seal, we calculated the median depth and duration of all dives associated with each 2-hourly location. We also identified the CTD profile from that seal that was closest in time to that location. In order to investigate temporal and regional differences in habitat use, we also allocated each location to a season and a geographic region. Season was defined as one of four 3-month periods: Postbreeding (*pm*, November–January), Postmolt 1 (*pm1*, February–April), Postmolt 2 (*pm2*, May–July), Postmolt 3 (*pm3*, August–October), encompassing the four distinct periods in the annual cycle of the elephant seals (Hindell and Burton 1988). The four regions were the Antarctic Peninsula (longitude > −110° and ≤ −50°), Southern Atlantic (> −50° and ≤ 60°), Southern Indian Ocean (longitude > 60° and ≤ 175°), and Southern Pacific (> 60° and ≤ −110°) regions.

Analyses of broad-scale habitat use in terms of shelf, Deep Ocean, and sea ice with respect to time of year and geographic region

Our data set comprised over 1,000,000 individual dives from 287 seals with more than 100,000 CTD profiles, and 568 136 estimated locations. We allocated a bathymetric depth under each location, based on the ETPOPO1 bathymetric data set (http://www.ngdc.noaa.gov/mgg/global). Locations that had median dive depths within 20 m of the ocean floor were classified as locations where the seal had made benthic dives, and all others were classified as locations where the seal made pelagic dives. Due to uncertainty in both the dive depth and bathymetry maps, some median depths at some locations were deeper than the ocean floor and we classified these locations as benthic dives. We also associated each location with the sea ice concentration at that location on that day using the blended optimal interpolation Version 2 ECDC AMSR+AVHRR 0.25 degree global ice charts from the NASA Coastwatch site (http://coastwatch.pfeg.noaa.gov/coastwatch).

Each location was then assigned to one of the two broad-scale habitat types: Continental *Shelf* (where the bathymetry was ≤1000 m) and *Deep Ocean* (where the bathymetry was >1000 m). This definition of shelf habitat was chosen so that locations that were associated with the upper edge of the shelf break, a region that has been reported to be important to elephant seals were included with the shelf (O'Toole et al. 2014). While this broad definition may fail to distinguish between subantarctic and Antarctic shelf habitats, the physical processes that dominate either shelf area are likely to differ greatly to those in open seas, and it is this broad-scale difference that were trying to capture in our analyses.

For each location, we also included information on the individual's, sex and age class. In practice, the seals in our study fell into two categories, adult females (169–583 kg) or subadult males (218–1200 kg). Finally, because elephant seals typically display pronounced diel movement patterns, and thereby potentially use different habitats (at least in terms of water masses, which have strong vertical distribution patterns) at different times of day, we allocated each location to either *day* or *night* using the *sunriset* function in R.

Using in situ CTD data to identify the different water masses used by the seals at their foraging depths

While seals were diving, CTD data were collected every 4 s during the ascent phase of each of the deepest dives recorded within 6-h periods and processed on-board for transmission via the ARGOS satellite system when the seals surfaced (Boehme et al. 2009). Temperature, conductivity, and salinity profiles were transmitted in an abstracted form with 17 inflection points determined by an on-board "broken stick algorithm" (Boehme et al. 2009). Even though a subset of the tags were calibrated prior to deployment (Charrassin et al. 2008), all the temperature and salinity data derived from the CTD profiles were also calibrated *post hoc* (Roquet et al. 2011).

For each location we determined which water mass the seal was using. To account for the three-dimensional nature of elephant seal habitat use, we identified the water mass that the seal occupied at the bottom of its dive at each location. This is typically the depth at which the seal spends most of its time, and presumably performs most of its foraging. The criteria for defining water masses are described in Table 1 and Appendix S1. The Antarctic Circumpolar Current (ACC) provides the primary pathway for exchange of water masses between the ocean basins and between the surface and deep ocean in the Southern Ocean. The shoaling of a wide range of isopycnals across the Southern Ocean toward Antarctica brings deep and intermediate Circumpolar Deepwater (CDW) close to the surface. Here, the Southern Ocean exchanges heat, freshwater, and momentum with the atmosphere and ice, leading to the physical and chemical transformation of water properties across densities to create lighter mode and intermediate waters—Subantarctic Mode Water (SAMW) and Antarctic Intermediate Water (AAIW) respectively, as well as Antarctic Bottom Water (AABW) (Fig. 1). The properties of the Southern Ocean water masses show spatial variability reflecting their circulation along the ACC, as well as the intrinsic characteristics of their source waters. Therefore, each water mass has been defined according to the region/sector where it was observed (Table 1), following the basic water mass definitions of Whitworth et al. (1998) and Orsi and Wiederwohl (2009).

Table 1. The three physical characteristics: (1) water density (γ^n), (2) water temperature (θ), and (3) water depth (P), used to define the 12 water masses across the Southern Ocean in which southern elephant seals spent their postbreeding and postmolt foraging trips.

Geographic zone	Water mass and characteristic	AP	Atlantic	Indian	Pacific
North of SAF	SASW				
	γ^n	≤ 26.95	≤ 26.80	≤ 26.80	≤ 26.95
	SAMW				
	γ^n		≤ 26.95	≤ 26.95	≤ 27.15
	AAIW				
	γ^n		≤ 27.40	≤ 27.40	≤ 27.40
	CDW north				
	γ^n	≤ 27.40	≤ 27.40	≤ 27.40	≤ 27.40
Antarctic PF to SAF	SASW				
	γ^n	≤ 26.95	≤ 26.80	≤ 26.80	≤ 26.95
	SAMW				
	γ^n		≤ 26.95	≤ 26.95	≤ 27.15
	AAIW				
	γ^n		≤ 27.40	≤ 27.40	≤ 27.40
	CDW south				
	γ^n	≤ 27.40	≤ 27.40	≤ 27.40	≤ 27.40
Antarctic shelf break to Antarctic PF	AASW				
	γ^n	≤ 28.00	≤ 28.00	≤ 28.00	≤ 28.00
	CDW				
	γ^n	≥ 28.00, ≤ 28.27	≥ 28.00, ≤ 28.27	≥ 28.00, ≤ 28.27	≥ 28.00, ≤ 28.27
	θ	>1.5°C	>1.5°C	>1.5°C	>1.5°C
	mCDW				
	γ^n	≥ 28.00, ≤ 28.27	≥ 28.00, ≤ 28.27	≥ 28.00, ≤ 28.27	≥ 28.00, ≤ 28.27
	θ	≤ 1.5°C	≤ 1.5°C	≤ 1.5°C	≤ 1.5°C
	mSW-north				
	γ^n	> 28.27	> 28.27	> 28.27	> 28.27
	P	< 2500	< 2500	< 2500	< 500
Continental shelf	ISW				
	θ	≤ −1.95°C	≤ −1.95°C	≤ −1.95°C	≤ −1.95°C
	AASW				
	γ^n	28.00	28.00	28.00	28.00
	mCDW south				
	γ^n	≥ 28.00, ≤ 28.27	≥ 28.00, ≤ 28.27	≥ 28.00, ≤ 28.27	≥ 28.00, ≤ 28.27
	θ	≤ 1.5°C	≤ 1.5°C	≤ 1.5°C	≤ 1.5°C

Note: SAF, Subantarctic Front; SASW, Subantarctic Surface Water; SAMW, Subantarctic Mode Water; AAIW, Antarctic Intermediate Water; CDW, Circumpolar Deepwater; PF, Polar Front; AASW, Antarctic Surface Water; mCDW, modified Circumpolar Deepwater; mSW, modified Shelf Water; ISW, Ice Shelf Water; DSW, Deep Shelf Water.

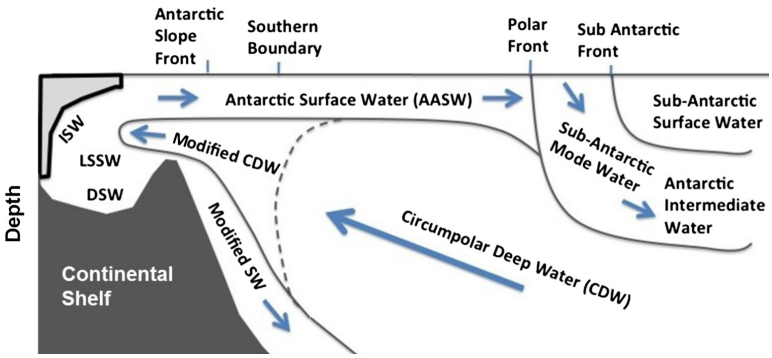

Fig. 1. A schematic illustration of the vertical arrangement of the major water masses identified in this study.

CDW becomes modified Circumpolar Deepwater (mCDW) from when it moves south of the Southern Boundary. Thereafter, it can access up the upper continental slope and move onto the shelf region in discrete locations. Dense Shelf Water forms from the cooling and salt-rejection resulting from the intense air-sea fluxes during sea ice formation in polynya regions around the Antarctic shelf. As this Deep Shelf Water (DSW) interacts with mCDW, it becomes modified Shelf Water that can migrate across the shelf break and descend the continental slope. With an export pathway and sufficient negative buoyancy, this Modified Shelf Water (mSW) will undergo further mixing with mCDW to produce AABW.

Comparing elephant seal population trends to seasonal habitat use

We collated current estimates of population size to determine the number of southern elephant seals in the Southern Ocean and compared these numbers to those that had been published previously to determine overall rates of change (McMahon et al. 2005*a*). Annual estimates of seal numbers were determined using the standard method of complete counts of all adult female seals hauled out during peak breeding on or as close to the 15th October as was practicable (McMahon et al. 2005*a*).

