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ORIGINAL PAPER

Habitat use and diving behaviour of macaroni *Eudyptes chrysolophus* and eastern rockhopper *E. chrysocome filholi* penguins during the critical pre-moult period

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Abstract After the breeding season, penguins must replenish body condition and accumulate sufficient energy stores before their annual moult ashore; failure to do so may lead to starvation. Knowing where and how adult penguins find adequate resources during this energy-intensive stage is vital to understanding their susceptibility to ecosystem changes. GPS and TDR loggers were used to track movements and record diving behaviour of macaroni *Eudyptes chrysolophus* and eastern rockhopper *E. chrysocome filholi* penguins from Marion Island (46°S, 37°E) during the pre-moult foraging trip in 2012, 2013 and 2014. Both species consistently travelled in a southerly direction to forage in cooler (~3.5 °C) Antarctic Zone waters south of the Antarctic Polar Front where they associated with mesoscale eddies and sub-mesoscale filaments. Dives were predominantly to depths of 30 to 60 m, but macaroni penguins dived deeper more often. Mean trip durations of both species were similar (33 ± 6 days), but maximum foraging ranges of macaroni penguins (903 ± 165 km) were greater than eastern rockhopper penguins (696 ± 152 km). Spatial overlap of core foraging areas between species was high, but a 2- to 3-week difference in departure dates reduced potential interspecific competition at sea. Trip durations were longer in 2014 compared to 2013, when decreased productivity may have reduced prey availability, forcing penguins to remain longer at sea. Continued monitoring is vital to understand how crested penguins at Marion Island adapt to the predicted southward shift of major frontal boundaries.

Introduction

Knowing where and how predators find prey is vital to understanding their susceptibility to ecosystem changes. Marine environments are dynamic in space and time, with physical processes driving patchiness in primary production (Sokolov and Rintoul 2007) and prey distribution (Ansorge et al. 2009). Oceanographic features that retain and enhance predictable prey aggregations, such as fronts (Bost et al. 2009), shelf edges (Phillips et al. 2008), mesoscale eddies (Cotté et al. 2007) and sub-mesoscale filaments (Nordstrom et al. 2013; Cotté et al. 2015), act as important foraging areas for many pelagic mesopredators.

Penguins (Spheniscidae) are key predators on a global scale, consuming more than 23 % of the estimated 70 million tonnes consumed by all seabirds annually (Brooke 2004). Perhaps the most energy-demanding stage of a penguin's annual cycle is the period preceding the moult (Brown 1989; Adams and Brown 1990; Green et al. 2009a). Unlike most seabirds that stagger their moult, penguins replace their entire plumage in just 2–5 weeks (Adams and

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Brown 1990). Reduced waterproofing and insulation during this period force penguins to remain on land, making them entirely dependent on endogenous fat and protein reserves for sustenance (Cherel et al. 1994). Penguins typically lose 40–50 % of their body mass during this time (Brown 1986). Such dependence on reserves requires penguins to commence the moult in excellent body condition, as failure to do so may result in starvation and impact survival (Keymer et al. 2001). For most penguins, which moult 3–7 weeks after breeding (Williams 1995), finding adequate resources to accumulate sufficient energy stores is particularly challenging, as they must do so within a limited time period.

Among extant penguins, crested penguins (genus *Eudyptes*) are the most abundant and diverse group, ranging from temperate to Antarctic climates (Williams 1995). Moult duration is similar across eudyptids (24–28 days; Adams and Brown 1990), but the duration of pre-moult foraging trips varies considerably, ranging from 13 days for macaroni penguins *E. chrysolophus* at South Georgia (Williams and Croxall 1991) to 70 days for Fiordland penguins *E. pachyrhynchus* in New Zealand (Warham 1974). Previous studies have reported large-scale dispersal (>400 km) of macaroni penguins during pre-moult trips (Brown 1987; Waluda et al. 2010), but at most localities, the foraging strategies of crested penguins during this crucial period remain poorly known.

We use GPS loggers and time-depth recorders (TDRs) to investigate the pre-moult habitat use and diving behaviour of macaroni penguins and the eastern race of the southern rockhopper penguin *E. chrysocome filholi* at the sub-Antarctic Prince Edward Islands. Approximately 302,000 and 80,000 pairs of macaroni and eastern rockhopper penguins breed at the islands, which together constitute 41 % of the total avian biomass (Ryan and Bester 2008; Crawford et al. 2009). Eudyptids breed sympatrically at many localities—usually involving the smaller rockhopper and the larger royal *E. schlegeli*, erect-crested *E. sclateri* or macaroni penguins (Warham 1975)—but it is uncommon for large numbers of both species to coexist, such as at the Prince Edward Islands. Macaroni and eastern rockhopper penguins have similar breeding cycles at the islands, but a 2- to 3-week difference in the onset of breeding means that macaroni penguin chicks fledge in mid-February and eastern rockhopper penguin chicks in early March (Crawford et al. 2003a, b). Adult penguins typically depart just before chicks fledge, but previous studies have not recorded the timing of adult departures from the Prince Edward Islands.

Unlike breeding penguins that are constrained in terms of the distance they can travel by the need to provision offspring, pre-moult penguins are free to travel larger distances to potentially more profitable foraging areas. Thus, pre-moult penguins offer a good model to explore habitat preferences and may provide insights into fine-scale habitat preferences during the non-breeding season when high accuracy data are not available. In this paper, we (1) identify core foraging areas of each species, (2) determine whether foraging behaviour varies with environmental correlates, (3) quantify spatial and temporal overlap between species and (4) identify potential drivers of inter-annual variation in foraging trip duration and range.

Methods

Study site

The Prince Edward Islands (46.9°S, 37.8°E) are located in the south-west Indian Ocean sector of the Southern Ocean. Among the pairs breeding at the islands, 96 % of macaroni penguins and 53 % of eastern rockhopper penguins occur at the larger Marion Island (Crawford et al. 2009). At-sea data were collected from adult penguins breeding at Funk Bay, south-east Marion Island, during the pre-moult foraging trip in 2012 (macaroni penguins only), 2013 and 2014.

