Geographic variation in at-sea movements, habitat use and diving behaviour of female Cape fur seals

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ABSTRACT: Knowledge of animal foraging behaviour has implications for management and conservation. While Cape fur seals *Arctocephalus pusillus pusillus* comprise a major proportion of the southern African marine predator biomass, little is known about their at-sea movements. We investigated foraging distribution, habitat use and diving behaviour for 35 adult female Cape fur seals from 3 breeding colonies experiencing contrasting oceanographic regimes. Animals from Black Rocks, the smallest and eastern-most colony, undertook shorter foraging trips and utilised shallower waters over the shelf. In comparison, animals from the larger west coast colonies, at Kleinsee and False Bay, travelled further and utilised deeper shelf and shelf-slope waters. However, across colonies, females typically preferred depths of <500 m and slopes of <5°. Kleinsee and False Bay seals selected sea surface temperatures within the range typically preferred by pelagic prey species such as round herring, sardine and anchovy (14–19°C). Black Rocks individuals showed bimodal preferences for colder (16°C) and warmer waters (>22°C). Dive behaviour was similar between Kleinsee and False Bay individuals (unavailable from Black Rocks), with both pelagic and benthic foraging evident. Diel patterns were apparent at both sites, as dive depth and benthic diving increased significantly during daylight hours, likely reflecting vertical movements of prey species. We provide the first assessment of Cape fur seal movement behaviour for the South African component of the population. Observed geographic differences likely reflect the availability of suitable habitat but may also indicate differences in foraging strategies and density-dependent effects throughout the range of this species.

KEY WORDS: *Arctocephalus pusillus pusillus* · South Africa · Benguela · Agulhas · Habitat selection · Movement ecology · Inter-colony differences · Top predators

1. INTRODUCTION

Marine top predators are a crucial component of the marine food web and play a key role in ecosystem structure and function (Coleman & Williams 2002, Roman et al. 2014). These animals forage in a highly dynamic environment, and their foraging strategies largely depend on the spatiotemporal distribution of their prey (Croxall et al. 1985, Weimerskirch et al. 1994). As such, the importance of identifying productive foraging areas of marine predators, and their association with oceanographic features and metrics of biological productivity, has increasingly been recognized (Guinet et al. 2001, Lea &

Dubroca 2003, de Bruyn et al. 2009, Wakefield et al. 2009, Kirkman et al. 2016b, Pistorius et al. 2017). This spatial information is fundamental for ecosystem-based management, informing bycatch reduction measures, reducing competition with fisheries and developing specific area-based management measures (Lombard et al. 2007, Corrigan et al. 2014, Hays et al. 2016, 2019, Augé et al. 2018). In addition, marine top predators are often advocated as sentinels, with knowledge of their foraging behaviour considered useful as a proxy to measure environmental change (Hindell et al. 2003, Hazen et al. 2019). This is especially relevant for land-breeding predators such as seals and seabirds, many of which must balance foraging trips at sea with regular periods of offspring attendance at breeding colonies (Shaffer et al. 2003, Costa 2007, Harding et al. 2007). These attendance patterns thus restrict their distributional range and may increase their sensitivity to environmental change (Fretwell & Trathan 2019).

Ecological studies using animal-borne data loggers have proven valuable towards identifying areas of ecological importance which may warrant protection (Raymond et al. 2015, Reisinger et al. 2018, Hindell et al. 2020) and for the purpose of monitoring changes in the marine environment (Biuw et al. 2010, McIntyre et al. 2011, Hoskins & Arnould 2014). However, despite a marked increase in the number of tracking studies involving seals and seabirds in recent years, information is still lacking for many species. In addition, foraging behaviour has often been inferred from the study of a small component of a population (e.g. individuals from a single breeding colony), which may not be representative of the entire population (Wege et al. 2016). This is of concern, as conspecifics inhabiting geographically distinct breeding areas are often subject to different oceanographic conditions which may drive variability in foraging behaviour. Indeed, there is increasing evidence of geographic differences in the foraging strategies (Lea et al. 2008, Staniland et al. 2010, Hückstädt et al. 2016), habitat use (Lowry et al. 2000, Robson et al. 2004, Baylis et al. 2018) and diet or trophic ecology (Drago et al. 2016, Handley et al. 2017, de Lima et al. 2019) within marine top predator species.

The Cape fur seal *Arctocephalus pusillus pusillus* is endemic to southern Africa and breeds at numerous colonies extending from the south coast of Angola to the southeast coast of South Africa (Kirkman et al. 2013). The total population size is estimated at 1.5–2 million individuals, the majority of which are concentrated within the Benguela Ecosystem (Benguela) (Kirkman et al. 2007). The species comprises a major proportion of southern Africa's marine predator biomass, previously estimated to consume ca. 2 million tonnes of prey per year (Punt et al. 1995). While Cape fur seals are generalist feeders, the bulk of their diet consists of commercially important species such as sardine *Sardinops sagax*, anchovy *Engraulis encrasicolus*, Cape horse mackerel *Trachurus trachurus capensis*, hake (*Merluccius* spp.), West Coast rock lobster *Jasus lalandii* and chokka squid *Loligo vulgaris reynaudii* (de Bruyn et al. 2003, 2005, Mecenero et al. 2006a,b, Huisamen et al. 2012, Connan et al. 2014). The composition of their diet also varies both spatially (David 1987, de Bruyn et al. 2003, Mecenero et al. 2006a) and temporally (de Bruyn et al. 2005, Mecenero et al. 2006b). Although the diet of Cape fur seals has been relatively well researched, surprisingly little is known about their foraging behaviour, including horizontal and vertical utilisation of the marine environment. A single study has reported the at-sea movements of foraging Cape fur seals, focussing on the Namibian component of the population (Skern-Mauritzen et al. 2009). In addition, published information on Cape fur seal diving behaviour is available for 2 individuals followed in 1977 (Kooyman & Gentry 1986) and 32 individuals in 2006–2008 (Kirkman et al. 2019), from a single breeding colony on the northwest coast of South Africa.

Continuation and enhancement of scientific monitoring of Cape fur seals has been petitioned for, partly based on increasing concerns over competitive interactions between seals and fisheries, as well as the need to establish indicators of ecosystem change in the Benguela (Kirkman et al. 2011). Baseline data on at-sea distribution and behaviour is a prerequisite for identifying potential overlap and interactions with fisheries and monitoring the ecological responses of Cape fur seals to environmental change. The latter is especially relevant given the vulnerability of the Benguela to climate change (O'Toole et al. 2001, Jarre et al. 2015) and potential effects of overfishing throughout the system (Coetzee et al. 2008, Roux et al. 2013). Shifts in the distribution of several important foraging species, including sardine, anchovy and West Coast rock lobster have already been documented throughout the Benguela (Roy et al. 2007, Coetzee et al. 2008, Blamey et al. 2012). Several studies have identified considerable implications of these shifts on the demographics and foraging ecology of seabird species including the Cape gannet *Morus capensis* (Pichegru et al. 2007, Grémillet et al. 2008), African penguin *Spheniscus demersus* (Crawford et al. 2011, Sherley et al. 2014) and Cape cormorant

Phalacrocorax capensis (Crawford et al. 2016). For these and other seabird species, consequences have been more detrimental for colonies in Namibia and on South Africa's west coast, while some colonies on South Africa's southeast coast may have benefited from the eastward shift in prey species, particularly anchovy (Crawford et al. 2009, 2014, Green et al. 2015, Grémillet et al. 2016). However, in the absence of baseline information on key attributes of the foraging ecology of Cape fur seals, the effects of these prey shifts on fur seals remains poorly understood.