Statistical analyses

We used linear mixed effects models (LMM) to compare response variables to sex, region, and season, with individual seal ID included as a random term. Where appropriate (i.e., those analyses with depth as a consideration), we also included the time of day (*day* or *night*) as an additional random term in the models. Where the response variable was normally distributed, or rendered as such by transformation, we used linear mixed effects models (package *nlme* in R) in the ANOVA function to test the importance of the main effects. When the response variable was binary (i.e., the SSM-derived behavioral mode), we used generalized linear mixed effects models (GLMM) with a binary family and logistic link function and individual seal as a random term (package lme4 in R). We used the Kullback–Leibler (K-L) information loss index to assign relative strengths of evidence to the different competing models (Burnham and Anderson 2002) and Akaike's information criterion (AIC) to indicate the best fit model(s). This measure of model parsimony identifies the/those model(s) from a set of candidate models that minimizes K-L information loss (Burnham and Anderson 2004, Burnham et al. 2011) with the relative likelihoods of candidate models calculated using AIC weights. Thus, the weight (wAIC) of any particular model varies from 0 (no support) to 1 (complete support), relative to the entire model set. Single-term relationships were assessed using information theoretic evidence ratios (ER = wAIC of the slope model ÷ wAIC of the intercept [null] model) (Burnham et al. 2011).

Results

Circumpolar distribution of southern elephant seals

Our combined data set includes location, behavioral and physical oceanographic data from 287 seals, with deployments made at eight major breeding sites, representing three of the four Southern Ocean stocks (Table 2). Tagging effort was not balanced between the sexes; more adult females (229) were tracked than subadult males (58). Tagging effort also varied among deployment sites. Isles Kerguelen had the most deployments (70), followed by South Georgia (65) and Livingston Island (52). All other sites had 30 or less tags deployed. Animals from particular deployments sites often used more than one at-sea geographic region. For example, adult females from Macquarie Island used the South Pacific and South Indian regions in almost equal amounts (41% and 59%, respectively). Females from Livingston Island used all four regions, although the Antarctic Peninsula was the most commonly used (59%). Females from Isles Kerguelen used both the South Indian (41% of locations) and South Atlantic (59% of locations) regions. Females from South Georgia used both the South Atlantic (70% of locations) and Antarctic Peninsula (30% of locations).

The overall mean maximum distance traveled from the deployment sites was 1765 ± 576 km (Table 3), with a maximum distance of 5482 km performed by an adult female seal from Livingston Island. This high level of dispersal, which was typical for seals at all locations (Table 3), ensured complete circumpolar coverage of the

Table 2. The number of 2-hourly at-sea locations (mean ± SD) obtained for female and male southern elephant seals from the Antarctic Peninsula (ap, *n*[females] = 159,832, *n*[males = 17,321]), South Atlantic (sa, *n*[females] = 172,988, *n*[males = 45,699]), Southern Indian (sp, *n*(females) = 92,049, *n*[males = [46,633]]), and Southern Pacific Ocean regions (sp, *n*[females = 33,614], *n*[males = [33,614]]) regions (identified in Fig. 1). The regional counts are divided into the mean number of locations (mean ± standard deviation) from seals of each sex at each of the deployment sites. Also indicated are the genetic stocks (Slade et al. 1998) for the seals at each deployment site and the mean proportion of time (mean ± standard deviation) that seals spent in ARS, i.e., foraging mode, and in transit/traveling mode.

			ap		sa		si		sp	
Deployment site	Genetic stock	No. seals	No. locations	%ARS	No. locations	%ARS	No. locations	%ARS	No. locations	%ARS
Females										
Bouvet Island	SG	12	0	0.0	2664 ± 725	46.9 ± 11.3	0	0.0	0	0.0
Elephant Is	SG	24	2014 ± 945	55.5 ± 17.2	513 ± 532	25.6 ± 17.8	0	0.0	1386 ± 112	55.9 ± 7.3
Falkland Is	SG	3	1837 ± 1292	34.8 ± 25.3	2358	54.11	0	0.0	0	0.0
Iles Kerguelen	Kerg	38	0	0.0	841 ± 667	52.3 ± 16.7	1195 ± 983	46.8 ± 19.9	0	0.0
Livingston Is	SG	51	1957 ± 987	59.7 ± 20.5	323 ± 326	59.7 ± 20.4	382	51.6	943 ± 617	49.6 ± 20.6
Marion Is	Kerg	19	0	0.0	1883 ± 888	46.2 ± 13.7	0	0.0	0	0.0
Macquarie Is	Macq	30	0	0.0	0	0.0	1541 ± 1107	41.9 ± 24.5	1314 ± 895	59.7 ± 24.8
South Georgia	SG	52	675 ± 635	61.7 ± 25.6	1535 ± 1136	61.7 ± 25.6	0	0.0	0	
Female total		229	1795 ± 1031	57.9 ± 20.7	1445 ± 914	41.4 ± 21.2	1040 ± 595	44.6 ± 21.9	1215 ± 238	56.2 ± 22.7
Males										
Bouvet Island	SG	7	0	0.0	1559 ± 1018	50.8 ± 14.5	0	0.0	0	0.0
Elephant Is	SG	5	1559 ± 1018	61.0 ± 28.7	21.0 ± 28.28	0.0	0	0.0	0	0.0
Falkland Is	SG	0	–	–	–	–	–	–	–	
Iles Kerguelen	Kerg	32	0	0.0	38	0.0	1457 ± 1997	54.7 ± 14.3	0	0.0
Livingston Is	SG	1	2391	18.3	0	0.0	0	0.0	0	0.0
Marion Is	Kerg	0	–	–	–	–	–	–	–	–
Macquarie Is	Macq	0	–	–	–	–	–	–	–	–
South Georgia	SG	13	2378 ± 935	71.3 ± 15.0	2081 ± 1279	50.1 ± 30.6	0	0.0	0	0.0
Male total		58	2109 ± 476	59.7 ± 27.1	1198 ± 1369	50.4 ± 25.4	1457 ± 997	54.7 ± 14.3	–	–
Overall total no. locations		287	177,153		218,687		138,682		33,614	

Note: Genetic stock abbreviations are: SG, South Georgia; Kerg, Kerguelen; Macq, Macquarie; ARS, Area-restricted search.

Southern Ocean by the seals in this study (Fig. 2a). There were sex (one-way ANOVA, $F_{1,2} = 7.713$, $P = 0.005$) and regional (one-way ANOVA, $F_{1,3} = 20.543$ $P < 0.001$) differences in the maximum distance traveled by the seals from their deployment sites. On average, male seals traveled slightly shorter distances than the females (1765 ± 576 km and 1833 ± 920 km, respectively). Female seals in the South Pacific region traveled the furthest (2975 ± 1098 km), perhaps due to the low number of breeding sites in the region, followed by the Southern Indian (1843 ± 853 km) and Southern Atlantic (1834 ± 810 km) regions. Females in the Antarctic Peninsula Region trav-

Table 3. Average trip diagnostics (mean ± standard deviation) for southern elephant seals from each of the geographic regions used in this study, according to sex. On average females traveled further than males did and travel rates (mean ± standard deviation) were higher when seals were in transit than when in area-restricted search (ARS).

	Distance from deployment (km)		Mean speed (km/h)	
Geographic region	Mean	Maximum	ARS mode	Transit mode
Female				
Antarctic Peninsula	1464 ± 767	3547	1.01 ± 0.63	3.46 ± 1.54
South Atlantic	1834 ± 810	4033	1.22 ± 0.88	3.98 ± 2.26
South Indian	1843 ± 853	5481	1.36 ± 0.99	4.46 ± 3.15
South Pacific	2975 ± 1098	4785	1.24 ± 0.39	3.36 ± 1.79
Mean	1833 ± 920	5482	1.19 ± 0.81	3.88 ± 2.30
Male				
Antarctic Peninsula	1270 ± 1105	3133	0.52 ± 0.32	2.97 ± 0.93
South Atlantic	1372 ± 909	3071	0.81 ± 0.62	3.70 ± 2.72
South Indian	1597 ± 1224	4523	0.96 ± −0.51	3.72 ± 2.73
Mean	1470 ± 1095	4523	0.85 ± 0.53	3.61 ± 2.54
Overall mean	1765 ± 576	4082	1.13 ± 0.78	3.84 ± 2.35

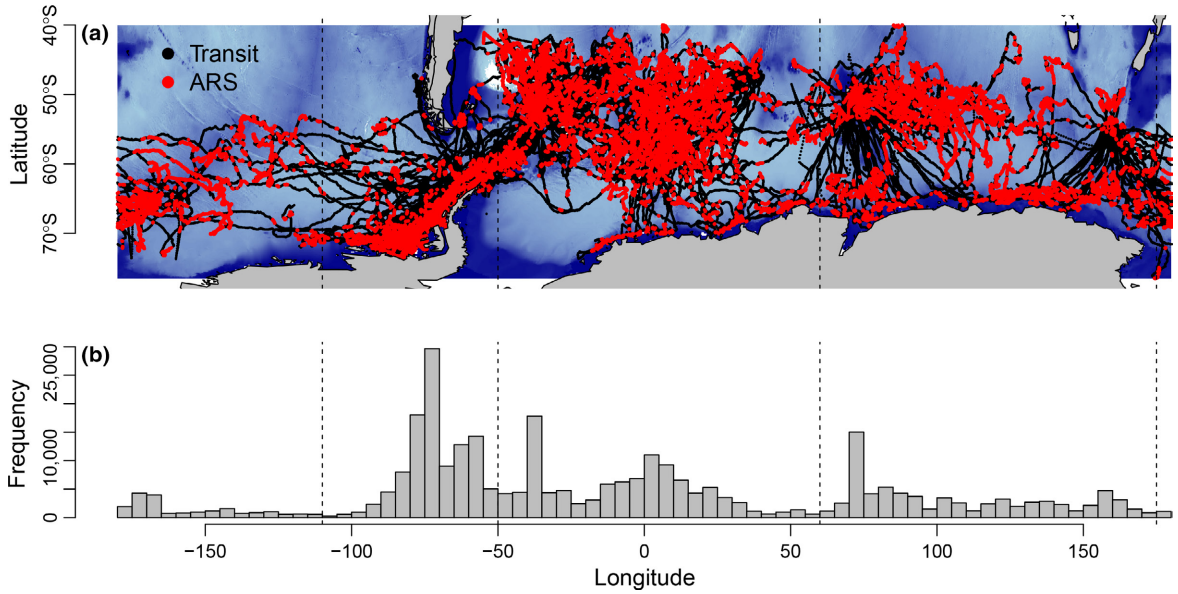

Fig. 2. The 568,136 locations after being processed by state-space movement models, extracted at 2-hourly time steps and categorized into one of two behavioral states, transit and area-restricted search (ARS). (a) A map of each estimated location showing the location of transit (black) and ARS (red). (b) The frequency of ARS locations in each 10 degrees of longitude. The vertical dotted lines represent the boundaries between each of the four regions identified by the troughs in the frequency distribution.

eled least far (1464 ± 767), covering only half the distance of seals in the South Pacific.