Logger deployments

CatTraQ™ GPS loggers (16 Mb memory, 230 mA lithium-ion battery, Mr Lee Technologies, 45.7 × 30.5 × 12.7 mm, 25 g, accuracy < 10 m) were deployed in all 3 years. They were customised at the IPHC-DEPE (Strasbourg, France) by removing the original packaging, replacing the main switch with a reed switch, and moulded in resin. Each GPS was programmed using @trip PC (version 2.0) to sample position at variable intervals between years (Table S1). TDRs (2 Mb memory, G5, CEFAS Technology Ltd., UK, 35.5 × 11.5 mm, 2.7 g) were deployed in 2012 and 2014 and were programmed using G5 Host (version 4.0) to sample depth at variable intervals between years (Table S1) at 12-bit resolution with an accuracy of ±1 m. In 2014, TDRs also sampled temperature every 5 s at 8-bit resolution with an accuracy of ±0.1 °C. GPS loggers were sealed in black heat-shrink tubing and TDRs attached to the rear of the GPS unit. Birds were captured at the end of the breeding season prior to their expected departure for the pre-moult foraging trip. Adult body masses were measured using an electronic scale (±10 g) and culmen length and depth taken with Vernier callipers (±0.1 mm) to determine sex (inferred from bill measurements given by Williams and Croxall 1991, Poisbleau et al. 2010). Following Wilson et al. (1997), each unit (<2 % of total body mass) was attached to feathers on the dorsal midline of the penguin's lower back using waterproof Tesa tape (Beiersdorf AG, Germany) and the tape edges sealed with cyanoacrylate glue (Loctite 401, Henkel). Birds were marked with a temporary, biological dye (Porcimark, Jørgen Kruuse A/S, Denmark) for easy identification and returned to their nest within 15 min of capture. When birds returned to their nest site (at or near their nest) to moult, they were recaptured, reweighed (2014 only) and the logger removed.

Trip characteristics

Data were analysed using R (version 3.1.0; R Development Core Team 2015) and the 'Spatial Analysis' tool of Ethographer (Sakamoto et al. 2009) in Igor Pro (WaveMetrics Inc., USA, version 6.2.2.2). Duplicated and on-land locations were removed in Igor Pro. Maximum foraging range was defined as the great circle distance between the colony and the furthest point of the trip. Bearing of the furthest point of the trip in relation to the colony was calculated using the function 'bearing' in the R package 'CircStats' and circular statistics (Kuiper's test) used to determine whether travel direction of individuals within each species was random. Due to the low acquisition rates of locations during the daytime when penguins were predominantly diving (Fig. S1), as well as unequal sampling intervals between years (Table S1), tracks were linearly rediscretised at 6-h intervals using the function 'redisltraj' in the R package 'adehabitatLT' (Calenge et al. 2009) to minimise inclusion of false locations. Travel speed was computed as a daily mean based on the total minimum distance travelled per day.

If GPS tracks were incomplete (Table S2) and temperature data were available from a TDR, landing date was determined by a rapid increase in ambient temperature when penguins left the water. When temperature data were not available, the change point at which each bird started its journey back to the colony was determined using a non-parametric segmentation of daily travel speeds (Lavielle 2005). Mean travel speed of the return journey was calculated for complete tracks, averaged among all birds by species and used to estimate the landing dates of incomplete tracks by calculating the time taken to travel the outstanding distance to the colony. Penguins typically maintain a constant speed travelling to and from the colony (Trathan et al. 2008), making the assumptions for such extrapolations reasonable.

Linear mixed-effect models (LMEs; R package 'nlme'; Pinheiro et al. 2013) were used to determine whether trip parameters (duration and maximum foraging range) differed between years for each species. Potential differences between sexes were not considered due to small sample sizes, but sex was still included as a random effect. Post hoc pairwise comparisons were made using the function 'glht' in the R package 'multcomp'. For interspecific and inter-annual comparisons, data were only considered for years when available for both species (2013 and 2014), and trip parameters modelled in relation to species and year, with sex included as a random effect.

Environmental data

Oceanographic variables likely to characterise the marine environment used by penguins included absolute dynamic topography or sea surface height (SSH), chlorophyll-a concentration, eddy kinetic energy (EKE), sea level anomaly (SLA) and sea surface temperature (SST) (see Table S3 for data resolution and sources). Additionally, sub-mesoscale filaments were identified using finite-size Lyapunov exponent (FSLE) which is a measure of local stirring by mesoscale currents (see d'Ovidio et al. 2004 for details). Environmental variables were spatially and temporally matched with locations using the function 'extract' in the R package 'raster'. A buffer of 5 km around each location was used, and if more than one grid cell was included, the arithmetic mean was taken. The southern extent of the Antarctic Polar Front (APF) and Southern Antarctic Circumpolar Current Front (SACCF) was defined as SSH contours of −0.630 and −0.943 m following Swart et al. (2010) and the core Antarctic Zone (AAZ) considered as −0.8 m (midpoint between APF and SACCF).

Habitat use

When prey are aggregated, optimal foraging theory predicts that predators should travel quickly through areas of low prey density to maximise time spent in high-density patches (Kareiva and Odell 1987; Weavers 1992). For diving marine predators, travel speed is a useful proxy for foraging behaviour (Bost et al. 1997; Cotté et al. 2007; Trathan et al. 2008), with slower speeds (reduced horizontal displacement) typically associated with increased foraging activity (Sato et al. 2004) and prey ingestion (Bost et al. 1997). Although restricting analyses to habitats penguins chose to travel through may underestimate habitat preferences by ignoring the habitats that penguins avoided, modelling travel speeds in relation to environmental covariates provides a relative index of preference for the habitat characteristics encountered. Due to the nonlinearity between response variables and environmental covariates so common in species-habitat studies (Cotté et al. 2015), generalised additive models (GAMs) were used for their ability to automatically detect relationship shapes through flexible smoothers. GAMs were implemented using the function 'bam' in the R package 'mgcv' (Wood 2006) as this function allows for the inclusion of an autoregressive correlation structure ($rho = 0.1$) to account for the weak temporal autocorrelation present. To ensure normality of residuals, travel speeds were square root transformed and models fitted with a Gaussian error distribution and identity link function. Prior to modelling environmental covariates were checked for collinearity, with a cut-off criterion of $r_s = 0.6$ for inclusion in the same model. SSH and SST were highly correlated in all years ($r_s = 0.93$–0.96). Due to potential inter-annual variation in environmental conditions and preferences, models were fitted separately for each year. Smoothers were applied to each environmental covariate and a separate smoother specified for each species. Smoothers were fitted using cubic regression splines with extra shrinkage, which avoids over-parameterisation by allowing variables to be penalised out of the model during fitting (Wood 2006). Interaction terms were specified with a tensor smooth and were fitted with a thin-plate regression spline. As travel speeds may differ between individuals, individual identity was included as a random effect. Smoothing parameters were estimated via restricted maximum likelihood (REML) and model selection performed using Akaike's information criterion (AIC).

Days where travel speed was less than the individual's mean were considered as core foraging phases (Fig S2; Cotté et al. 2007). Environmental characteristics of core foraging phases were compared between years for each species using LMEs, with individual identity included as a random effect. At-sea distributions of core foraging phases were broadly characterised for each species by computing 50 and 90 % utilisation distributions (UDs) of pooled locations from years when data were available for both species (2013 and 2014). This was performed using kernel analysis in the R package 'adehabitatHR' (Calenge 2006). Due to small sample sizes, population UDs for each species were broadly characterised by using a smoothing parameter of 1°. Spatial overlaps between the two species' 50 and 90 % UDs were computed using the 'VI' method in the function 'kerneloverlaphr' (Fieberg and Kochanny 2005). This method returns the volume of intersection as a proportion of the 100 % UD ranging from 0 (no overlap) to 1 (complete overlap). Daily utilisation distributions were also calculated for each species based on daily locations when ≥ 3 individuals of each species were at sea and the daily overlap computed using the same method.