Throughout its South African distribution, the Cape fur seal population is subjected to a wide range of oceanographic conditions, with substantial differences between the west and southeast coasts. The west and southwest portion of their range in South Africa is influenced predominantly by the cold, nutrient-rich Benguela Current, which is characterized by high levels of wind-driven upwelling (Hutchings et al. 2009, Kirkman et al. 2016a). In contrast, much of the south and southeast coast of South Africa is largely under the influence of the warmer Agulhas Current (Hutchings et al. 2009, Kirkman et al. 2016a). While this region is generally less productive, significant upwelling still occurs at localized sites (i.e. capes and shelf edges) (Goschen et al. 2012, 2015, Kirkman et al. 2016a). In addition to the physical oceanographic characteristics, the width of the continental shelf also varies substantially along the South African coast (Dingle & Rogers 1972). Therefore, given the varying conditions across the range of Cape fur seals in South Africa, site-specific foraging strategies may be expected, highlighting the need for a range-wide assessment of Cape fur seal foraging behaviour.

In this study, we considered 3 geographically separate Cape fur seal colonies with divergent adjacent oceanographic conditions, and investigated intra- and inter-colony variation in (1) at-sea movements, (2) marine habitat selection and utilisation and (3) diving behaviour. This was done to obtain a better understanding of behavioural plasticity in Cape fur seals, and accordingly, their capacity to adapt to future ecosystem changes driven by climate change or other impacts, and to identify important habitat to inform spatial management planning and decision-making concerning Cape fur seals. Lactating adult females were the focus of the study as they provide a good indication of local feeding conditions during periods of central-place foraging while provisioning pups, whereas other sex and age classes are free to roam in search of optimal resources (Kirkman et al. 2019).

2. MATERIALS AND METHODS

2.1. Study sites and data collection

Data were collected in June–September of 2014 and 2015 at 3 Cape fur seal breeding colonies: Kleinsee; Seal Island (False Bay); and Black Rocks (Algoa Bay) (see Fig. 1). The mainland colony at Kleinsee is located on South Africa's west coast and hosts the largest South African Cape fur seal population (estimated annual pup production of 50 000–80 000), while False Bay, situated on the southwest coast, hosts the second-largest island breeding population (estimated annual pup production of 14 000–19 000) (Kirkman et al. 2007). In contrast, the colony at Black Rocks, located within a national park on the southeast coast, is spatially restricted owing to the small size of the island and, thus, significantly smaller (estimated annual pup production of 300–500) (Kirkman et al. 2007).

At each study site, female Cape fur seals nursing pups were selected at random and captured using a modified hoop net based on the design of David et al. (1990), following which animal-borne data recording devices were deployed. At Kleinsee and False Bay, 29 animals were anaesthetised using isoflurane by means of a portable vaporizer (Stinger, Advanced Anaesthesia Specialists; Gales & Mattlin 1998). Once anaesthetised, individuals were removed from the net, weighed on a platform with a suspension scale (±0.5 kg) and several measurements, including standard length, axillary girth and fore-flipper length, were taken using a fibreglass tape measure (±0.5 cm). At Black Rocks, the devices were fitted on animals through the open dorsal aperture in the net while animals were restrained within the hoop net.

Individuals captured at Kleinsee were instrumented with either a GPS dive-behaviour logger (MK 10, Wildlife Computers) or a combination of a FastLoc GPS logger (Sirtrack) and a dive-behaviour recorder (MK9, Wildlife Computers). Individuals at False Bay were instrumented with Argos-linked FastLoc GPS-dive behaviour loggers (Splash F297A, Wildlife Computers) and individuals at Black Rocks, with platform terminal transmitters (PTTs; SPOT-287C, Wildlife Computers). At all sites, devices were attached to the dorsal mid-line pelage of the animal using a quick-setting epoxy (Araldite AW2101, CIBA-GEIGY). Following deployment procedures, the animals were allowed to recover from anaesthesia, released back into the colony and monitored until full recovery and resumption of normal behaviours. All devices used in the present study constituted

<1 % of the body mass of sampled individuals. As such, and based on findings from previous studies (McMahon et al. 2008, Field et al. 2012), no adverse influences on individual performance or survival were expected.

Females at Kleinsee were recaptured after they returned from a single foraging trip. Animals were located within the colony with the assistance of VHF-based tracking, with a VHF transmitter (Sirtrack) fitted to study animals during deployment. Devices were removed by cutting the fur beneath the devices using a scalpel. Owing to logistical constraints, including the offshore location of the colonies and risk of disturbance, individuals at False Bay and Black Rocks could not be recaptured and, thus, devices continued to transmit data until the battery failed or the devices moulted off.

2.2. Data processing and statistical analyses

2.2.1. Location data

All data processing and statistical analyses were conducted in R version 3.5.1 (R Core Team 2018). GPS devices deployed at Kleinsee were programmed to log location data at 10 min intervals. At False Bay, PTTs were programmed to transmit location data to the CLS Argos system every 90 s while at sea. This produced a complementary data set comprising both Fastloc GPS and ARGOS locations, both of which were incorporated into the study to increase the spatiotemporal coverage. PTTs deployed at Black Rocks were programmed to transmit location data at 90 s intervals.

Prior to filtering, all ARGOS locations of class Z were removed from the data. The remaining ARGOS and GPS locations were then processed following the methods of Austin et al. (2003), using a 3-stage filtering algorithm implemented with the package 'diveMove' (Luque 2007). Firstly, the filter removed locations that required speeds >3 m s^{-1} to travel to the 4 nearest neighbouring points. Secondly, the filter implemented a simple forward/backward speed filter (McConnell et al. 1992) with a speed threshold of 3 m s^{-1}. Finally, the remaining ARGOS locations were passed through the third stage of the filter which removed locations exceeding distances from the previous location, based on a user-defined threshold. Threshold values of 30.6 and 45.24 km were specified for False Bay and Black Rocks, respectively, corresponding to the 95th percentile of inter-location distances calculated for ARGOS locations of classes 1, 2

and 3. The use of this filtering method permitted the inclusion of both GPS and ARGOS locations, subsequently allowing for consistency across sites.

A foraging trip was defined as the period at sea between departure from and arrival back at the breeding colony. Where available, haul out and dive information was used to identify trip start and end times. However, where necessary, arrival/departure times were estimated from the nearest at-sea location, based on the average travel speed during the individual's foraging trip. Only complete trips, where individuals returned to the breeding colony, were considered for all further analyses. Following Skern-Mauritzen et al. (2009), at-sea periods of less than 24 h were also excluded, as these short trips may represent periods of thermoregulation and not foraging. Foraging tracks were then linearly interpolated using the package 'adehabitatLT' (Calenge 2006) to provide locations at an even fix frequency of 10 min.

For each filtered track, trip duration (d), total distance travelled (km), maximum distance attained from the colony (km) and bearing of the distal point (°) were calculated using the geosphere package (Hijmans 2017). Foraging trip metrics were compared between colonies by employing a linear mixed effects (LME) modelling framework to accommodate multiple foraging trips per individual using the package 'lme4' (Bates et al. 2015). Each model included colony as a fixed effect and individual ID as a random effect to account for repeated measures. Barring distal bearing, all foraging trip metrics were left-skewed and were therefore log-transformed prior to inclusion in the LMEs. To validate the LMEs, quantile–quantile plots were used to assess normality of residual spread, and model residuals were plotted against fitted values to assess homogeneity of variance.

Individuals are expected to spend more time in areas where search behaviour and foraging effort is concentrated (Péron et al. 2012). Therefore, time spent per grid cell was used as a spatial proxy of foraging distribution. For each interpolated track, the number of locations per square 0.05° grid cell (selected to aggregate several seal locations) were calculated using the package 'raster' (Hijmans 2018) and converted to the proportion of the foraging trip spent per grid cell. For individuals tracked over multiple trips, the proportion of time per grid cell was calculated as the total proportion of time at-sea across all foraging trips to ensure that individuals contributed equally to the sample. Finally, the proportion of time per grid cell was summed across individuals to produce a single layer for each colony grouping.