We identified both behavioral states (transit and ARS) in all individuals (Fig. 2a). Seal locations, and importantly ARS locations, were widely distributed across the Southern Ocean but, noticeably concentrated along the Antarctic continental shelf, particularly in the region

Table 4. Summary dive metrics for female and male southern elephant seals diving in the seas along the western Antarctic Peninsula and in the South Atlantic, South Indian, and South Pacific oceans. The individual metrics are presented as the mean (±standard deviation) and include: the number of individual seals in an ocean region (*n*), the mean dive depth of the seals (in meters), the mean maximum dive depth (in meters), the single deepest dive by a seal (in meters), the mean dive duration (in minutes), the mean maximum dive duration (in minutes), the single longest dive by a seal (Abs. max.; in minutes), and the mean foraging index score. See Table 1 for a definition of water mass labels.

		Dive depth			Dive duration			Foraging score
Region	*n*	Mean	Mean max.	Deepest dive	Mean	Mean max.	Abs. max.	Mean
Female								
Antarctic Peninsula	96	368 ± 83	1099 ± 400	2378	24.6 ± 5.6	67.0 ± 18.2	92.3	−0.011 ± 0.116
South Atlantic	136	409 ± 86	1076 ± 325	2069	24.6 ± 6.2	60.0 ± 20.1	94.3	0.003 ± 0.126
South Indian	66	420 ± 7 5	1176 ± 396	2389	22.8 ± 5.1	60.7 ± 20.1	93.3	−0.045 ± 0.111
South Pacific	28	382 ± 53	1174 ± 387	2378	25.5 ± 6.6	66.1 ± 20.3	94.3	0.027 ± 0.108
All females		432 ± 71	1049 ± 315	2389	26.0 ± 5.3	62.6 ± 17.9	94.4	0.098 ± 0.020
Male								
Antarctic Peninsula	9	399 ± 49	1275 ± 282	1629	24.5 ± 3.8	70.6 ± 9.9	82.3	0.009 ± 0.021
South Atlantic	22	410 ± 140	1259 ± 522	2069	24.4 ± 5.4	68.2 ± 20.5	94.3	−0.009 ± 0.089
South Indian	30	416 ± 114	1146 ± 342	2058	21.8 ± 4.6	66.4 ± 18.4	94.3	0.000 ± 0.000
All males		439 ± 123	1170 ± 411	2069	24.8 ± 5.1	63.4 ± 17.8	94.3	0.080 ± 0.019

of the Antarctic Peninsula (Fig. 2a). Overall, 306,434 (53.9%) of the locations were allocated to ARS mode and 261,702 (46.1%) were allocated to transit. When considered within the regional framework, most of the ARS locations were in the Southern Atlantic region (38.1%), followed by the Antarctic Peninsula (33.4%), Southern Indian (22.9%), and finally the Southern Pacific (5.5%). The proportion of ARS locations for individual seals varied with region (Table 2), such that seals in the Antarctic Peninsula and the Southern Pacific had proportionally more ARS locations than seals in the Southern Atlantic and the Southern Indian. The mean travel speed between locations was more than three times higher for seals in transit mode compared to those performing ARS (Table 3).

Diving behavior

The seals all made long, deep dives, with overall maxima of 94.3 min and 2389 m (Table 4). Both dive duration and dive depth varied between the sexes and among the regions (Table S1c,d in Appendix S1). The top model comparing dive duration with sex and region was the full model containing both terms and their interaction. Males made slightly shorter dives than females, and these were shorter in the Southern Indian region than the Southern Atlantic or the Antarctic Peninsula. Females performed their shortest dives in the Southern Indian Ocean and their longest dives in the Antarctic Peninsula. Dive depths showed a different pattern. Despite making slightly shorter dives, males tended to make deeper dives than females. Male diving also varied regionally, with the deepest dives by males occurring in the Southern Indian sector and the shallowest dives in the Antarctic Peninsula sector. For females, the deepest dives were also in the Southern Indian region and the shallowest in the Antarctic Peninsula.

Broad-scale habitat use in terms of shelf, Deep Ocean, and sea ice with respect to time of year and geographic region

Overall, 47% of the 306 434 ARS locations were recorded in shelf waters, *i.e.,* the Antarctic continental shelf or the Kerguelen Plateau. However, the best model comparing behavioral state to sex and region was the full model (Table S1a in Appendix S1), with the ER indicating that it was 40 times better than the region only model. This indicates that male and female

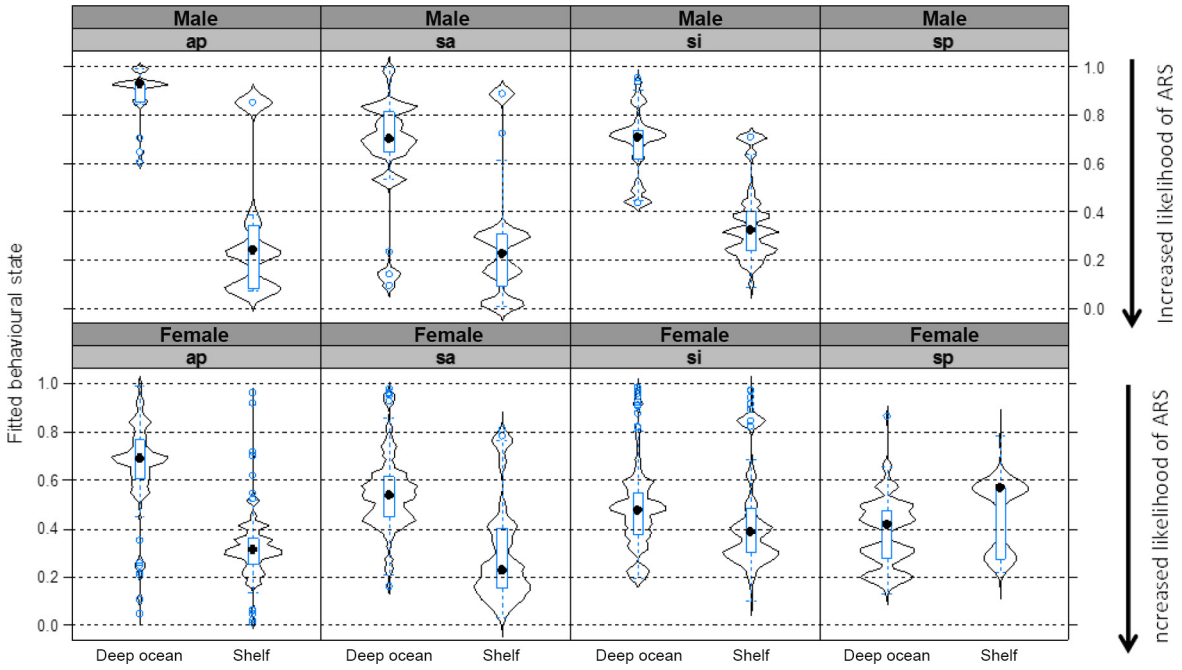

Fig. 3. Fitted values for mean behavioral state (0 = area-restricted search [ARS], 1 = transit) from the generalized linear mixed effects models relating behavioral state to broad-scale habitat use, geographic region, and sex. Shown are the kernel density plot for each habitat, superimposed on the boxplot, illustrating the median (black dot), interquartile range (box) and the range (dotted lines). The horizontal line indicates the 0.5 baseline, where there is equal likelihood of ARS and transit. Points above this line indicate that the behavior for that water mass was predominantly Transit while below the line the behavior was predominantly ARS.

elephant seals used Deep Ocean and Shelf waters differently, according to region (Fig. 3). Male seals were more likely to display ARS mode when in the shelf habitat, and this effect was most pronounced in the Antarctic Peninsula region, and least pronounced in the Southern Indian region. The pattern was broadly similar for females, with them being generally more likely to be in ARS mode when in the shelf habitat. However, the effect was not as pronounced as for the males. The effect was strongest on the Antarctic Peninsula, and less pronounced in the Southern Indian region. In the Southern Pacific region, ARS and transit behaviors were equally likely to occur in both habitats. This analysis suggests that, even though both habitats had similar amounts of ARS locations overall, the Shelf habitat can be considered a better quality habitat than Deep Ocean, as there were relatively more ARS than transit locations in the shelf habitat, most likely as a consequence of the seals transiting through the Deep Ocean habitat from their subantarctic breeding sites to reach the shelf where they concentrate their foraging.