Dive data analysis

Depth data from 2012 were manually corrected for a drifting surface level (as temperature was not recorded), whilst 2014 data were corrected using Ethographer in Igor Pro (Sakamoto et al. 2009). To separate potential merged dives resulting from large sampling intervals (Table S1), all depth values <1 m were replaced with zero. A dive was considered when depth >3 m (Tremblay and Cherel 2003) and dive parameters (maximum depth, duration, descent rate and ascent rate) extracted for each dive. As shallow dives are typically associated with travelling, only dives >10 m were considered as foraging dives following a distinct mode in dive depth distributions (Green et al. 2005). For each day at sea, the number of dives performed (total, >10 m and >80 m), the amount of time spent underwater and the vertical travel distance (VTD; sum of maximum dive depths) were also calculated. To account for the delayed response time of the temperature sensor to detect changes (28 s to reach 66 % of the step from 5 to 30 °C) and avoid the influence of air temperature, sea surface temperature (T_{surface}) was considered as the first temperature reading after 15 s of continual submersion. Additionally, the minimum temperature (T_{bottom}) of each dive was determined. For each dive, the difference between T_{surface} and T_{bottom} (ΔT) was used to detect the presence of a thermocline, with a threshold of $\Delta T > 1$ °C used following temperature-depth changes associated with thermoclines in previous studies (Charrassin and Bost 2001). As positional data in 2014 were not available for entire trips, and daily means of satellite-derived sea surface temperatures and T_{surface} (hereafter referred to as SST_{TDR}) were highly correlated ($r_s = 0.92$, $n = 304$ days), SST_{TDR} was used for further analyses. LMEs were used to compare daily means of dive parameters between species and water masses (< and >4.5 °C SST_{TDR}), with individual identity nested within year included as a random effect. Kernel density plots were used to visualise the variation of maximum dive depths in relation to SST_{TDR}. LMEs were used to determine whether mean daily dive depths, durations, number of dives >10 m and time spent underwater differed in relation to the presence/absence of sub-mesoscale filaments (only 2014), with individual identity included as a random effect.

Results

Trip characteristics

Twenty macaroni and 13 eastern rockhopper penguins were tracked (Table 1). A large number of incomplete tracks resulted from insufficient battery life of GPS loggers (Table S2). For relatively complete trips (>70 %) where the furthest point from the colony was confidently discernable, maximum ranges were reached at 58 ± 6 % (macaroni, $n = 12$) and 56 ± 8 % (eastern rockhopper, $n = 5$) of the total trip duration. Thus, the inclusion of maximum ranges of incomplete trips in subsequent analyses was determined by criteria based on the lower confidence intervals of these means (i.e. 52 % of total trip duration for macaroni and 48 % for eastern rockhopper penguins). Mean daily travel speeds of the return journey for trips where return dates were known were 3.8 ± 0.4 km h^{-1} ($n = 9$) for macaroni and 3.5 ± 0.7 km h^{-1} ($n = 5$) for eastern rockhopper penguins.

Table 1 Trip characteristics (mean ± SD) of macaroni and eastern rockhopper penguins during the pre-moult foraging period

Species	Year		Departure date	Trip duration (days)	Maximum foraging range (km)	Minimum total distance travelled (km)	Bearing at furthest point (°)
Macaroni penguin	2012	All (5)	19-Feb ± 1	35 ± 7	1018 ± 166	2349 ± 364	192 ± 9
		Male (2)	20-Feb ± 1	29 ± 3	932 ± 260	2094 ± 527	188 ± 8
		Female (3)	18-Feb ± 1	40 ± 6	1075 ± 95	2519 ± 130	195 ± 10
	2013	All (6)	16-Feb ± 2	29 ± 3	780 ± 60	1954 ± 230	180 ± 16
		Male (3)	17-Feb ± 1	27 ± 1	756 ± 78	1913 ± 226	189 ± 18
		Female (3)	16-Feb ± 2	30 ± 4	803 ± 35	1994 ± 276	170 ± 6
	2014[a]	All (9)	18-Feb ± 1	35 ± 6	873 ± 104	2164 ± 202	193 ± 9
		Male (5)	18-Feb ± 1	34 ± 6	841 ± 109	2141 ± 254	193 ± 11
		Female (4)	18-Feb ± 0	38 ± 8	938 ± 76	2211 ± 57	192 ± 8
Eastern rockhopper penguin	2013	Male (4)	8-Mar ± 1	26 ± 3	626 ± 165	1640 ± 288	182 ± 12
	2014[b]	All (9)	4-Mar ± 1	37 ± 5	743 ± 137	1718 ± 250	182 ± 12
		Male (5)	4-Mar ± 1	34 ± 6	827 ± 138	1851 ± 242	183 ± 19
		Female (4)	4-Mar ± 2	40 ± 3	658 ± 79	1585 ± 212	181 ± 5

[a] Maximum foraging range and trip duration calculated for 6 individuals (4 males and 2 females)

[b] Maximum foraging range calculated for 6 individuals (3 males and 3 females) and trip duration calculated for 7 individuals (4 males and 3 females)

Travel direction was non-random (Kuiper's test $D_{\text{macaroni}} = 4.1$ and $D_{\text{rockhopper}} = 3.4$; $P < 0.01$); all individuals from both species travelled south (Fig. 1). For macaroni penguins, maximum foraging ranges were 232 ± 65 km further in 2012 compared to 2013 (LME, $t_{13} = 3.6$, $P = 0.001$), but were similar between other inter-annual comparisons ($\text{LME}_{2012–2014}$, $t_{13} = 2.0$, $P = 0.12$; $\text{LME}_{2013–2014}$, $t_{13} = -1.7$, $P = 0.21$). Trip durations were 7 ± 3 days longer in 2014 compared to 2013 (LME, $t_{13} = 2.4$, $P = 0.042$), but were similar between other inter-annual comparisons ($\text{LME}_{2012–2013}$, $t_{13} = 1.9$, $P = 0.15$; $\text{LME}_{2012–2014}$, $t_{13} = -0.5$, $P = 0.89$). For eastern rockhopper penguins, maximum foraging ranges were similar between years (LME, $t_7 = 1.7$, $P = 0.14$), but trip durations were 13 ± 3 days longer in 2014 (LME, $t_8 = 4.4$, $P = 0.0022$). For interspecific comparisons, maximum foraging ranges of macaroni penguins were slightly further (153 ± 76 km) than eastern rockhopper penguins, but this difference was only near significant (LME, $t_{17} = -2.03$, $P = 0.058$). Overall trip durations were similar between species (LME, $t_{18} = -1.02$, $P = 0.32$). For inter-annual comparisons, maximum foraging ranges were similar in 2013 and 2014 (LME, $t_{17} = 1.4$, $P = 0.18$), but trip durations were longer in 2014 compared to 2013 (LME, $t_{18} = 2.2$, $P = 0.039$).