Oceanographic variables including depth, sea floor slope and sea surface temperature (SST) have previously been identified as important determinants of habitat use by marine predators (Reisinger et al. 2018, Hindell et al. 2020). Therefore, as a broad assessment of habitat use, data for each of these variables were collated for the at-sea range of the Cape fur seals from each colony. Depth data were obtained from the GEBCO 15-arc second grid (https://www.gebco.net) at 0.004° resolution, and used to calculate sea floor slope by means of the 'terrain' function in the 'raster' package. Daily SST values were obtained from the Multi-scale Ultra-high Resolution (MUR) SST data set (https://coastwatch.pfeg.noaa.gov) at 0.01° resolution. Environmental covariates were then spatiotemporally matched to each real and interpolated location. For each foraging trip, the proportion of time associated with pre-determined classes of depth (20 m), slope (0.5°) and SST (0.5°C) intervals was calculated. Environmental covariates were compared between colonies using LMEs with depth, sea floor slope and SST modelled in response to colony as a fixed effect. To account for repeated measures, a random effect of trip nested within individual was included in each model.

To determine habitat selection, knowledge of the habitat utilised in relation to potentially available habitat is required. Presence–pseudoabsence approaches have been used effectively for marine predators (Pistorius et al. 2017, Reisinger et al. 2018, Hindell et al. 2020) and were adopted in the present study. Following the methods of Raymond et al. (2015), 20 pseudo-tracks were simulated for each real track using a first-order vector autoregressive model, implemented using the 'availability' package (Raymond et al. 2016). Simulated pseudo-tracks were bound by a land mask, and characteristics of the real tracks were maintained through constraints on sampling frequency, distances, turning angles and departure and arrival locations. Locations of each pseudo-track were then spatiotemporally matched with the above environmental covariates.

The influence of depth, sea floor slope and SST on the probability of occurrence (presence) in relation to available habitat (pseudo-absence) were investigated using a binomial generalized additive model (GAM). The model fitted a binomial response variable of presence (1) represented by each real location and absence (0) represented by each pseudo-location. Response variables were modelled in relation to the environmental covariates fitted as smooth predictor effects, with separate splines fitted for each colony grouping. While it is possible to account for repeated

measures of individuals through the use of generalized additive mixed models (GAMMs), the incorporation of a random effects structure into the present study resulted in the model failing to converge. In addition, as the response intercept in question represents a constant ratio of presence (observed locations) to absence (simulated locations), including a random effects structure to account for individual variability presents little advantage (Raymond et al. 2015). Therefore, standard GAMs were used for habitat selection analysis.

2.2.2. Diving data

Data on dive behaviour were collected for females from Kleinsee and False Bay. At Kleinsee, dive behaviour data, obtained through archival dive recorders, provided complete dive records for each foraging trip at a resolution of 1 or 5 s. Dive data were corrected for depth drift, and summary statistics for each dive were produced using the 'diveMove' package (Luque 2007). In contrast, devices used at False Bay were programmed to store and transmit (at user-defined intervals) summaries of the diving data at 0.5 m depth resolution. To account for these differences, comparisons of diving behaviour were limited to the maximum dive depth and the probability of benthic diving.

Only dives greater than 4 m in depth were considered for further analysis (Kirkman et al. 2019). Dives were classified as either benthic or pelagic using a custom written, 2-stage routine based on the dive depth to bathymetric depth ratio (Baylis et al. 2015) and a modified version of the intra-depth zone (Tremblay & Cherel 2000). Firstly, the location of each dive was determined based on the nearest 10 min location linearly interpolated along the trajectory. Bathymetric depth data were then extracted for each dive location and the ratio of dive depth was divided by bathymetric depth. Secondly, the routine compared the depth of each dive to the depth of the previous and following dive. Dives were classified as benthic if the dive depth to bathymetric depth ratio was >0.9 (i.e. max depth was within 10% of the sea floor), and if the dive depth was within ±10% of either the previous or following dive, provided that the dives occurred within 1 h of each other.

GAMMs were used to investigate the influence of colony and time of day on diving behaviour using the 'mgcv' package (Wood 2015). Two separate GAMMs were fitted, the first using dive depth as a response variable and the second using a binomial response

variable indicating whether a dive was pelagic (0) or benthic (1). In each GAMM, colony grouping was fitted as a categorical parametric coefficient, and time of day (hour) was fitted as a smooth predictor with separate splines fitted for each colony grouping. To account for repeated measures across foraging trips and individuals, a random effect structure consisting of foraging trip nested within individual was incorporated into the GAMM. A significance threshold of $\alpha = 0.05$ was assumed throughout, and unless stated otherwise, all results are presented as mean ± SE.

3. RESULTS

At-sea distributions from 87 complete foraging trips were obtained for 35 female Cape fur seals between June and September of the respective study years (Table 1; Table S1 in the Supplement at www.int-res.com/articles/suppl/m649p201_supp.pdf). The number of foraging trips per individual ranged from 1 to 13. While the inclusion of multiple trips per individual may influence the results, preliminary analyses using only the first trip for each individual were not different from the results obtained when all trips per individual where included. Therefore, to increase the temporal coverage, all foraging trips per individual were retained for further analyses. During longer foraging trips of some of the females from the Kleinsee and False Bay colonies, haul-out behaviour at sites away from the breeding colonies was frequently recorded. One individual from Kleinsee hauled out at the Buchu Twins seal colony (15 km south of Alexan-

der Bay) during 2014 and remained at this site for 4 d, during which time she conducted 2 short trips to sea lasting 1.8 and 2.4 d and covering distances of 80.9 and 144.3 km, respectively (Fig. S1A). During 2015, another individual hauled out at the Strandfontein Point seal colony (30 km south of Hondeklip Bay) for 1 d before returning to the breeding colony at Kleinsee (Fig. S1B). Females from False Bay often hauled out at the Geyser Rock breeding colony, situated approximately 100 km southeast of False Bay (Fig. S1C), with haul-out durations lasting between 7 and 22 h. In all cases, haul-out periods on land were noted, and all at-sea periods in between haul-outs were considered as part of a single foraging trip until the individual returned to the breeding colony. Cape fur seals from the Black Rocks colony did not haul out elsewhere during foraging trips.

3.1. Foraging trip metrics and at-sea movements

Foraging trips of female Cape fur seals lasted between 1.3 and 29.0 d, during which time individuals traversed distances of 38.2 to 1342.8 km and reached maximum distances ranging from 13.7 to 335.8 km from the breeding colonies. For individuals from the Kleinsee colony, foraging trips were slightly longer during 2015 (duration: 7.4 ± 1.1 d, total distance: 412.3 ± 55.7 km) compared with 2014 (duration: 6.1 ± 1.03 d, total distance: 353.5 ± 60.1 km). However, these differences were not statistically significant (linear models, all p > 0.1, Table S2), and data were pooled over the 2 years.

The effect of colony on foraging trip duration and total distance travelled was not significant (LMEs, all p > 0.1), but there was a significant influence on maximum distance (LME, p < 0.05) and distal bearing from the colony (LME, p < 0.001) (Table 2). Foraging trip durations and distances of Black Rocks individuals were substantially shorter than individuals from Kleinsee and False Bay (Tables 1 & 2). However, across all sites, there was a high degree of variability among individuals. This was particularly evident for the False Bay colony, where 2 of the 5 individuals either remained in False Bay or traversed short distances (mean: 3.4 d, 138.4 km) to the neighbouring bays, travelling close to shore (Fig. S2B). The 3 remaining individu-

Table 1. Summarized foraging and dive metrics, as well as values of environmental variables encountered along trajectories of female Cape fur seals tracked from Kleinsee (n = 23 females), False Bay (n = 5) and Black Rocks (n = 7). Values are presented as mean ± SE; na: parameters not available

	Kleinsee	False Bay	Black Rocks
No. of trips	23	38	26
Duration (d)	6.9 ± 0.6	8.8 ± 2.5	5.4 ± 0.9
Total distance (km)	389.3 ± 30.1	469.1 ± 136.4	260.5 ± 34
Maximum distance (km)	137.4 ± 9.6	134.4 ± 37.9	81.2 ± 10.4
Distal bearing (°)	250.7 ± 8.6	143.5 ± 4.9	148.2 ± 22.2
No. of dives per trip	1134.6 ± 137.4	470.3 ± 100.1	na
Dive depth (m)	88.9 ± 6.0	75.6 ± 26.9	na
Dive duration (min)	2.9 ± 0.2	2.5 ± 0.5	na
Proportion of benthic dives per trip	0.35 ± 0.04	0.42 ± 0.1	na
Depth (m)	171.2 ± 10.1	125.5 ± 35.8	130.6 ± 31.9
Mean sea floor slope (°)	0.2 ± 0.02	0.5 ± 0.1	0.9 ± 0.3
Mean SST (°C)	13.6 ± 0.2	14.9 ± 0.5	18 ± 0.3