There were considerable regional differences in how female seals used the two habitats, and this was to a large extent due to seasonal expansion of the sea ice (Fig. 4). During the postbreeding (PB1) season, females from both the Southern Indian and Southern Atlantic regions made relatively little use of the shelf habitat with a median value of <20% of all ARS locations occurring there (Fig. 5). In contrast, the postbreeding females in the Antarctic Peninsula had a median value of over 90% of their ARS locations on the shelf (Fig. 5). At this time, the pack-ice extent was close to its minimum and very few of the seals encountered it.

During the first part of the postmolt (winter) trip (PM1), the female seals ranged throughout much of the Southern Ocean (Fig. 4). This was also the time of year when they made the most use of the shelf habitat; almost all ARS locations in the Antarctic Peninsula region occurred in this

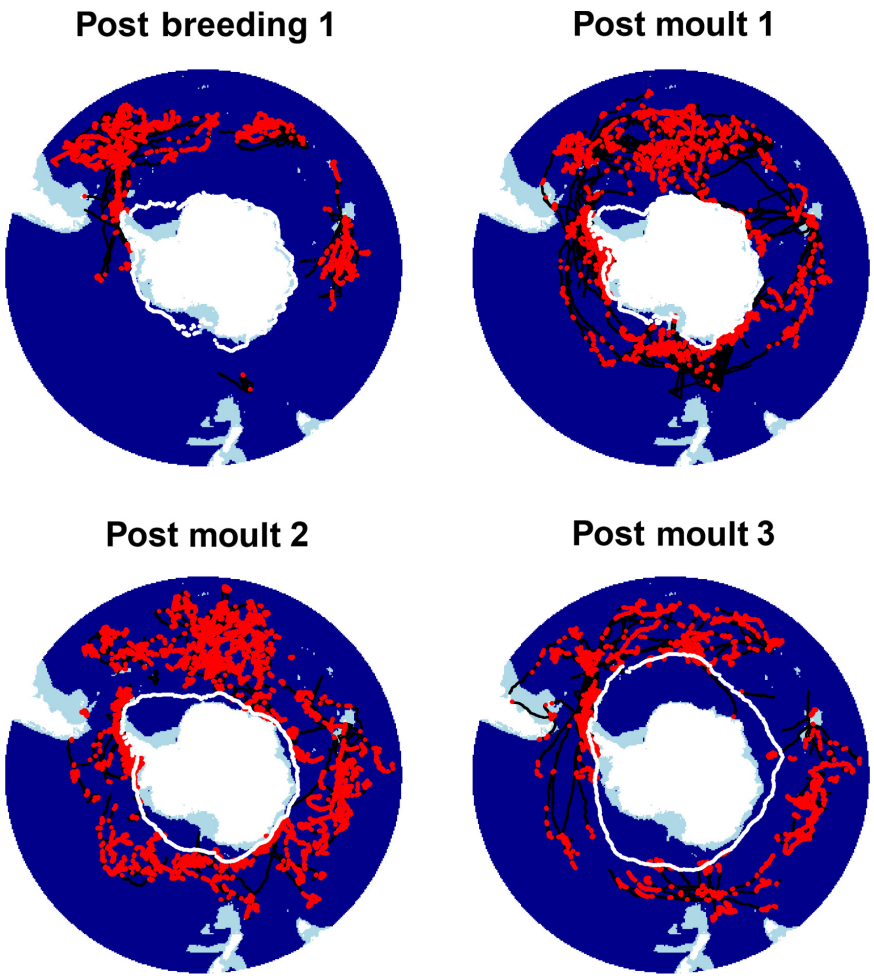

Fig. 4. For adult females, the distribution of area-restricted search (red dots) and transit (black dots) in each of the four seasons superimposed on the two broad-scale habitats, shelf (light blue) and deep ocean (dark blue). Very few locations fall within the sea ice, and the locations move northwards with the season growth of the sea ice. The seasons were defined as one of four 3-month periods: Postbreeding (*pm*, November–January), Postmolt 1 (*pm1*, February–April), Postmolt 2 (*pm2*, May–July), Postmolt 3 (*pm3*, August–October).

habitat, and approximately 50% of ARS locations from the Southern Indian and Pacific regions also occurred on the shelf (Fig. 5). The females from the Southern Atlantic region made least use of the shelf habitat with <10% of their ARS locations made there. At this time of year, the sea ice is at its minimum and even seals on the shelf encountered little ice. The region with the greatest sea ice extent at this time is the Weddell Sea in the South Atlantic region, and no seals used that area (Fig. 5).

The sea ice expanded northwards during the second postmolt foraging period (Fig. 4). This corresponded to a reduction in the average number of ARS locations made in the shelf habitat in all regions but in the Antarctic Peninsula where more than 90% of ARS locations still occurred on the shelf. In the Southern Indian region, the proportion of ARS locations made on the shelf habitat dropped to < 20%, and most of these were associated with the Kerguelen Plateau rather than the Antarctic Continental Shelf. In the Southern Pacific Region, there were no ARS locations made in the shelf habitat.

By the final postmolt period (PM3), the pack-ice was at its maximum extent and very few ARS locations occurred within the pack-ice. Those that did were associated with its outer margins

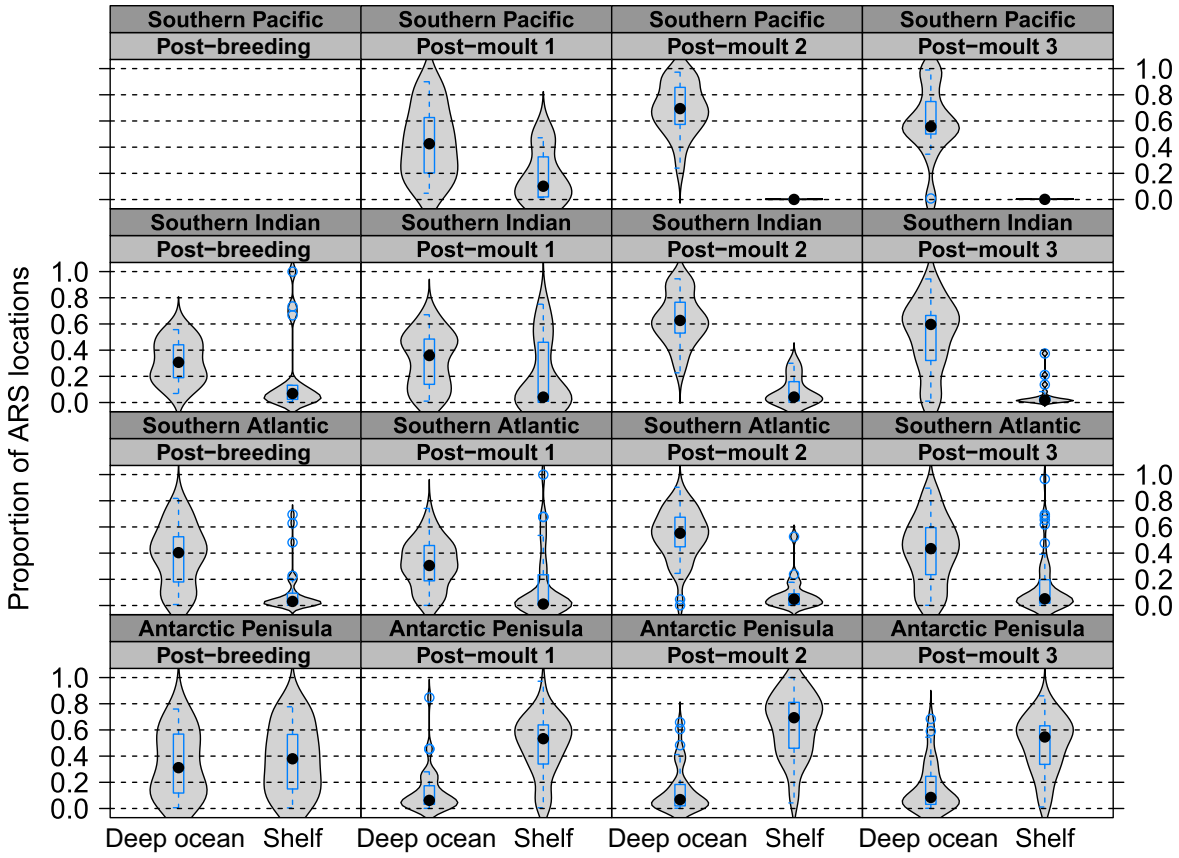

Fig. 5. For females, the mean proportion of area-restricted search (ARS) locations made by an individual that occurred in each habitat in each season. The use of the habitat varied among regions and season: for all regions but the Antarctic Peninsula, more ARS locations were in the Deep Ocean, and in the Southern Indian and Pacific regions, the use of Shelf habitats decreased throughout the winter, corresponding to the growth of ice in Fig. 4.

(Fig. 4). The exception to this general pattern occurred in the Antarctic Peninsula where female seals continued to use the shelf habitat despite the present of ice over the Continental Shelf. In the Southern Pacific region, the females continued to use the *deep ocean* habitat exclusively. The use of shelf habitat declined slightly in the Southern Indian region, but the increased breadth of the quartile range indicated that some individuals were making extensive use of the shelf habitat associated with the Kerguelen Plateau. Similarly, the seals using the Southern Atlantic region showed a slight increase in the use of the shelf habitat, but this was due to animals using the shelf regions around South Georgia rather than the Antarctic Continental shelf.

Overall, adult female elephant seals exhibited a pattern of moving northwards as the winter progressed and the ocean area covered by sea ice increased. This coincided with a reduction in the use of the Antarctic continental shelf, presumably due to the ice acting as a barrier to the seals as they spent very little time in the pack-ice zone. The seals in the Antarctic Peninsula region deviated from this pattern and continued to make the majority of their ARS locations over the shelf despite the presence of ice there.