Mean body mass of macaroni penguins prior to departure (3.9 ± 0.4 g, $n = 20$) was 50 % larger than eastern rockhopper penguins (2.6 ± 0.2 g, $n = 13$). In 2014, mass gain during a trip as a proportion of individual body mass was 53 ± 21 % ($n = 9$) for macaroni penguins and 44 ± 16 % ($n = 9$) for eastern rockhopper penguins. Mass gains of macaroni penguins (2.0 ± 0.7 kg, $n = 9$) were similar to those at Kerguelen (49.1°S, 70.3°E) instrumented with miniature GLS loggers (Thiebot et al. 2014), suggesting minimal impact of GPS loggers. Mass gains of eastern rockhopper penguins in the present study averaged 1.1 ± 0.4 kg ($n = 9$).

Travel speed and marine habitat characteristics

Mean daily travel speeds of macaroni and eastern rockhopper penguins were 2.6 ± 0.3 km h^{-1} ($n = 20$) and 2.3 ± 0.4 km h^{-1} ($n = 13$), respectively. Mean maximum travel speeds of raw locations for the two species were 6.1 ± 0.8 km h^{-1} ($n = 20$, max = 7.59 km h^{-1}) and 5.9 ± 0.7 km h^{-1} ($n = 13$, max = 7.5 km h^{-1}), respectively. The relationships of travel speed with SSH and SST were striking, with both species slowing down as they moved into cooler AAZ waters (Fig. 2). Change points in the mean daily travel speed were detected at −0.65 m SSH and 5 °C SST for macaroni penguins and at −0.65 m SSH and 4.5 °C SST for eastern rockhopper penguins. More than 90 % of locations within core foraging phases were in waters where SSH was <−0.65 m and SST was <4.5 °C for both species. Table 2 shows the summary of environmental characteristics within core foraging phases, and Table 3 shows the GAM results. GAMs revealed an interaction between SST and EKE in 2012 and 2013, with both species travelling slower in cooler waters (<4.5 °C SST) characterised by relatively low EKE (Fig. S3). Travel speed only varied in relation to SLA in 2014 when both species travelled

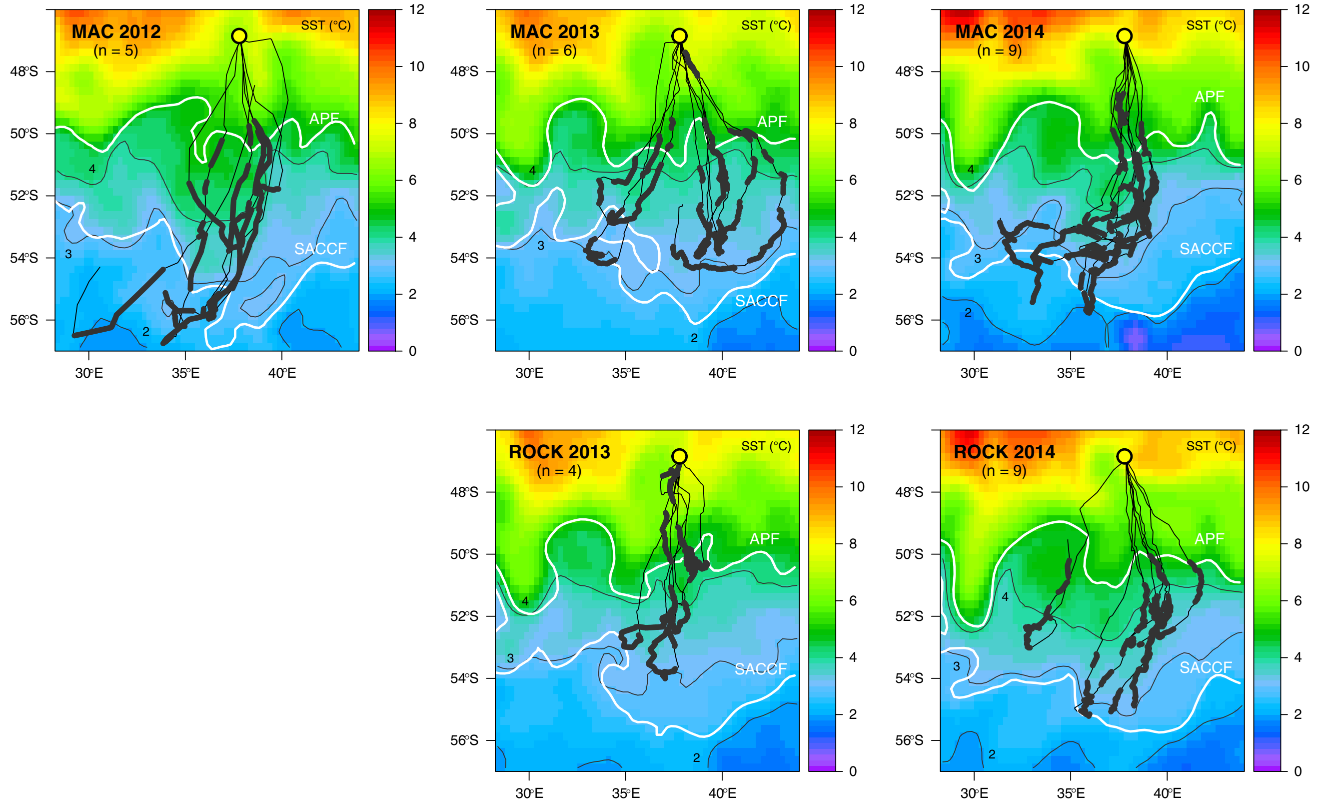


Fig. 1 Tracks of macaroni (MAC) and eastern rockhopper (ROCK) penguins during the pre-moult foraging trip from Marion Island. Thicker lines represent core foraging phases where daily travel speeds were less than each individual's mean. *Maps* depict sea surface temperature for the duration that penguins were at sea with 2, 3 and 4 °C isotherms shown as faint *black lines* (*source*: NASA), and *white lines* show the locations of the Antarctic Polar Front (APF) and Southern Antarctic Circumpolar Current Front (SACCF) (*source*: Aviso). Eastern rockhopper penguins departed 2–3 weeks after macaroni penguins

slower in waters characterised by positive SLA (Fig. S4), but core foraging phases in all years were generally characterised by weak positive SLA (Table 2). Travel speeds only varied in relation to chlorophyll-a concentrations in 2013, when penguins travelled fast through the less productive waters (<0.2 mg m^{-3}) of the Polar Frontal Zone (PFZ) and slowed down in the more productive waters of the AAZ (Fig. S5). Additionally, eastern rockhopper penguins travelled slower in marginally less productive waters in 2014 (Fig. S4). FSLE did not influence travel speeds and was thus excluded from the model selection process; however, the association of both species with sub-mesoscale filaments (FSLE > 0.1 day^{-1}) was striking. Macaroni penguins associated with sub-mesoscale filaments (FSLE > 0.1 day^{-1}) during 57 ± 7 % (range 48–65 %, $n = 5$), 49 ± 11 % (range 38–69 %, $n = 6$) and 67 ± 8 % (range 59–83 %, $n = 9$) of trip locations (6 h intervals) in 2012, 2013 and 2014, respectively, and eastern rockhopper penguins during 70 ± 4 % (range 65–74 %, $n = 4$) and 56 ± 19 % (range 36–93 %, $n = 9$) of trip locations in 2013 and 2014, respectively.