Table 2. Summary results of the linear mixed effects models for the effect of colony on foraging trip metrics and environmental covariates encountered during foraging trips of female Cape fur seals. KS: Kleinsee, FB: False Bay, BR: Black Rocks. Significant p-values (p < 0.05) are highlighted in **bold**

Response	Predictor	CE	SE	df	t	p
Duration	Intercept (KS)	1.9	0.1	68.4	13.5	**<0.001**
	FB	−0.1	0.2	28.1	−0.3	0.77
	BR	−0.4	0.2	40.5	−1.9	0.06
Total distance	Intercept (KS)	5.9	0.2	64.0	38.7	**<0.001**
	FB	−0.2	0.3	30.5	−0.8	0.44
	BR	−0.5	0.3	41.6	−1.9	0.06
Maximum distance	Intercept (KS)	4.9	0.1	62.7	33.7	**<0.001**
	FB	−0.4	0.3	30.1	−1.4	0.18
	BR	−0.6	0.3	40.9	−2.3	**0.02**
Distal bearing	Intercept (KS)	250.7	9.4	41.1	26.6	**<0.001**
	FB	−107.5	19.0	21.6	−5.7	**<0.001**
	BR	−107.1	17.7	27.9	−6.0	**<0.001**
Bathymetric depth	Intercept (KS)	5.0	0.1	36.2	45.7	**<0.001**
	FB	−0.5	0.2	27.9	−2.1	**<0.05**
	BR	−0.4	0.2	31.0	−1.9	0.05
Sea floor slope	Intercept (KS)	−1.9	0.1	42.1	−19.7	**<0.001**
	FB	0.7	0.2	19.6	3.7	**<0.001**
	BR	1.0	0.2	26.5	5.5	**<0.001**
Sea surface temperature	Intercept (KS)	2.6	0.01	43.5	181.7	**<0.001**
	FB	0.1	0.03	22.9	3.1	**<0.001**
	BR	0.3	0.02	29.7	10.4	**<0.001**

als undertook longer foraging trips (12.5 ± 2.9 d) and travelled substantial distances (688.5 ± 146.0 km), with foraging trip trajectories extending over much of the Agulhas Bank (Fig. S2A). Most animals from Kleinsee travelled to the west and southwest of the colony, although there was substantial variation between individuals (range: 45–243°; Table 1). Individuals from the False Bay population travelled mainly to the east and southeast of the colony (range: 99–189°). Distal bearings of animals from Black Rocks varied widely between individuals (range: 60–236°), with most travelling either to the southwest or east of the colony. Individuals tracked over multiple trips from False Bay and Black Rocks were relatively consistent in their durations, distances and headings across foraging trips (Table S1).

The at-sea movements from all 3 colonies were confined mainly to shelf (<200 m) and shelf-slope waters (<1000 m) (Fig. 1). The total at-sea range of Cape fur seals (sum of all 0.05° grid cells used) from Kleinsee, False Bay and Black Rocks covered an area of 4545, 4825 and 1975 km², respectively. For animals from Kleinsee, several grid cells incorporating a high proportion of time at-sea were associated with the shelf break (200 m) and deeper waters of the shelf-slope (200–1000 m) (Fig. 1). Individuals also spent a high proportion of time over the shelf in waters of

100–200 m directly to the west of the colony (Fig. 1). For False Bay individuals, the at-sea range was spread mainly southeastward over the Agulhas Bank (Fig. 1). Distribution patterns were similar to those of Kleinsee animals, with several 'hotspots' associated with the deeper waters of the shelf, shelf break and, to a lesser extent, the shelf-slope waters (Fig. 1). The eastern section of False Bay and the neighbouring Walker Bay also appeared to be an important foraging area (Fig. 1). This was, however, almost exclusively accounted for by the 2 individuals that remained close to the colony and travelled between these 2 bays (Fig. S2). The at-sea range of the Black Rocks animals was substantially smaller compared with individuals from the Kleinsee and False Bay colonies, with several 'hotspots' associated with the shelf break situated south of Cape Recife. However, individuals from Black Rocks also spent a large proportion of time in shallower waters (<100 m) on the shelf (in close proximity to the colony) but with minimal time spent within Algoa Bay (Fig. 1).

3.2. Habitat use and habitat selection

Seals moved over depths down to 1456 m and sea floor slopes up to 14°, with encountered SSTs ranging between 11 and 22°C. Available habitat as estimated by simulated locations ranged broadly at all colonies for depth (down to 4743 m), sea floor slope (0–52°) and SST (11–23°C). Analysis of habitat selection (presence) in relation to availability (pseudo-absence) revealed all fitted slopes to be significant (GAM, p < 0.001) (Table 3).

Depths encountered varied significantly (LME, p < 0.05) between colonies (Tables 1 & 2) with animals from Kleinsee, on average, encountering deeper areas more often than individuals from False Bay and Black Rocks (Tables 1 & 2). In addition, inter-colony differences in the proportion of time spent within pre-determined depth classes were apparent (Fig. 2). Individuals from Kleinsee spent the greatest proportion of time at sea in relatively deep waters ranging between 140 and 360 m (Fig. 2). Some individuals from the False Bay colony used similar depth classes to Kleinsee animals, on average spending a large
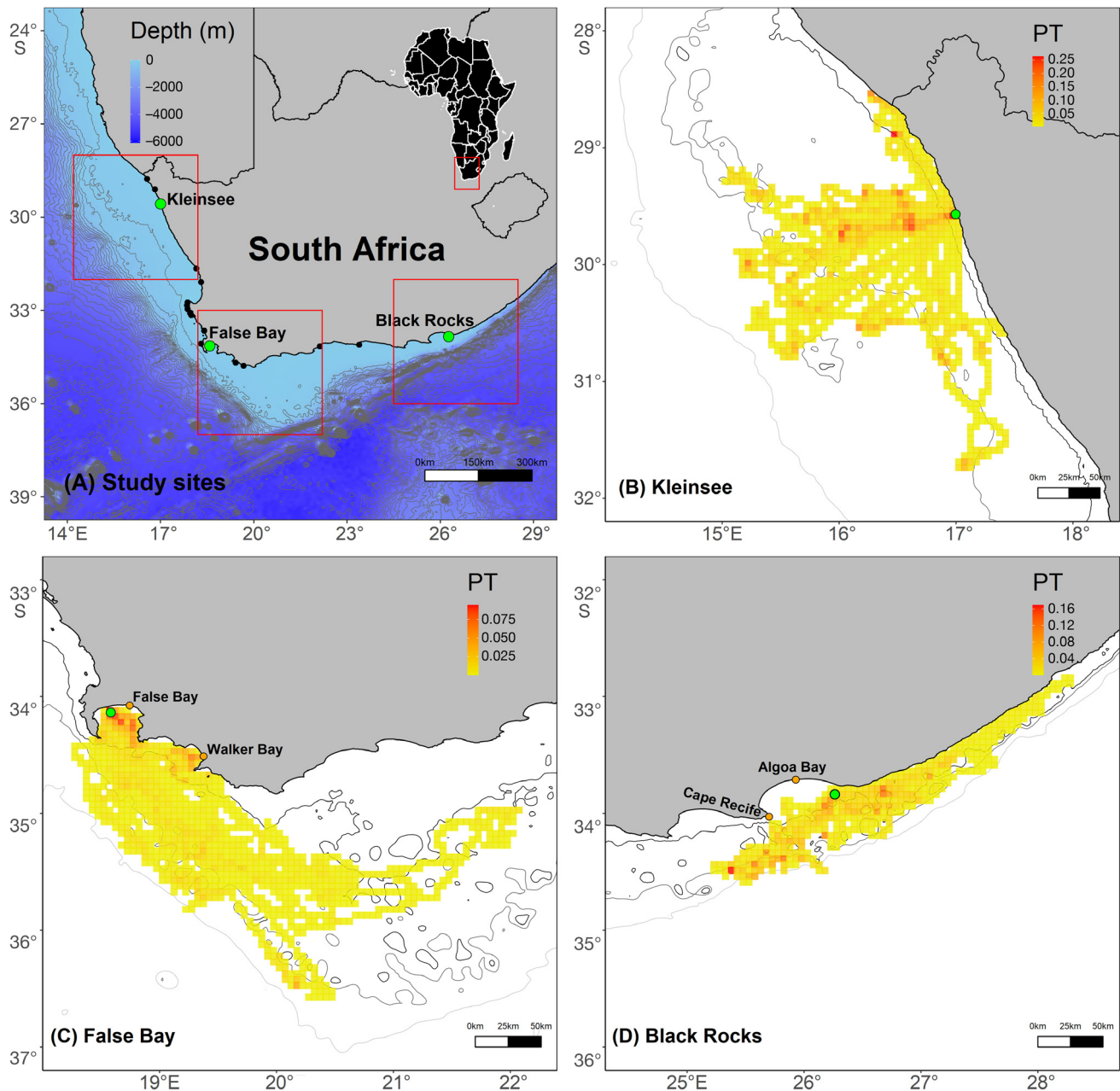
Fig. 1. (A) Study sites in South Africa and (B–D) the proportion of time (PT) spent per 0.05° grid cell for Cape fur seals from (B) Kleinsee, (C) False Bay and (D) Black Rocks. Study colonies are represented by a green dot and all other South African Cape fur seal breeding colonies by black dots. Bays and headlands are represented by orange dots. In (A), isobaths between 200 and 5000 m are shown in 200 m intervals. In (B–D), isobaths representing the 100 m (black lines), 200 m (dark grey lines) and 1000 m (light grey lines) depth contours are shown