Subadult males differed markedly from the females (Fig. 6). Males used the shelf habitat in all four seasons. Even in PM2 and PM3, when sea ice covered the Antarctic continental shelf, individual males continued to use it, doing most of their ARS in the shelf habitat in all regions in all seasons. In part this was due to individuals using the subantarctic shelf regions, but unlike the females, some individuals remained in the sea ice

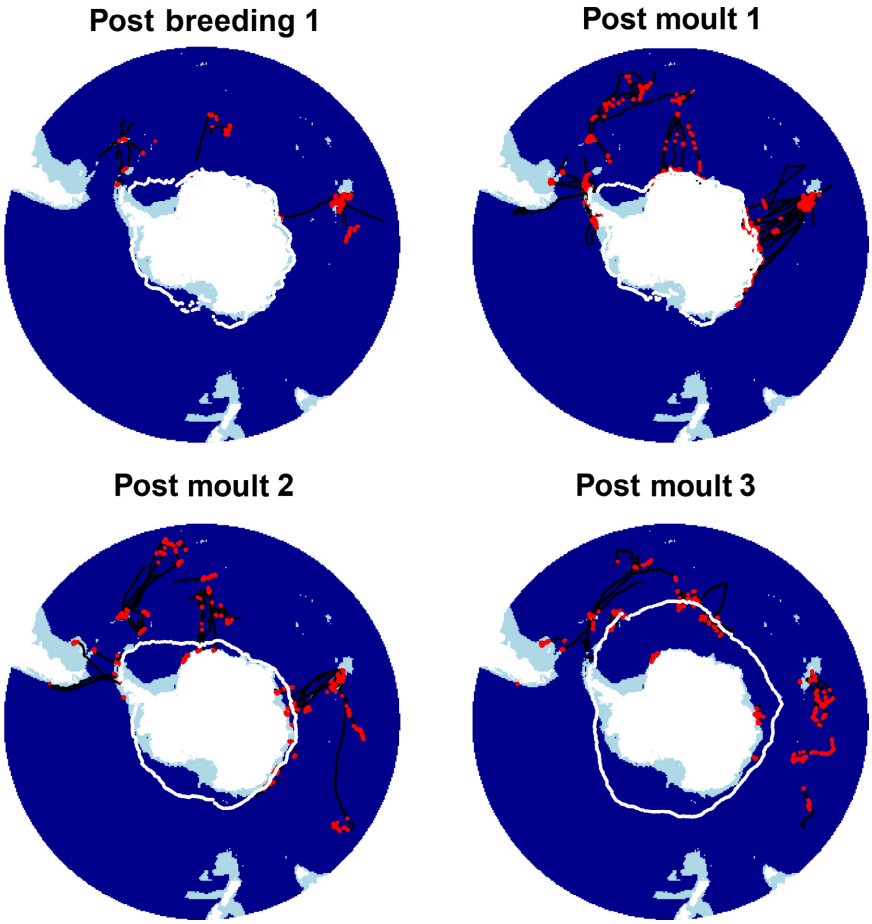

Fig. 6. For adult male seals, the distribution of area-restricted search (red dots) and transit (black dots) in each of the four seasons, superimposed on the two habitats, shelf (dark blue) and deep ocean (light blue). The locations of the males were less influenced by the presence of sea ice than the females (Fig. 4) with some individuals remaining in the sea ice zone year-round.

zone and continued using the continental shelf year-round (Fig. 7).

Use of the different water masses by region and sex

The seals encountered 12 different water masses at their foraging depths (Table 5) but only six were commonly used by seals from all the regions: Antarctic Surfacewater (AASW, 39.4% of all locations), mCDW off the shelf break ($mCDW_D$, 19.0%), mCDW south of the shelf break ($mCDW_S$, 10.1%), CDW south of the polar front (CDW_S, 10.5%), AAIW (9.4%), and CDW north of the polar front (CDW_N, 8.6%). The distribution of these water masses is shown in Fig. 8.

To assess the relative importance of the various water masses to each sex, we used GLMMs relating *behavioral state* to *sex* and water mass at each location, including individual seals and time of day as random terms. Only seven of the 12 water masses were used by both sexes and could therefore be included in this analysis (Table 5). The best fitting model was the full model including both *sex* and *water mass* and their interaction (Table S1b in Appendix S1). The ER indicated that this model was vastly more informative than the next model which contained water mass alone. For females, two water masses were strongly associated with a greater likelihood of being in ARS mode, mSW_n and $mCDW_s$ (Fig. 9). The other five water masses had equal likelihoods of being used for ARS or transit. For males, only $mCDW_s$ was associated with a greater likelihood of being

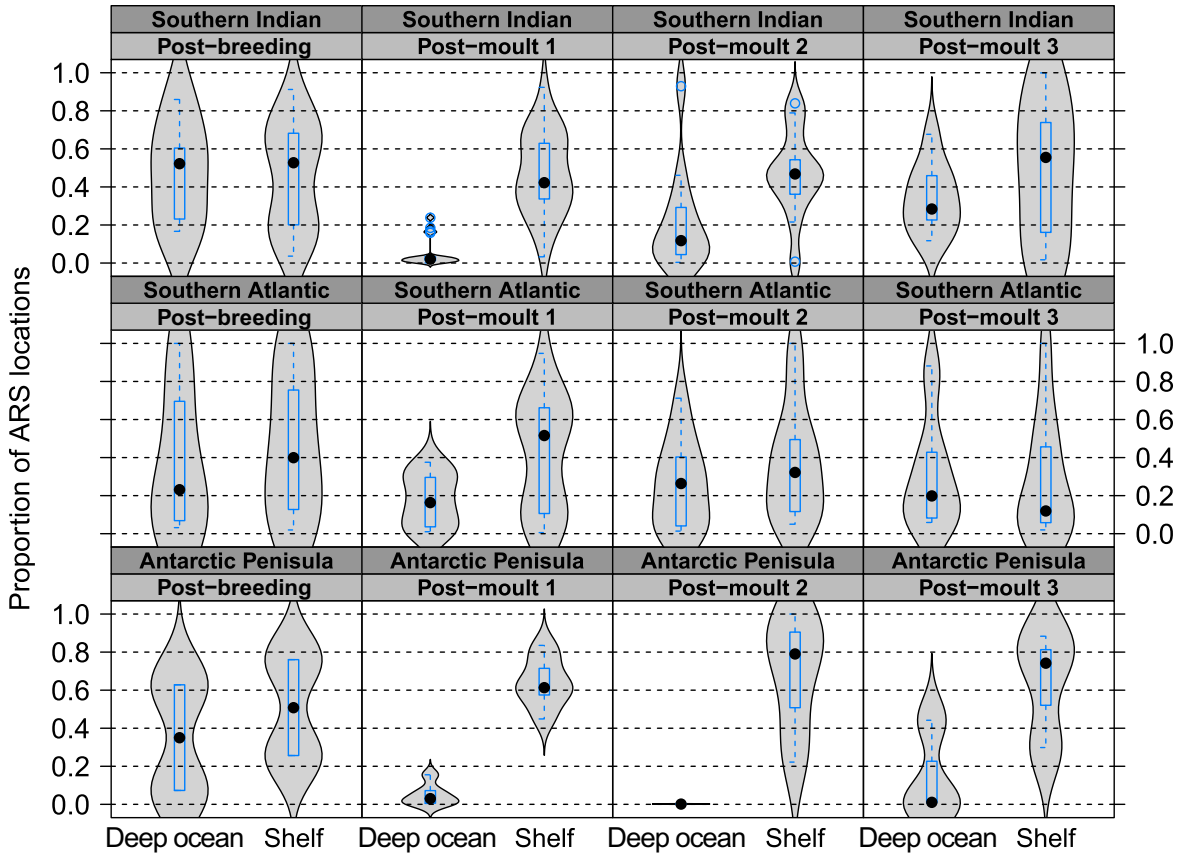

Fig. 7. For males, the mean proportion of area-restricted search locations made by an individual that occurred in each habitat in each season.

in ARS mode; however, CDW_n and $mCDW_d$ were associated with an increased likelihood of being in transit mode.

Comparing elephant seal population trends to seasonal habitat use

Since the last review of southern elephant seal population status in 2005 (McMahon et al. 2005*a*), there has been a modest (0.61%) increase (% change = $[(N_{t+1} - N_t)/N_{t+1}] \times 100$) in the global abundance of elephant seals from 744,755 to 749,385 seals (Table 6). This increase has not been uniformly spread across populations; it is principally due to a few rapidly growing populations such as the one at Peninsula Valdés, and the stabilization of several of the previously decreasing populations such as the Kerguelen stock. The suggested increase in the South Georgia stock is an artifact of the inclusion of the previously excluded population at Elephant Island, so it is likely that this population has actually remained stable. The Macquarie Island population stands out as anomalous compared to all of the others, as it continues to decrease (Table 6).

Discussion

Air-breathing marine predators, (whales, seabirds, and seals), can be regarded as either "divers", such as fur seals and petrels which spend most of their time on the ocean surface making brief excursions into the water column, or "surfacers", such as elephant seals and beaked whales, which spend most of their time at depth only returning briefly to the surface to re-oxygenate (Kramer 1988, Houston and Carbone 1992). Regardless of their classification in this regard, all diving predators inhabit a complex three-dimensional environment (i.e., one that

Table 5. The proportion of locations (%) occurring in each of the 12 water masses used by the southern elephant female and male seals equipped with CTD-SLDRs in this study by season; Postbreeding (PB = November to January) and the three Postmolt (PM1 = February–April), PM2 = May–July, PM3 = August–October) periods. The water mass at a location was determined by the physical characteristics of the water mass at the median dive depth of individual seals within 4 h of the time of that location. There were 295,284 locations out of a total of 568,136 for which a water mass could be assigned. See Table 1 for abbreviations.