Mean chlorophyll-a concentrations in the region of interest (48–56°S and 28–42°E) during January to March were 0.23 ± 0.10 mg m^{-3} in 2012, 0.22 ± 0.09 mg m^{-3} in 2013 and 0.12 ± 0.06 mg m^{-3} in 2014. Along-track chlorophyll-a concentrations within core foraging phases confirmed that the productivity of waters exploited by penguins in 2014 was significantly lower than in 2012 and 2013 (Table 2). The mean distance from the colony to the core AAZ south of the islands (33–41°E) whilst macaroni penguins were at sea was 724 ± 119 km in 2012, 677 ± 107 km in 2013 and 734 ± 123 km in 2014, and 680 ± 106 km in 2013 and 722 ± 115 km in 2014, whilst eastern rockhopper penguins were at sea. Mean SSTs within core foraging phases were ~3.5 °C (Table 2). The mean distance from the colony to the 3.5 °C isotherm south of the islands (33–41°E) whilst macaroni penguins were at sea was 657 ± 102 km in 2012, 606 ± 54 km in 2013 and 681 ± 83 km in 2014, and 679 ± 47 km in 2013 and 632 ± 94 km in 2014, whilst eastern rockhopper penguins were at sea. Positions of the APF and SACCF, and cooler isotherms (2–4 °C), during the pre-moult foraging trip varied marginally between years (Fig. 1; see also Fig. S6). Interestingly, a negative SST anomaly occurred south of the SACCF (~57°S, 38°E) at the end of February 2014

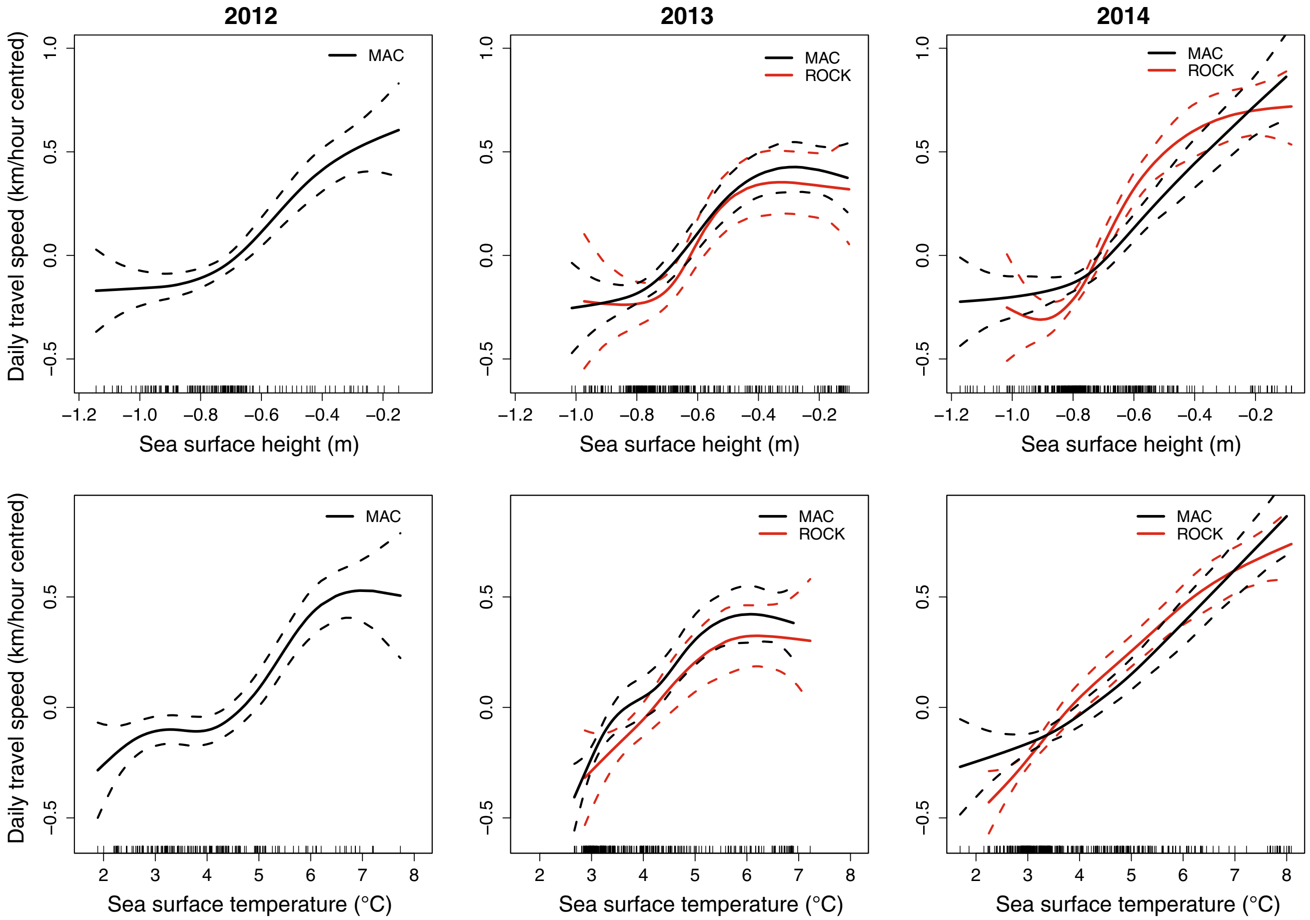


Fig. 2 Daily travel speeds of macaroni (MAC) and eastern rockhopper penguins (ROCK) in relation to sea surface height and sea surface temperature. *Solid lines* are predicted curves from generalised additive models, and *dashed lines* represent 95 % confidence intervals

Table 2 Summary of environmental covariates associated with core foraging phases (daily travel speeds less than the individual's mean) of macaroni and eastern rockhopper penguins during the pre-moult foraging trip

	Macaroni				Eastern rockhopper		
	2012	2013	2014	*P* value	2013	2014	*P* value
Chlorophyll-a concentration (mg m^{-3})	0.27 ± 0.02^a	0.28 ± 0.02^a	0.15 ± 0.02^b	<0.001	0.25 ± 0.03	0.12 ± 0.01	<0.001
Eddy kinetic energy (cm^2 s^{-2})	169 ± 89	129 ± 97	157 ± 106	0.67	231 ± 166	142 ± 247	0.44
Finite-size Lyapunov exponent (d^{-1})	0.13 ± 0.01	0.12 ± 0.04	0.16 ± 0.5	0.21	0.19 ± 0.03	0.12 ± 0.05	0.02
Sea level anomaly (m)	0.10 ± 0.01^a	0.09 ± 0.04^a	0.06 ± 0.03^b	0.05	0.03 ± 0.01	0.07 ± 0.03	0.01
Sea surface height (m)	−0.81 ± 0.06	−0.76 ± 0.06	−0.79 ± 0.09	0.53	−0.68 ± 0.05	−0.80 ± 0.04	<0.001
Sea surface temperature (°C)	3.6 ± 0.3	3.4 ± 0.2	3.5 ± 0.5	0.50	4.0 ± 0.3	3.2 ± 0.3	0.001

[a,b] Significant differences

and temporarily pushed the 2 °C isotherm further north (Fig. 1).