proportion of time in waters ranging from 140 to 240 m. However, there was also a substantial proportion of time spent over shallower depth classes (20–80 m). While deeper waters of over 1400 m were encountered by Black Rocks individuals, very little time was spent in waters deeper than 140 m, with a clear peak over depths between 80 and 120 m (Fig. 2). Selection for depth in relation to availability

was similar across colonies, with animals selecting depths shallower than 500 m and with the probability of occurrence decreasing substantially between 500 and 1000 m (Fig. 3).

Sea floor slope varied significantly between colonies (LME, p < 0.001), with individuals from Black Rocks generally encountering steeper sea floor slopes compared to individuals from Kleinsee and False Bay

Table 3. Results from the generalized additive models for the influence of depth (m), sea floor slope (degrees) and sea surface temperature (°C) on the probability of occurrence (presence) in relation to the potential habitat available (pseudo-absence) of female Cape fur seals at Kleinsee (KS), False Bay (FB) and Black Rocks (BR). Dashes specify where either parametric coefficients or smooth terms were not fitted for a particular predictor effect. All smooth terms were significant (p < 0.05)

Response Predictor	Parametric coefficients			Approximate significance of smooth terms	
	Est	SE	z	Edf	F
Probability of occurrence					
Intercept	−2404.3	126.9	−18.95	–	–
Depth:KS	–	–	–	7.6	12883.8
Depth:FB	–	–	–	8.1	3313.3
Depth:BR	–	–	–	7.2	792.9
Sea floor slope:KS	–	–	–	5.5	1296.6
Sea floor slope:FB	–	–	–	5.0	127.4
Sea floor slope:BR	–	–	–	8.9	5347.2
Sea surface temperature:KS	–	–	–	7.4	1243.8
Sea surface temperature:FB	–	–	–	8.9	20243.0
Sea surface temperature:BR	–	–	–	8.7	2075.3

(Table 2). However, the use of sea floor slope classes was similar across colonies, with the greatest proportion of time spent over flat bottom areas with slopes of <1° (Fig. 2). Similarly, across colonies, animals showed a higher selection for flat bottom areas with the probability of occurrence peaking at slope values of <5° (Fig. 3).

There was a significant difference in the SST between colonies (LME, p < 0.001) (Table 1), with encountered SST values increasing along the coast from Kleinsee to Black Rocks (Table 2). Kleinsee individuals spent a high proportion of time associated with SSTs ranging from 13 to 14.5°C with a second peak around 16°C (Fig. 2). Although less marked for False Bay seals, slight peaks in the proportion of time were apparent around 13, 15.5 and 18°C (Fig. 2). Individuals from Black Rocks on average spent a high proportion of time associated with temperatures in the colder end of the recorded range (16–18°C), although some individuals spent a substantial proportion of time in warmer waters, in excess of 20°C (Fig. 2). While availability and use of SST varied substantially among sites, animals tended to select temperatures towards the upper end of the range at each of the 3 colonies
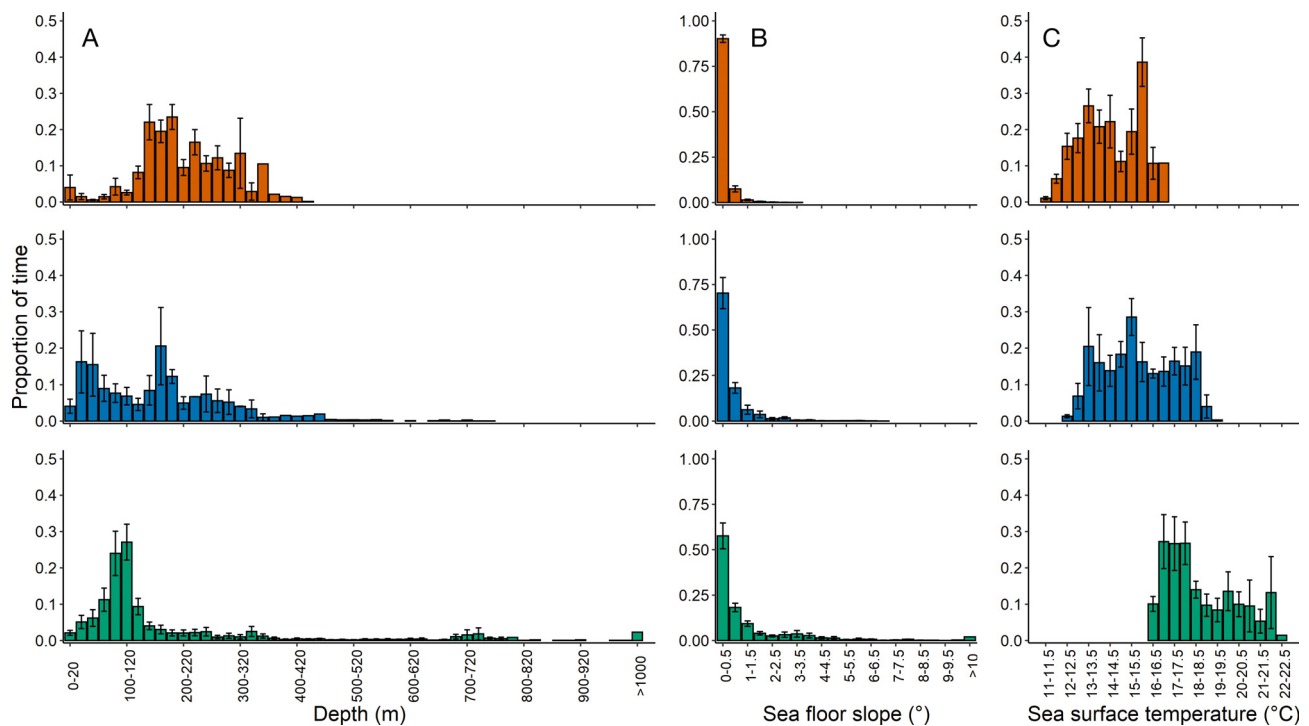