	Post breeding		Postmolt 1		Postmolt 2		Postmolt 3	
Water mass	Females	Males	Females	Males	Females	Males	Females	Males
SASW	0.1	0.0	0.0	0.8	0.6	0.9	1.1	0.3
SAMW	0.3	0.0	0.1	0.1	0.9	0.6	1.7	1.0
AAIW	17.3	0.3	3.7	5.8	10.1	10.7	15.2	8.1
CDWn	22.0	2.4	5.6	4.0	7.7	7.0	11.7	7.9
AASW	37.8	41.9	46.7	46.8	39.8	40.9	27.3	25.8
CDWs	11.4	29.8	7.8	13.9	9.4	12.7	13.6	8.6
mCDW	6.0	20.5	22.1	20.4	18.8	22.1	15.8	39.1
MSWn	0.1	0.7	0.4	1.8	0.4	3.0	2.2	7.8
mCDWs	4.8	2.7	12.9	4.4	12.1	1.4	10.6	1.2
MSWs	0.2	1.4	0.5	0.7	0.2	0.6	0.9	0.0
DSW	0.0	0.3	0.2	0.7	0.0	0.0	0.0	0.0
ISW	0.0	0.0	0.1	0.7	0.0	0.1	0.0	0.0
Total locations	23,490	2971	84,244	20,226	89,383	11,930	54,335	8705

varies in time and space), as they use the water column, often to considerable depths, to forage. Quantitatively describing the habitats of marine predators is an essential task for ecologists, as this forms the basis of our understanding of their responses to varying environmental conditions and population viability. This is vital information for developing conservation oriented management policies and actions. For surfacers, this requires the integration of information not just on where animals occur geographically, but where they are within the water column. This requires multidimensional information on the environmental characteristics in the marine environment. Previous attempts to model habitat usage of diving species have only rarely included a vertical component in the analyses, and this might be part of the reason why the resulting models have relatively poor predictive capacity (Bradshaw et al. 2004*a*, Heerah et al. 2013).

In this study, we present a data set from the quintessential "surfacer"; the southern elephant seal, that performs extremely deep (2389 m) and extremely long dives (up to 2 h [Hindell et al. 1992]), returning to the surface for only short periods (approximately 2 min). This data set combines a large sample size of tracked animals that exhibited broad geographic coverage (the entire Southern Ocean) along with at-sea foraging metrics to: (1) describe the geographic distribution of core foraging areas and behavior of southern elephant seals in the Southern Ocean, (2) assess the relative quality of the habitats regionally, and (3) show how elephant seal population growth rates at the population (or stock) level may be related to at-sea habitat use. A great strength of this study was that it could use a comparative approach to contrast elephant seal populations across their range, which display a diversity of foraging ranges and habits to understand the differing population trends in this species.

Geographic distribution of foraging areas

Southern elephant seals are wide ranging, with most individuals traveling long distances from their breeding and molting sites to forage, and in so doing traversing all of the Southern Ocean. The circumpolar coverage offered by this vast International Polar Year, MEOP data set provided a unique opportunity to study how seals behave in different habitats and to compare regional differences in behavior. There were differences in the distances that seals traveled to foraging zones with respect to both sex and geographic

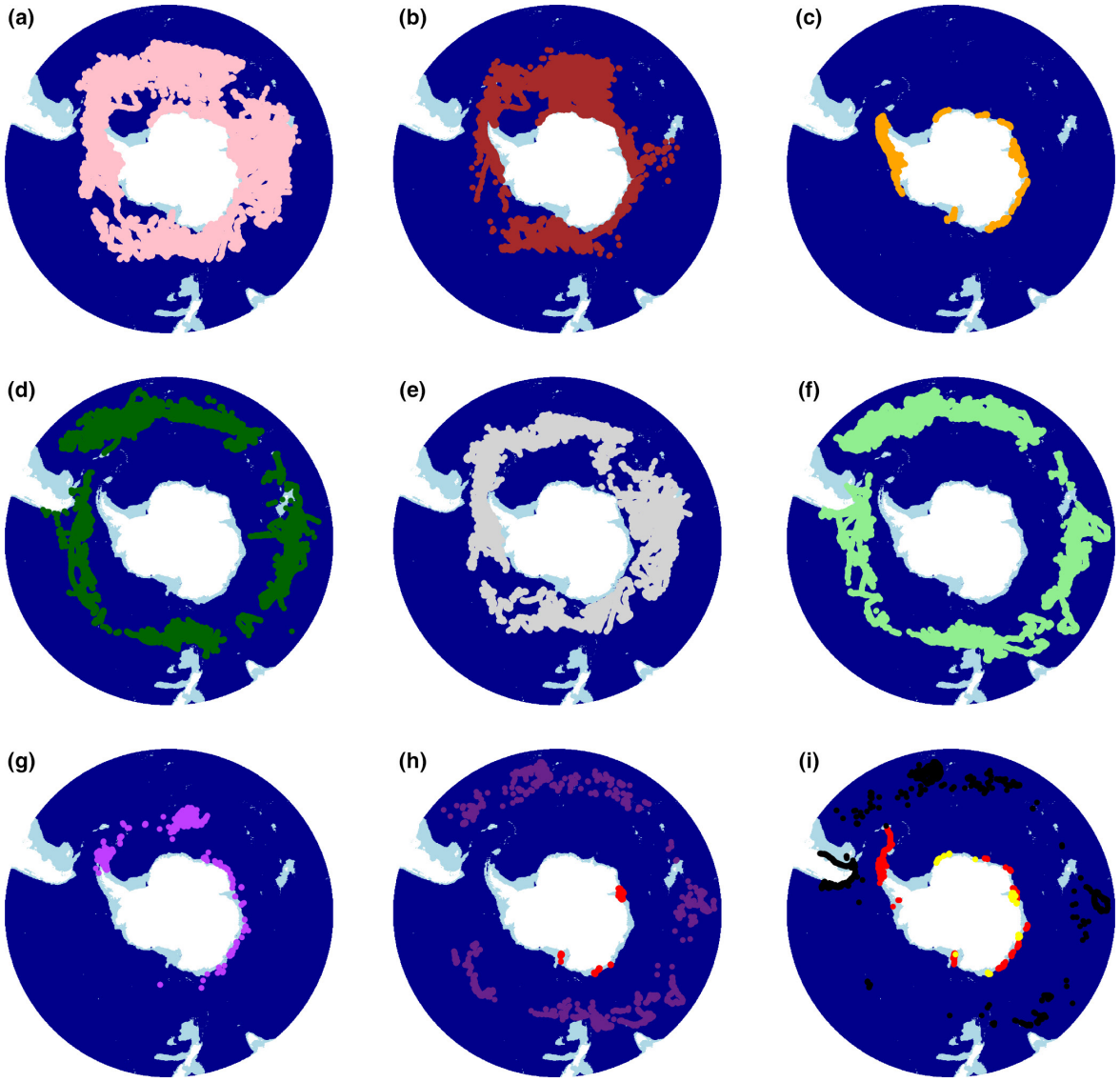

Fig. 8. The distribution of the 12 water masses used by seals. (A) Antarctic Surface water (AASW), (B) Modified Circumpolar Deepwater (deep) (mCDWd), (C) Modified Circumpolar Deepwater (shelf) (mCDWs), (D) Circumpolar Deepwater (north of Polar Front) (CDWn), (E) Circumpolar Deepwater (south of Polar Front) (CDWs), (F) Antarctic intermediate Water (AAIW), (G) Modified Shelf Water (north) (mSWn), (H) Subantarctic Mode Water (SAMW-purple dots) and Deep Shelf water (DSW- red dots), (I) Modified Shelf Water (south) (mSWs – red dots), Subantarctic Surface Water (SASW – black dots) and Ice Shelf Water (ISW – yellow dots).

region. Female seals in the South Pacific region traveled on average twice as far as those in the Antarctic Peninsula region (2975 ± 1098 km vs. 1464 ± 767 km). On average male seals traveled less far than female seals, most likely due to their greater use of the shelf regions with in particular males from Elephant Island, the Antarctic Peninsula and South Georgia remaining close to their island haul-out sites.