Spatial and temporal overlap between species

At-sea distributions of core foraging phases were similar between species with an overlap index of 0.32 (64 %) and 0.69 (77 %) for 50 and 90 % utilisation distributions, respectively (Fig. 3). Despite this large spatial overlap, spatiotemporal overlap was minimal because macaroni penguins started their pre-moult trip 2–3 weeks earlier than eastern rockhopper penguins (Table 1; Fig. 4). In 2013, the peak daily spatiotemporal overlap (0.66) occurred when macaroni penguins were travelling back to the island and eastern

Table 3 Summary of selected generalised additive models explaining variance in the daily travel speed of macaroni (mac) and eastern rockhopper (rock) penguins in relation to environmental covariates during the pre-moult foraging trip (see Table S4 for model rankings)

Year	Model	Term	edf	F	*P* value	Dev. expl. (%)
2012	SST*EKE	SST*EKE	11.8	9.5	<0.001	61
	SSH + CHLA + SLA	SSH	2.6	30.7	<0.001	55
		CHLA	3.8	2.5	0.04	
		SLA	0.9	1.7	0.18	
2013	SST*EKE + SLA	SST*EKE:mac	6.6	13.2	<0.001	55
		SST*EKE:rock	12.1	6.3	<0.001	
		SLA:mac	0	0.3	1	
		SLA:rock	2.79	2.2	0.08	
	SSH*CHLA + EKE + SLA	SSH*CHLA:mac	5.7	15	<0.001	51
		SSH*CHLA:rock	7.4	5.9	<0.001	
		EKE:mac	0	0	1	
		EKE:rock	2.2	4.7	0.006	
		SLA:mac	1.1	2.8	0.07	
		SLA:rock	0	0.1	1	
2014	SST	SST:mac	2.4	55.8	<0.001	63
		SST:rock	2.5	78.9	<0.001	
	SSH*EKE + CHLA + SLA	SSH*EKE:mac	3	3	<0.001	63
		SSH*EKE:rock	6.5	7.3	<0.001	
		CHLA:mac	0	1.2	1	
		CHLA:rock	2.1	2.6	0.02	
		SLA:mac	1.2	1.4	0.001	
		SLA:rock	9.8	1.2	0.01	

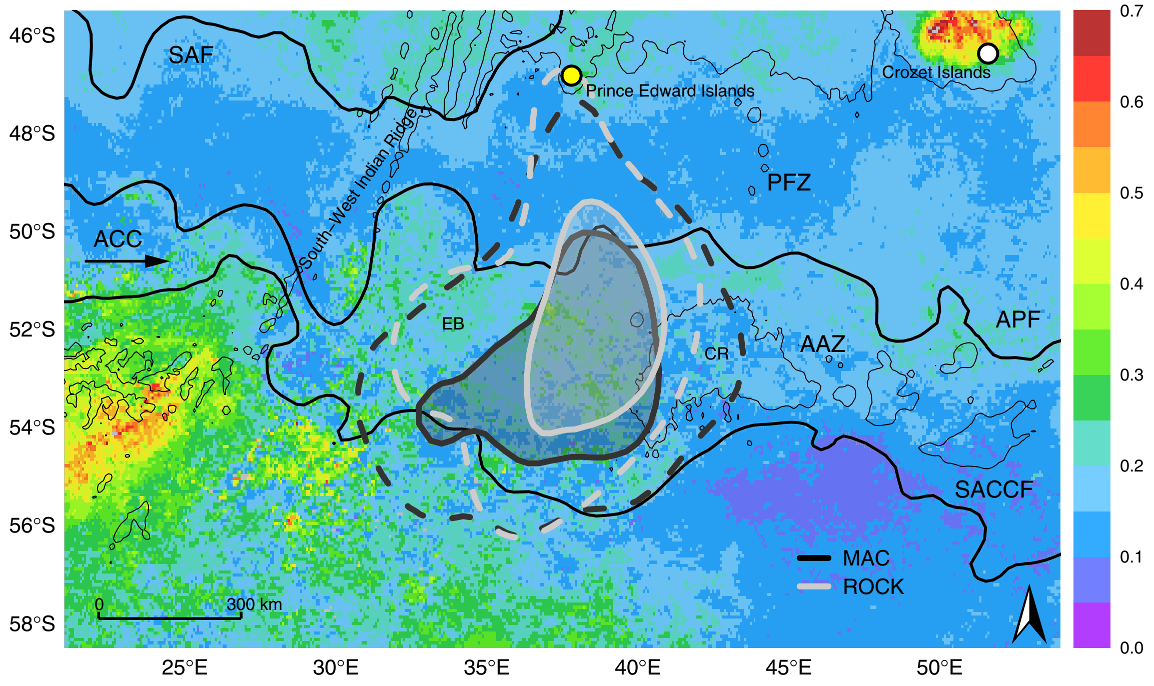


Fig. 3 Kernel utilisation distributions of macaroni (MAC) and eastern rockhopper (ROCK) penguins during 2013 and 2014 pre-moult foraging trips in relation to a composite map of satellite-derived chlorophyll-a concentrations (mg m^{-3}) during January to March 2013 and 2014 (*data source*: Aqua Modis). *Solid* and *dotted lines* represent 50 and 90 % kernel density contours, respectively, of locations where travel speeds were less than the individual's mean. Positions of the Sub-Antarctic Front (SAF), Antarctic Polar Front (APF) and Southern Antarctic Circumpolar Current Front (SACCF) are shown following Swart et al. (2010), and *thin black lines* represent the 3000-m-depth contour. *PFZ* Polar Frontal Zone, *ACC* Antarctic Circumpolar Current, *AAZ* Antarctic Zone, *EB* Enderby Basin, *CR* Conrad Rise