Fig. 2. Mean (±SE) proportion of foraging trips associated with pre-determined classes of (A) depth (20 m), (B) sea floor slope (0.5°) and (C) sea surface temperature (0.5°C) for female Cape fur seals from Kleinsee (red), False Bay (blue) and Black Rocks (green)
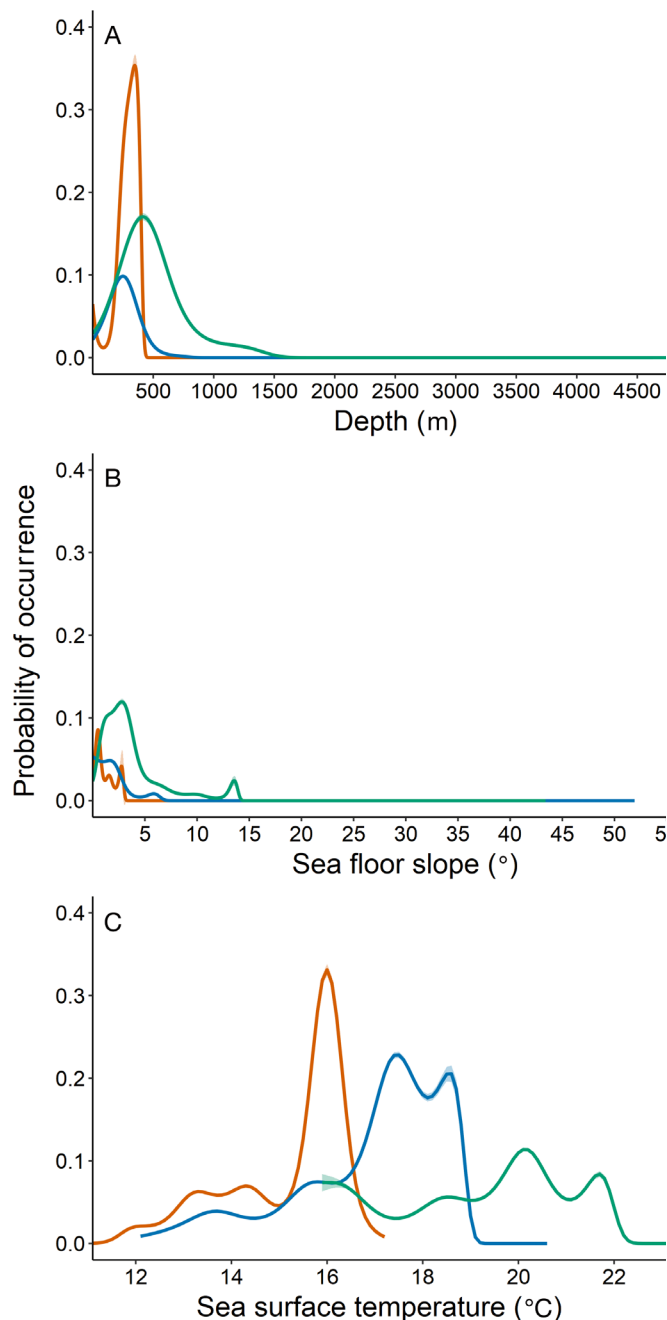
Fig. 3. Results of the generalized additive model for the influence of (A) depth (m), (B) sea floor slope (°) and (C) sea surface temperature (°C) on the probability of occurrence (presence) in relation to available habitat (pseudo-absence) of female Cape fur seals from Kleinsee (red), False Bay (blue) and Black Rocks (green). Shaded areas represent SE estimates from the model

3.3. Diving behaviour

A total of 42 325 dives were recorded for the 23 individuals from Kleinsee (n = 26 095) and the 5 individuals from False Bay (n = 16 230) (Table 1). The number of dives recorded per trip ranged from 382 to 2890 (86–279 dives d^{-1}) and from 50 to 1057 (15–239 dives d^{-1}) for individuals from Kleinsee and False Bay, respectively. For seals from Kleinsee, the deepest dive depth and longest dive duration recorded were 361 m and 8.1 min, respectively, while for seals from False Bay, the deepest dive depth and longest dive duration recorded were 411.5 m and 8.8 min. Most dives occurred at night (18:00 to 06:00 h SAST), although the percentage of nocturnal dives was higher for seals from Kleinsee (63%) than for those from False Bay (38%). Benthic dives accounted for 32% of all recorded dives, but were present for all individuals. While individuals from Kleinsee dived slightly deeper and performed a greater proportion of benthic dives during 2014 (depth: 90.7 ± 11.3, percentage benthic dives: 42 ± 9%) compared with 2015 (depth: 87.7 ± 7.1, percentage benthic dives: 29 ± 4%), these differences were not significant (LME, p > 0.1) (Table S2), and data were pooled for analysis of dive metrics.

Dive depth and the probability of benthic diving did not vary significantly among colonies (Table 3). Indeed, mean dive depths and the average proportion of benthic dives per trip were remarkably similar between Kleinsee and False Bay animals, but each parameter varied substantially between individuals (Kleinsee: mean dive depth: 13.8–146.7 m, percentage benthic dives: 4–97%, False Bay: mean dive depth: 29.2–201.9 m, percentage benthic dives: 3–94%). For the 2 individuals from False Bay that undertook short trips within the bay and to neighbouring bays, dives were consistently shallower (43.1 ± 11.5 m), and were mainly benthic (62 ± 4.3%). In contrast, mean dive depths (96.8 ± 14 m) and the percentage benthic diving (27.6 ± 4.9%) for the 3 individuals from False Bay that travelled further over the Agulhas Bank were more similar to those recorded at Kleinsee. At both sites, foraging trips with a higher proportion of benthic dives were, on average, shorter than trips comprising more pelagic dives (LMEs, all p < 0.05, Table S3, Fig. S3). A diel pattern in diving behaviour was also evident, with time of day significantly influencing both dive depth and the probability of benthic diving (GAMM, all p < 0.001) (Table 4). In general, dive depths and the probability of benthic diving were greater during daylight hours (06:00–

(Fig. 3). For Kleinsee individuals, the probability of occurrence increased around 16°C, while peaks were apparent at False Bay between 17 and 19°C. For individuals at Black Rocks, marginal peaks in the probability of occurrence were observed at both colder (<17°C) and warmer (20–22°C) temperatures.

Table 4. Results from the generalized additive mixed models for the influence of colony grouping and time of day on dive depth and the probability of benthic diving for female Cape fur seals from Kleinsee (KS) and False Bay (FB). Dashes specify where either parametric coefficients or smooth terms were not fitted for a particular predictor effect. Significant p-values (p < 0.05) are highlighted in **bold**

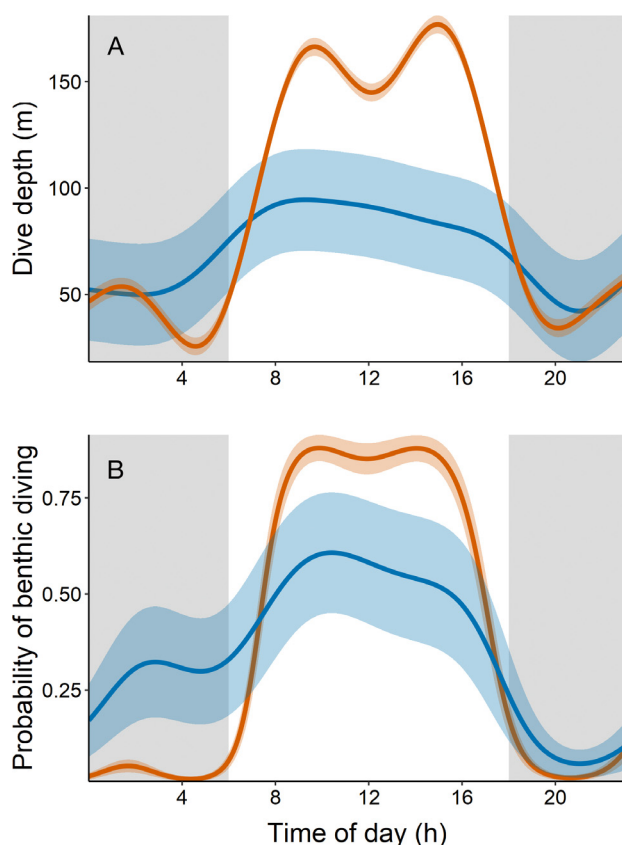| Response Predictor	Parametric coefficients			Approximate significance of smooth terms		p
	Est	SE	z	Edf	F	
Dive depth						
Intercept (KS)	93.1	6.7	14.0	–	–	**<0.001**
FB	−21.9	14.5	−1.5	–	–	0.13
Hour:KS	–	–	–	8.9	2374.3	**<0.001**
Hour:FB	–	–	–	8.6	157.6	**<0.001**
Probability of benthic diving						
Intercept (KS)	−1.1	0.3	−3.2	–	–	**<0.01**
FB	0.3	0.7	0.5	–	–	0.60
Hour:KS	–	–	–	8.9	700.6	**<0.001**
Hour:FB	–	–	–	8.7	139.3	**<0.001**