We used hierarchical behavioral switching state-space models to distinguish between rapid and directed "transit" behavior and "ARS" behavior, where the animals slowed down and made numerous changes in direction. ARS is an accepted

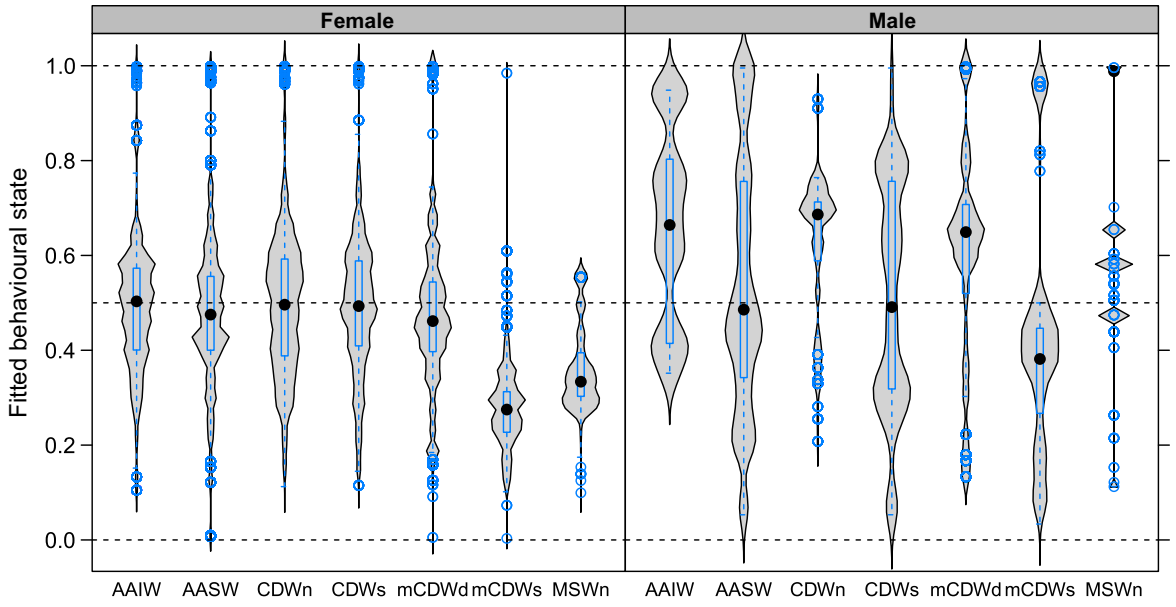

Fig. 9. Fitted values for mean behavioral state (0 = area-restricted search [ARS], 1 = transit) from the generalized linear mixed effects models relating behavioral state to sex and water mass. Shown are the kernel density plot for each water mass, superimposed on the boxplot, illustrating the median (black dot), interquartile range (box), and the range (dotted lines). The horizontal line indicates the 0.5 baseline, where there is equal likelihood of ARS and transit. Points above this line indicate that the behavior for that water mass was predominantly Transit, while below the line the behavior was predominantly ARS.

indication of foraging activity among pinnipeds. Although we have no independent confirmation that ARS behavior was actually associated with foraging in this study, all the evidence to date points to a strong positive correlation between ARS and active foraging (Thums et al. 2011, Dragon et al. 2012). Overall, the seals spent similar amounts of time in transit and ARS, but this varied regionally and with sex. The seals from the Southern Pacific regions traveled furthest to get to their foraging sites and spent the least amount of time engaged in ARS (38% of all locations).

The Southern Ocean is characterized by fronts, inter-frontal zones, and gyres, which are persistent in space and time, as well as numerous eddy systems associated with the fronts, particularly the Antarctic Polar Front. Due to mixing and concentration of nutrients, fronts and eddies have long been known to be associated with increased primary production, and also increased densities of predators (Hyrenbach et al. 2002, Bost et al. 2009, Joiris and Dochy 2013). However, despite the greater productivity associated with fronts, they are often not focal sites for foraging activity (Bestley et al. 2010, Staniland et al. 2012) as we found in this study. While ARS did take place in the Antarctic Polar Frontal zone, ARS also occurred widely across the Southern Ocean with the least used areas being the Weddell Sea and the waters south of Marion Island. However, it must be noted in this regard that there were relatively few data south of Marion Island, so the apparent absence of foraging activity by elephant seals in this area might be due to under-sampling rather than it being a region of low interest to the seals. However, since the IPY MEOP project period, there have been over 100 animals tracked from Marion Is and there is little evidence that they use this area (McIntyre et al. 2011*b*, 2012). In contrast, the Weddell Sea was within the potential range of the seals from South Georgia and the Antarctic Peninsula and was well sampled in terms of a high number of seals that could potentially have used this area, suggesting that they choose not to use it, perhaps because of the heavy pack-ice that is common in this region. These areas of relatively low use also correspond to the three major Southern Ocean gyres.

Table 6. The estimated populations sizes and trends in southern elephant seals. Overall the circumpolar population has remained stable. Numbers in brackets are the number of female seals counted at a breeding site on the 15th October, i.e., the day of maximum female haul-out during the breeding season and the day when all censuses are done.

Stock and location	Pre-1970s	1990s	2000s	Size –2010s	References	Current status
South Georgia						
South Georgia	350,000	357,000	397,054	397,054	Boyd et al. (1996)	Stable
South Orkney Island	350	20	20?	20?	Laws (1994)	Unknown
South Shetland Island	1050	2300	8050 (2300)	8050 (2300)	Laws (1994)	Unknown
Livingston Island				5530	Gil-Delgado et al. (2013)	Increasing
Elephant Island				696		Increasing
Falkland Island	3500	3500	1827	1929 (551)	Galimberti and Boitani (1999)	Stable
Gough Island	350	105		63	Bester et al. (2001)	Decreasing
Bouvet Island				329 (94)	Kirkman et al. (2001)	Unknown
Stock total	355,250	362,925	406,951	413,671		Increase/ stable
Kerguelen						
Isles Kerguelen	157,500	143,500	153,237	153,237	Authier et al. (2011)	Stable
Heard Island	80,500	40,355	61,933	61,933	Slip and Burton (1999)	Stable?
Marion Island	3850	2009	2009	1582 (452)	McMahon et al. (2009)	Increasing
Prince Edward Island	Unknown	782		410	Bester and Hofmeyr (2005)	Decreasing
Isles Crozet and Possession I	10,500	2023	1995	1995	Guinet et al. (1999)	Increasing
Stock total	252,350	188,669	219,174	219,157		Stable
Macquarie						
Macquarie Island	136,500	77,791	76,000	60,298 (17,228)	van den Hoff et al. (2014)	Decreasing
Antipodes Island	Unknown	400	249	249	Anonymous	Decreasing
Campbell Island	455	20	<10	<10	McMahon et al. (2005*a*,*b*)	Decreasing
Maatsuyker Island	1	1	3	4	This study	
Stock total	136,956	78,212	76,262	60,561		Decreasing
Peninsula Valdés						
Peninsula Valdés	13,800	33,726	42,371	56,000	Ferrari et al. (2013)	Increasing
Stock total	13,800	33,726	42,371	56,000		Increasing
Total population estimate	758,355	663,531	744,755	749,385		Stable

Broad-scale use of the inter-frontal regions of the Southern Ocean have been reported for a number of predators, including elephant seals (Campagna et al. 2006, Dragon et al. 2010, McIntyre et al. 2011*a*), Antarctic fur seals (Lea and Dubroca 2003, Staniland et al. 2012), and king penguins (Trathan et al. 2008). Animals may respond to prey being concentrated by eddy-induced isopycnal shoaling and upwelling in the inter-frontal zones (Dragon et al. 2010, d'Ovidio et al. 2013). However, the degree to which eddies are important in the overall energy budget of predators is yet to be quantified (Bailleul et al. 2010). What is apparent from this comprehensive study is that predators can forage successfully in the deep ocean utilizing relatively sparse and patchily distributed prey. There is clearly sufficient food in the deep ocean for the seals in our study that foraged there to meet their energetic requirements for traveling, breeding, gestation, and maintenance.

Habitat quality

Habitat quality can be measured in many ways for different types of animals. For elephant seals,

relative change in body condition is detectable via changes in buoyancy of the animals themselves measured as the drift rates of dives (Crocker et al. 1997, Schick et al. 2013, New et al. 2014) and this measure has been shown to be a useful assessor of habitat quality (Biuw et al. 2003). However, due to the data compression algorithms used in the CTD-SLDRs, this metric was not available to us in this study. We therefore assessed the relative quality of the various habitats in terms of the proportion of locations in that water mass when the seals were performing ARS, with water masses with relatively more ARS locations being indicators of higher quality habitat than those with more transit locations.

Using this interpretation, Shelf waters were consistently higher quality locations than Deep Ocean waters for both sexes although the difference was less pronounced in the South Pacific region. Shelf waters were used by seals in all four regions, indicating that overall the shelf is important to elephant seals. However, the relative importance of the shelf for elephant seal foraging varied geographically and with sex, with seals on the Antarctic Peninsula using shelf waters more than in any other region, while those in the Southern Pacific used deepwater areas most often. The importance of the shelf waters is confirmed by the rates and amount of resources adult female elephant seals can accumulate and store when frequenting these waters. Adult female seals from Macquarie Island increase their lipid content faster when feeding on the shelf than in off-shelf waters (Thums et al. 2011, Schick et al. 2013), confirming that this is a particularly rich area for the seals from this population even though they use it relatively rarely. The preference exhibited by males for these productive shelf waters may be due to their higher absolute energetic demands in this highly dimorphic species. Given that only the largest and fittest males hold harems, and sire the most offspring (but see de Bruyn et al. (2011) for evidence suggesting an alternative strategy by some males), if follows that they would evolve foraging strategies that maximize growth rates via maximizing their residence times in the best foraging habitats.

It seems that Antarctic shelf waters provide prime habitat for both sexes, but that males use them more than female seals because female seals generally leave, or are forced to leave, by the advancing sea ice. Seals from all regions and both sexes moved northward during the winter, but this movement away from the Shelf waters was most pronounced for females. However, even females remained in the ice year-round in the Antarctic Peninsula region, but they used it least in late winter when the ice was densest and at its most northerly extreme. Female seals move north as the ice expands up the Antarctic Peninsula, along the shelf rather than off it, which helps explain the high use of the shelf year-round by female seals in this region. Further, the female seals on the Antarctic Peninsula seem to be more tolerant of sea ice than females from other regions, given that more ARS locations were made in the sea ice on the Peninsula (up to 30%) than in other regions. The ability to forage in sea ice may be related to body size (Bailleul et al. 2008); large females have been reported to use higher ice concentrations than smaller females (Muelbert et al. 2013) and females that breed on the islands of the Antarctic Peninsula and South Georgia are larger than those from other breeding sites (Burton et al. 1997, Postma et al. 2013), which may confer an advantage in terms of foraging success, and ultimately offspring survival (McMahon et al. 2000*a*, 2003). The ability of large females to use the sea ice zone efficiently related to them being physically more capable of breaking through the ice to breath, and consequently being able to remain in these resource rich zones for longer.