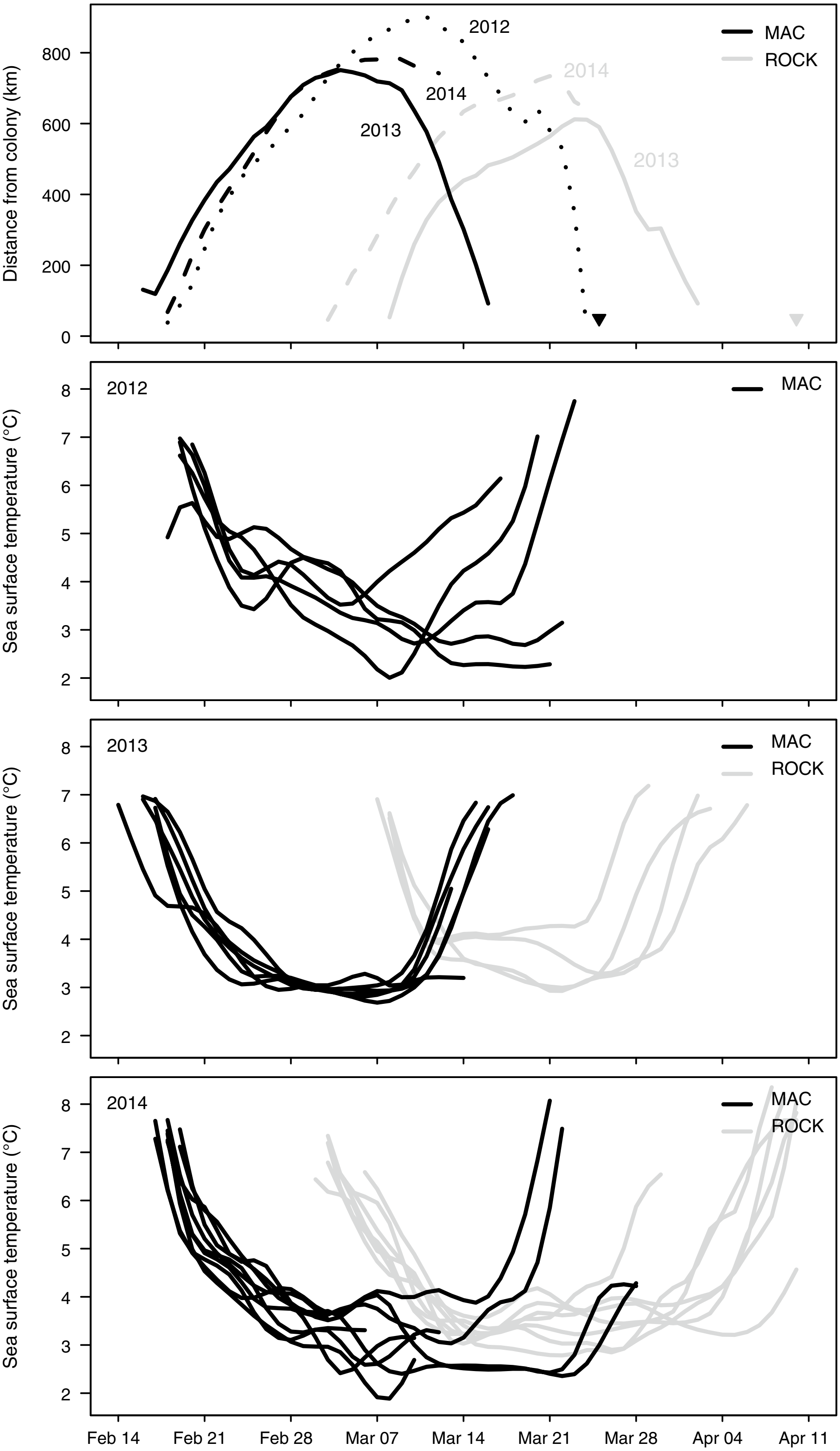


Fig. 4 The evolution of distance from the colony (*top panel*) and sea surface temperatures of macaroni (MAC) and eastern rockhopper (ROCK) penguins during the pre-moult foraging trip. Locations were only included when ≥3 individuals were at sea. *Triangles* denote mean return dates of trips in 2014 when GPS tracks were incomplete

Table 4 Summary of daily diving behaviour of macaroni and eastern rockhopper penguins during the pre-moult foraging trip from Marion Island

	Macaroni penguin ($n = 7$)				Eastern rockhopper penguin ($n = 7$)					
	>4.5 °C	<4.5 °C		All	>4.5 °C	<4.5 °C		All	P_{All}	$P_{<4.5}$
Days (*n*)	54	163		217	80	175		255		
Dive rate (dives day^{-1})	292 ± 77	260 ± 31	**	269 ± 38	452 ± 69	300 ± 47	***	351 ± 54	**	ns
Dives > 10 m (%)	70 ± 11	86 ± 6	***	82 ± 6	68 ± 7	87 ± 5	***	81 ± 6	ns	ns
Dives > 80 m (%)	16 ± 9	25 ± 10	*	22 ± 8	2 ± 3	4 ± 3	ns	4 ± 2	**	**
Time underwater (h day^{-1})	8.3 ± 1.7	8.3 ± 0.9	ns	8.3 ± 0.7	9.3 ± 1.2	7.1 ± 0.8	***	7.9 ± 0.8	ns	ns
VTD (km day^{-1})	10.6 ± 1.7	12.6 ± 1.6	*	12.1 ± 1.1	11.2 ± 1.8	12.5 ± 1.4	*	12.2 ± 1.1	ns	ns
Maximum depth (m)[a]	39 ± 9	51 ± 8	**	48 ± 7	27 ± 3	43 ± 4	***	38 ± 3	***	**
Dive duration (s)[a]	127 ± 13	130 ± 12	ns	130 ± 11	95 ± 5	95 ± 7	ns	95 ± 5	***	***
Descent rate (m s^{-1})[a]	1.08 ± 0.1	1.17 ± 0.07	**	1.15 ± 0.06	1.0 ± 0.07	1.12 ± 0.07	***	1.08 ± 0.06	ns	ns
Ascent rate (m s^{-1})[a]	1.0 ± 0.12	1.13 ± 0.05	***	1.10 ± 0.05	0.88 ± 0.07	1.15 ± 0.07	***	1.07 ± 0.04	ns	ns

Significances of linear mixed-effect model results comparing dive parameters between water masses (< and >4.5 °C SST_{TDR}) and species with individual identity nested within year are shown: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$, *ns* not significant