Fig. 4. Results of the generalized additive mixed models for the influence of time of day on (A) dive depth and (B) the probability of benthic diving of female Cape fur seals from Kleinsee (red) and False Bay (blue). Lighter shaded bands represent standard error estimates from the models; gray background shading indicates night time

18:00 h SAST), although the trend was more distinct and showed less variability across individuals from Kleinsee compared to those from False Bay (Fig. 4).

4. DISCUSSION

Information on the at-sea distribution and behaviour of marine predators is useful for informing ecosystem-based management and predicting the response of species to future environmental changes (McGowan et al. 2017, Arthur et al. 2018, Hays et al. 2019). This study provides the first detailed assessment of at-sea movement and habitat use of Cape fur seals from 3 different sites in South Africa. Results reveal that the foraging ranges of females from all sites were generally limited to the shelf (up to 200 m) and shelf-slope waters (up to 1000 m). However, geographic differences in distributions and habitat use were apparent, which likely indicates the variability in local foraging conditions and habitat availability. In addition, this study compared the dive behaviour of individuals from 2 of these colonies and found little difference in dive depth and the proportion of benthic dives between study sites, although substantial differences were apparent between individuals from both sites. Diel variation in diving parameters was apparent at both study sites.

4.1. Foraging trip metrics and at-sea movements

Foraging trip metrics of Cape fur seals recorded in the present study varied widely among individuals at each colony. However, mean trip duration and distances across colonies were within the winter range previously recorded for lactating females of other temperate latitude fur seal species (Harcourt et al. 2002, Hoskins et al. 2015, 2017). During this time, female fur seals are central-place foragers and generally limited in their at-sea distribution. Individuals from Black Rocks, on average, undertook shorter foraging trips compared with animals from Kleinsee and False Bay. For all colonies, movements were confined to the shelf, shelf-break and shelf-slope. However, the Kleinsee and False Bay populations appeared to spend a relatively high proportion of time

over the deeper portion of the shelf, and in particular over the shelf-break and shelf-slope waters. This is typical of epipelagic foragers, which forage closer to the surface and target areas and features of high prey concentration (Guinet et al. 2001, Page et al. 2006, de Bruyn et al. 2009). In comparison, the distribution of the Black Rocks animals was more restricted to the shallower shelf region closer to the colony, although several apparent hotspots were associated with the shelf break and slope south of Cape Recife, an area of known localized upwelling (Goschen et al. 2015).

Geographic differences in foraging behaviour and distribution have previously been documented in other otariid species (Staniland et al. 2010, Baylis et al. 2018) and for Cape fur seals breeding in Namibia (Skern-Mauritzen et al. 2009). There are several possible explanations for such differences between breeding sites. For central-place foraging marine predators, longer foraging trips and extensions in foraging range are attributes thought to reflect poor local foraging conditions (e.g. Boyd et al. 1994, Pichegru et al. 2007). It is possible that at Black Rocks, shorter trips and smaller foraging ranges are a result of higher quality local foraging conditions compared to conditions at Kleinsee and False Bay colonies. Indeed, over the past 2 decades, large-scale eastward shifts in the distribution of several forage species, primarily anchovy, have been beneficial for several seabird colonies on the southeastern coast (Crawford et al. 2009, 2014). In addition, large proportions of anchovy have previously been reported in the diet of Cape fur seals at Black Rocks (Connan et al. 2014) and Robberg (Huisamen et al. 2012), the closest neighbouring colony. However, given the lower and less predictable productivity characteristic of this sub-region of the Benguela, it is unlikely that prey availability alone is able to explain the shorter foraging trips and more restricted at-sea movements for the Black Rocks colony.

A more likely explanation, perhaps, is that foraging trip durations and distances reflect the availability of suitable foraging habitat. While published information is limited, available evidence on Cape fur seal foraging distributions suggest that individuals feed predominantly over the continental shelf and shelf-slope and features associated with this area (David 1987, Skern-Mauritzen et al. 2009, present study). As such, the broad continental shelf off Kleinsee and, particularly, the Agulhas bank southeast of False Bay may provide more suitable foraging habitat to Cape fur seals breeding at these colonies. In contrast, the continental shelf and shelf-slope narrow

considerably towards the east and may thus restrict the range of Cape fur seals breeding at Black Rocks. Foraging trip metrics and movement patterns may also be related to other oceanographic influences such as current speeds, eddies and upwelling cells, which vary substantially along the South African coast (Roberson et al. 2017). Although the spatial distribution and foraging strategies of pinnipeds are often related to environmental influences (Foo et al. 2019, 2020), other factors such as competition may also be implicated, particularly at smaller spatial scales (Wege et al. 2019). Thus, the longer foraging trips observed for animals from Kleinsee and False Bay could be linked to higher levels of intra-specific competition at these larger colonies and may reflect strategies of resource partitioning (e.g. Staniland et al. 2011, Wakefield et al. 2013).

Individuals from the False Bay colony appeared to utilise 2 different foraging strategies, either remaining within False Bay and the neighbouring Walker Bay, or travelling significantly further and spending a large proportion of time over the Agulhas Bank. Although the sample size of animals for this colony was small (n = 5), individuals were remarkably consistent in their trip durations, distances travelled, distal bearings and at-sea distribution. Within pinniped populations, the use of multiple individual foraging strategies has been documented for several species, including Galapagos sea lions *Zalophus wollebaeki* (Villegas-Amtmann et al. 2008), southern sea lions *Otaria flavescens* (Baylis et al. 2015), Antarctic fur seals *Arctocephalus gazella* (Arthur et al. 2015) and New Zealand fur seals *A. fosteri* (Hoskins et al. 2017). In most cases, this has been suggested as a strategy to reduce intra-specific competition or may be related to individual-level specialization. Given the size of the colony at False Bay and its proximity to other Cape fur seal breeding sites, it is possible that some individuals may adopt foraging strategies to reduce competition, and become specialized in their behaviour. High levels of productivity and consequent availability of epipelagic forage fish over the Agulhas Bank suggest that longer foraging trips might be more profitable for female Cape fur seals at False Bay. However, short travel distances and reliable food sources, albeit of lower quality, could outweigh the costs of travelling extensive distances and searching for preferred prey types (e.g. Botha & Pistorius 2018). To fully assess this seemingly bimodal foraging strategy in Cape fur seals, larger sample sizes are required for this colony.