Why is the shelf a high-quality habitat?

Our ability to collect ocean data concurrently with diving data is a relatively recent, and important, technological development (Lydersen et al. 2002) that greatly improves our capacity to quantify the oceanic habitats used by marine animals at spatial and temporal scales that are appropriate to their own movements (Biuw et al. 2007, Charrassin et al. 2008). Prior to the availability of animal-borne CTD-SRDLs, habitat models had to rely largely on remotely sensed data which often only provide information on the ocean surface, and which are available at temporal and spatial scales that are much larger and coarser than those at which marine predators make foraging decisions. In this study, we used temperature, depth, and salinity profiles collected by the seals to derive neutral density values and then allocate a water mass type to

the vertical foraging locations of the seals. The three-dimensional distribution of water masses in the Southern Ocean is broadly predictable in terms of latitude and longitude, but can be highly dynamic at finer spatial and temporal scales (Klinck and Dinniman 2010). Water masses are a convenient and appropriate habitat descriptor as their differing origins and circulation patterns mean that they have divergent amounts of mixing, nutrients, phytoplankton, and zooplankton, which attracts different types and amounts of prey for higher trophic animals.

To better understand the biological differences between the shelf and deepwater habitats, we used the "target" water mass (*i.e.,* the water mass that the seal was in during the bottom phase of its dive). This was because each of these larger habitats is comprised of a number of water masses. For example, the Antarctic continental shelf (including the upper continental slope to 1000 m) has DSW, Ice Shelf Water (ISW), $mCDW_S$, and MSW_N. In contrast, the deep ocean north of the southern boundary front of the ACC and south of the Polar Front predominantly contains CDW and AAIW, while north of the Polar Front the deep ocean contains SAMW. mCDW is CDW that upwells onto the Antarctic Continental Shelf.

The effect of water temperature on diving performance of southern elephant seals has been reported previously, with seals performing longer dives in cooler waters (McIntyre et al. 2011*a*). Although McIntyre et al. (2011*a*) lacked the *in situ* salinity observations needed to identify specific water masses, the results of that study are consistent with seals responding to one of the primary characteristics that defines the different water masses. The behavioral mode of the seals in our study was also influenced by the water masses in which they were swimming/diving. ARS was most likely to occur in, $mCDW_S$ (both males and females) and MSW_N (females only). These two water masses are associated with the shelf region and upper continental slope, respectively, where cold nutrient rich mCDW move up into the eutrophic zone, stimulating primary productivity. Another earlier study, using a subset of the data in this study, also found that the seals acquired the most body fat in areas where upwelling of mCDW occurred (Biuw et al. 2007). The circulation and enhanced mixing patterns of these best quality habitats, and in particular the presence of mCDW, seem to explain why Antarctic Shelf waters are such an important region for elephant seals.

Habitats of marine predators are often described in terms of oceanographic properties and water masses because more direct measures of important habitat characteristics such as prey densities are very difficult to obtain in oceanic environments (Hindell 2008). Nonetheless, our analysis confirms that elephant seals use different water masses in the Southern Ocean differently, and that some are used more than others for foraging. However, rather than targeting a specific water mass, seals may simply be targeting areas of high mixing and presumably concomitant high prey concentrations due to the higher turnover of nutrients within the water column.

Habit use and population trends

The combined effects of differing habitat quality, differing responses to encroaching sea ice as the winter progresses and differing distances between breeding sites and the best foraging locations in combination explain the differing population trends observed among elephant seals across the Southern Ocean. The population from Macquarie Island (which used both the Southern Indian Ocean and Southern Pacific regions) is undergoing long-term and continuing declines, while seals from the Kerguelen Islands (which declined substantially in the recent past and have now stabilized) used the Southern Indian Ocean region. Seals from both of these areas spent relatively little time in high-quality Antarctic continental shelf waters, and their breeding sites are furthest from the shelf. In contrast, the population breeding on South Georgia, which has been stable for many decades, used both the Southern Atlantic and the Antarctic Peninsula. The Peninsula is relatively close to South Georgia. Seals used this particular shelf habitat more and for longer than any other region, even when sea ice formed during winter. And although relatively small currently, the population of seals that breed on the islands closest to the Antarctic Peninsula are currently increasing. In this study, this stock comprises animals from Livingston and Elephant islands. These seals do not have to travel far at all to reach shelf habitats, and may even have the added advantage of being more tolerant to sea ice, by being substantially

bigger, enabling them to remain on the shelf further into the winter season, despite the presence of sea ice (Burton et al. 1997, Carlini et al. 1997, Muelbert et al. 2013, McIntyre et al. 2014). Further, the Antarctic Peninsular region is highly dynamic with extensive inlets, fjords, and tide cracks relative to other regions, which might increase the availability of leads in the ice so the seals can remain in the area longer.

This broad pattern, linking population growth rates and their relative access to high-quality habitat, strongly suggests that net energy gain during the winter months by foraging seals, and in particular gestating females, influences recruitment into the breeding population (van den Hoff et al. 2014). This is most likely mediated through weaner and juvenile survival both of which are sensitive to maternal condition (McMahon and Burton 2005, McMahon et al. 2005*b*). Female southern elephant seals, like other capital breeders, rely on the energy acquired and stored during their postmolt foraging trip to subsequently raise their pups (Arnbom et al. 1993, 1997). The amount of energy collected and stored during these trips influences both pup size at birth and at weaning and the subsequent survival of the pups in the first years of their life (McMahon et al. 2003, McMahon and Burton 2005). This early investment period has broad consequences at the population level so that survival during the juvenile phase is an important determinant of population growth rates (McMahon et al. 2005*b*). Because the annual number of female seals at their natal beaches is the primary metric used to determine population size (McMahon et al. 2009), it follows that lower rates of survival negatively affect recruitment rates and hence population size.

Long-term trends in sea ice extent around the Antarctic are correlated well with our broad interpretation of what is happening in the various stocks. Unlike the situation in the Arctic, where there have been major, broad-scale decreases in sea ice extent and duration, the Antarctic shows considerable regional variability in sea ice patterns (Cavalieri and Parkinson 2008). The Southern Pacific region in our study is a region in which sea ice extent has been increasing over the last several decades (Maksym et al. 2012). The Southern Annular Mode (SAM) has been in a positive phase for the past two decades (Simpkins and Karpechko 2012) and is associated with increasing sea ice extent in this region. Thus, the seals from Macquarie Island (ongoing population decline) that use the South Pacific region have been increasingly excluded from productive foraging areas, which is consistent with the long-term decrease in the number of breeding seals in this population (van den Hoff et al. 2014). The area encompassed by our Southern Indian region has been quite variable, experiencing both slight increases in sea ice extent in the East and slight decreases in sea ice extent in the West. This means that the Macquarie Island animals that use this region are also experiencing increases in ice extent in their foraging areas. Seals from the Kerguelen Islands (initial decrease and now a stable population), which use the entire southern Indian Ocean region will have had highly variable access to shelf waters dictated by annual ice extent across their range. In contrast, the Antarctic Peninsula region has exhibited marked decreases in sea ice extent (−7% *per annum*) and seasonal duration of the ice (Maksym et al. 2012), which has resulted in increased access to the favored shelf region for the seals from the Antarctic Peninsula (increasing population) and South Georgia (stable population). The situation at South Georgia is complex given that many of the animals from this island also feed in the South Atlantic sector, which has had slight increases in ice extent. This interpretation only holds true if the seals do not readily switch between foraging areas, but this appears to be the case, elephant seals have a high degree of individual foraging site fidelity over periods of up to 10 yr (Bradshaw et al. 2004*b*, Robinson et al. 2012).

The small population from Marion Island, which feeds in both the Southern Atlantic and in the Southern Indian regions, runs counter to the arguments outlined above. This population has been undergoing a steady population increase over the last decade. Simultaneously, ice has increased in the western part of their range and decreased in the eastern. The apparent contradiction between population trend and ice extent patterns might be due to the fact that the animals from this population make relatively little use of the Antarctic shelf (Jonker and Bester 1998, McIntyre et al. 2011*a*).

This study illustrates that deep ocean habitat, particularly the inter-frontal zone south of the

Antarctic Polar Front (APF), is at the very least, adequate habitat, which is used by individuals from all regions. Seals from each of the populations display two strategies (Deep Ocean vs. Shelf foraging), which are maintained in the population because presumably they have on average, resulted in similar fitness consequences (Brommer 2000). Seals feeding on the shelf have higher energetic returns in some years, but this is a riskier strategy because inter-annual variability in sea ice may mean that in some years seals foraging in these areas do less well (van den Hoff et al. 2014). Seals feeding in the deep ocean may have on average a lower, but a more certain return, and so are able to breed successfully each year (Authier et al. 2012). Changing sea conditions in recent decades may now favor the shelf-feeding strategy in the Antarctic Peninsula region by providing a more consistent energetic return across multiple years.

This study demonstrates clear advantages of integrating biological data with *in situ* physical oceanography data in order to explore marine predator behavior and population dynamics. This approach allowed us to quantify how changes in the environment, both within and among years, affected the behavior of animals and how this is likely translated into populations growth rates, which remains a central theme in ecology (New et al. 2014).

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Marine Mammals Exploring the Oceans Pole to Pole (MEOP) is an IPY (International Polar Year) project that coordinates researchers and institutions from eight different countries in its Southern Ocean team (http://www.meop.info/en/partners/). This synoptic project allowed us for the first time to quantify those factors determining habitat selection by key polar marine mammal species and we are grateful to all the field personnel who assisted us so ably in attaching instruments to elephant seals at the many sites where MEOP deployments took place.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1213/supinfo