4.2. Habitat use and habitat selection

Consistent with the spatial distributions identified in the present study, habitat use varied between the colonies. In particular, individuals from Black Rocks spent a greater proportion of time in the shallower waters of the shelf while individuals from Kleinsee and False Bay typically preferred deeper waters of the shelf, shelf-break and, to a lesser extent, the shelf slope. This may further reflect differences in habitat availability between sites, with the broad, gently sloping continental shelf at Kleinsee and False Bay providing a greater availability of suitable habitat for foraging Cape fur seals. In addition, individuals from Black Rocks that ventured further more regularly encountered steeper slopes of the shelf-edge, indicating its proximity to the colony. Inter-colony differences in habitat use could also reflect different foraging strategies between sites. For example, the movement patterns and habitat preferences observed for Black Rocks animals are analogous to those of female Australian fur seals foraging within Bass Strait (Arnould & Kirkwood 2007), which are almost exclusively benthic foragers. The extensive use of shallower depths by individuals from Black Rocks could therefore indicate a dominance of benthic foraging by seals from this colony. Indeed, the large proportion of time spent in shallower areas of less than 80 m by False Bay animals was mainly accounted for by the 2 individuals that remained inshore and whose dives were almost exclusively benthic. Furthermore, foraging trips of both Kleinsee and False Bay seals, incorporating a greater proportion of benthic dives, were significantly shorter than trips incorporating more pelagic dives. Overall, habitat selection in relation to total habitat availability was similar across colonies for both bathymetric depth and sea floor slope. The selection of shallow depth classes (<500 m) and gentle-sloping sea floor (<5°) is consistent with females of other generalist otariids (Villegas-Amtmann et al. 2008, Baylis et al. 2018) and further highlights the importance of the shelf and shelf-slope habitats to foraging female Cape fur seals.

As expected, encountered SST values varied widely between colonies. However, the proportion of time associated with SST classes and selection of SST values was somewhat similar across sites, with notable peaks at temperatures between 16 and 19°C, particularly at Kleinsee and False Bay. This falls within the preferred temperature range of several South African pelagic fish species, including red-eye round herring *Etrumeus whiteheadi* (15–18°C), sardine (14–19°C) and, to a lesser extent, anchovy (<15°C) (Agenbag et al. 2003). Interestingly, animals from Black Rocks also showed a bimodal preference, with individuals also selecting warmer SSTs, in excess of 20°C. This may reflect a higher degree of benthic foraging behaviour. While relationships between foraging activity and SST have mainly been identified for epipelagic foraging marine predators (Lea & Dubroca 2003, de Bruyn et al. 2009), preferences for specific SSTs have also been shown for benthic foraging species, particularly in shallow habitats, where high levels of mixing occurs throughout the water column (Fadely et al. 2005, Arnould & Kirkwood 2007). Thus, it is possible that the warmer surface temperatures selected by females at Black Rocks could reflect conditions and processes at depth. However, future studies should consider investigating fine-scale vertical habitat utilisation of Cape fur seals in relation to environmental covariates (e.g. Hindell et al. 2002).

4.3. Geographic and diel variation in diving behaviour

Mean dive depths recorded in the present study were within the range previously reported for Cape fur seals at Kleinsee (Kooyman & Gentry 1986, Kirkman et al. 2019). Maximum depths were similar between the 2 colonies, although on average, slightly deeper for individuals from Kleinsee compared to those from False Bay. In addition, benthic dives were included in the foraging trips of all individuals, and although the average degree of benthic diving was similar between Kleinsee and False Bay animals, it varied substantially between individuals. These results support recent findings that Cape fur seals exhibit both pelagic and benthic foraging strategies (Kirkman et al. 2019), and suggests that these strategies may occur throughout the range of the species.

Shorter foraging trips, consisting predominantly of benthic foraging, are typically characteristic of sea lions (Costa & Gales 2000, 2003). Fur seals, in turn, generally undertake longer foraging trips spanning multiple days and forage mainly on epipelagic prey (Guinet et al. 2001, Harcourt et al. 2002). However, several exceptions to these typical patterns have previously been documented. For example, California sea lions *Z. californianus* exhibit a predominantly pelagic foraging mode (Costa et al. 2004). In addition, female and male Australian fur seals *A. pusillus doriferus*, conspecifics of Cape fur seals, are almost exclusively benthic foragers (Arnould & Hindell 2001, Knox et al. 2017). These findings have largely been attributed to local environmental conditions

and productivity, and are thought to have important implications for population dynamics and recovery from previous overexploitation (Arnould & Costa 2006). The Cape fur seal thus presents an interesting case. Although previously considered to be a predominantly epipelagic forager in the highly productive Benguela, the diving behaviour of some individuals appears more similar to that of benthic foraging Australian fur seals in the less productive Bass Strait (Arnould & Kirkwood 2007, Kirkwood & Arnould 2011). Previous diet records suggest that benthic prey have always comprised at least some proportion of Cape fur seal diet in the Benguela (de Bruyn et al. 2003, 2005, Mecenero et al. 2006a). Despite this, the drivers of benthic foraging, as well as its ecological implications, remain unclear and warrant further investigation possibly spanning several years.

While no diving data were available for females at Black Rocks, the at-sea distributions and habitat use patterns of these individuals suggests a high level of benthic foraging at this colony. This would be consistent with recent evidence of benthic foraging in African penguins *Spheniscus demersus* breeding at colonies in close proximity to Black Rocks (Sutton et al. 2020). Historically (1992–1995), benthic prey species, particularly redspotted tonguefish *Cynoglossus zanzibarensis* and Cape flounder *Arnoglossus capensis*, were important components in the diet of Cape fur seals on the south coast of South Africa (Stewardson 2001). However, more recent diet studies at the same colonies identified a large proportion of pelagic prey, mainly anchovy, consumed by Cape fur seals (Huisamen et al. 2012, Connan et al. 2014). As such, knowledge of the specific foraging strategies at Black Rocks remains speculative at present. Future studies should therefore consider the use of dive behaviour loggers at this colony and elsewhere to validate the proposed benthic foraging behaviour of Cape fur seals on the south coast.

Diel patterns in dive behaviour observed in the present study are consistent with those recently documented for Cape fur seals (Kirkman et al. 2019). Deeper dives and a greater probability of benthic diving during daylight hours likely reflect diel vertical migrations of preferred prey. Indeed, several important prey species of Cape fur seals, including sardine and red-eye round herring, occur deeper during daylight, while moving closer to the surface at night (Roel & Armstrong 1991, Beckley & van der Lingen 1999). While diel patterns were evident at both colonies, the trend was more apparent at Kleinsee. At False Bay, a high level of inter-individual variability in the diel pattern was evident. This variability is most probably accounted for by the 2 individuals that remained close inshore and foraged at consistent depths, on the bottom, regardless of the time of day. The remaining individuals that travelled further over the Agulhas Bank showed diel patterns similar to those of individuals from Kleinsee. It is also possible that the diving behaviour and at-sea distributions observed in the present study could be related to predation risk. Indeed, spatiotemporal differences in the behavioural and physiological responses of Cape fur seals to predation by white sharks *Carcharodon carcharias* are apparent at several South African colonies (de Vos et al. 2015a,b, Fallows et al. 2016, Hammerschlag et al. 2017, Morse et al. 2019). However, quantifying predator–prey interactions at sea is inherently difficult, and could be investigated through simultaneous tracking of these 2 species.

5. CONCLUSION

This study provides important baseline information on the at-sea distribution, habitat selection and utilisation, and diving behaviour for the South African component of the Cape fur seal population. Geographical differences found in this study, which are likely to be caused by a number of related factors, highlight the need to consider geographic variability in the spatial distribution of marine predators for future management and spatial planning. Furthermore, while Cape fur seals are mainly epipelagic foragers, benthic foraging does occur and is dominant for some individuals. This raises further questions regarding observed changes in the availability of forage species and potential long-term effects on the Cape fur seal population.

Snyders, Lihle Skolo and Lieze Swart. Fieldwork at Kleinsee and False Bay was permitted by the Animal Ethics Committee of the then Department of Environmental Affairs (Ref: EC-2015-5). Ethics clearance for fieldwork at Black Rocks was issued by the Research Ethics Committee at the then Nelson Mandela Metropolitan University (reference: A13-SCI-ZOO-008). Fieldwork at Black Rocks was conducted in terms of research permits (RES2014-54 and RES2015-19), issued to the Port Elizabeth Museum by the then Department of Environmental Affairs, in terms of a research agreement between the Port Elizabeth Museum and South African National Parks.

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