[a] For dives > 10 m; *VTD* vertical travel distance

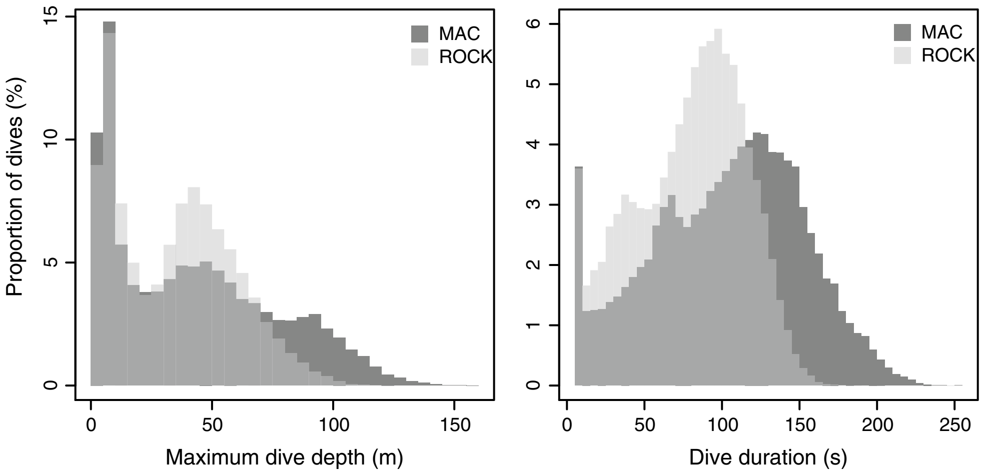


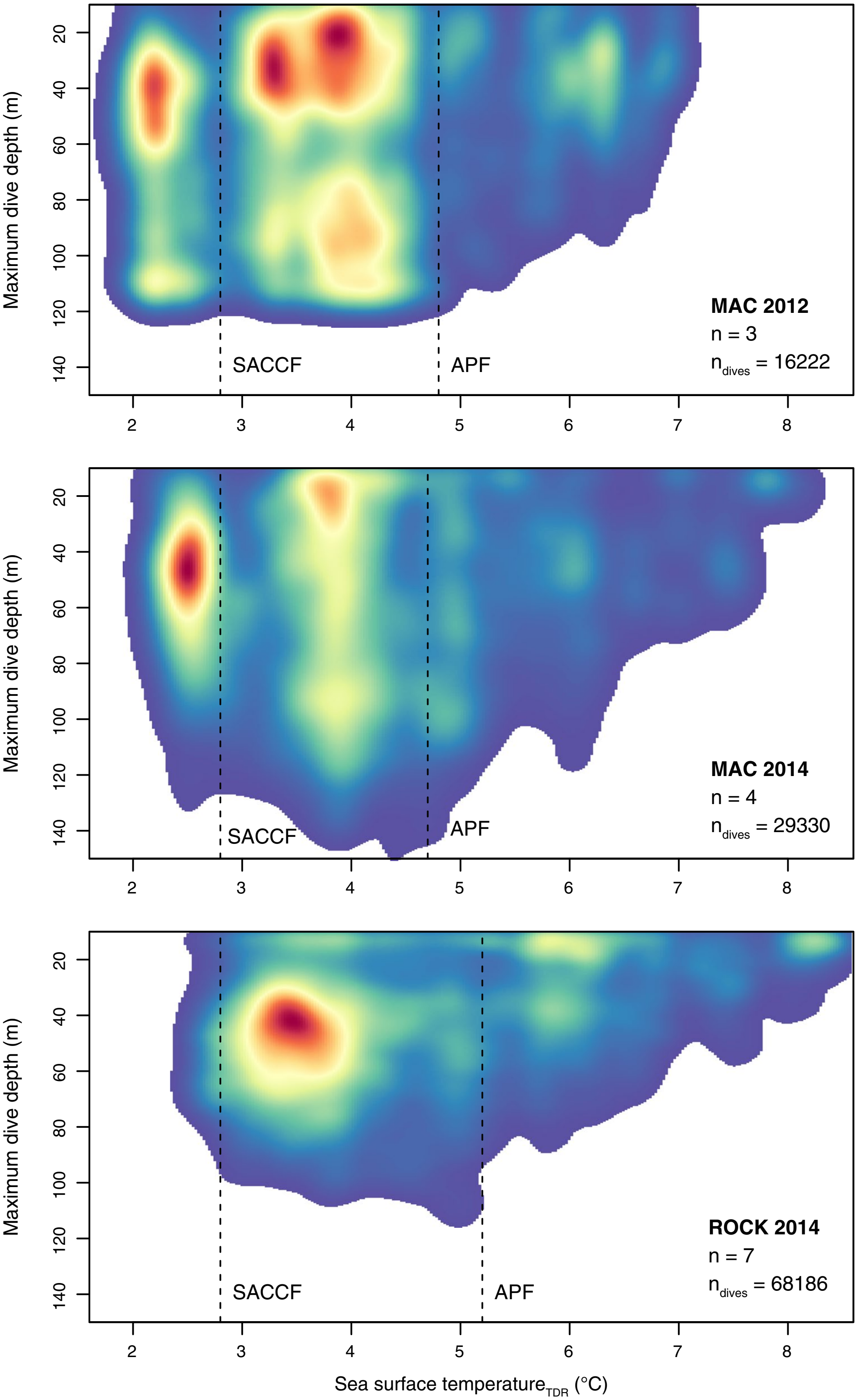
Fig. 5 Distribution of maximum dive depths (*left panel*) and dive durations (*right panel*) of macaroni (MAC) and eastern rockhopper (ROCK) penguins during the pre-moult foraging trip in 2014

rockhopper penguins were on their outbound journey. In 2014, the two species were at sea together for a longer period (23 days) than in 2013 (8 days; Fig. 4), but unfortunately the expected increase in spatiotemporal overlap could not be computed due to the early failure of GPS logger batteries.

Diving behaviour

Absolute maximum dive depths and durations were 156.3 m and 255 s for macaroni penguins and 122.3 m and 205 s for eastern rockhopper penguins. Both species most frequently dived to depths <10 m, but the distribution of deeper dives differed between species, with eastern rockhopper penguins exhibiting a distinct mode between 30 and 60 m and macaroni penguins exploiting depths >80 m more often (Table 4; Fig. 5). Dive durations differed markedly between species, with most (~50 %) dives of macaroni penguins and eastern rockhopper penguins lasting 110–150 and 70–120 s, respectively (Fig. 5). Table 4 shows the summary of daily diving behaviour of both species. Comparisons of daily diving behaviour of macaroni penguins in 2012 and 2014 revealed no significant differences, and thus, data were pooled. However, the distribution of dive depths in relation to SST_{TDR} differed between years (Fig. 6). In both years, dive depths of macaroni penguins south of the SACCF were predominantly to depths of 30–60 m, but within AAZ waters dives in 2014 were more homogenously distributed within the water column (Fig. 6). Eastern rockhopper penguins

Fig. 6 Kernel density estimates (99 %) of maximum dive depths (>10 m) of macaroni (MAC) and eastern rockhopper (ROCK) penguins in relation to sea surface temperature (SST_{TDR}) during the pre-moult foraging trip. Approximate positions of the Antarctic Polar Front (APF) and Southern Antarctic Circumpolar Front (SACCF) are shown based on the mean SST encountered by penguins at −0.63 m SSH and −0.943 m SSH, respectively (Swart et al. 2010)



concentrated diving activity in AAZ waters (3–4 °C) and dived predominantly to depths of 30–70 m (Fig. 6). Diurnal diving activity differed between water masses (Fig. 7), with penguins performing more night dives and diving more consistently throughout the day in warmer waters (>4.5 °C). Macaroni and eastern rockhopper penguins encountered a

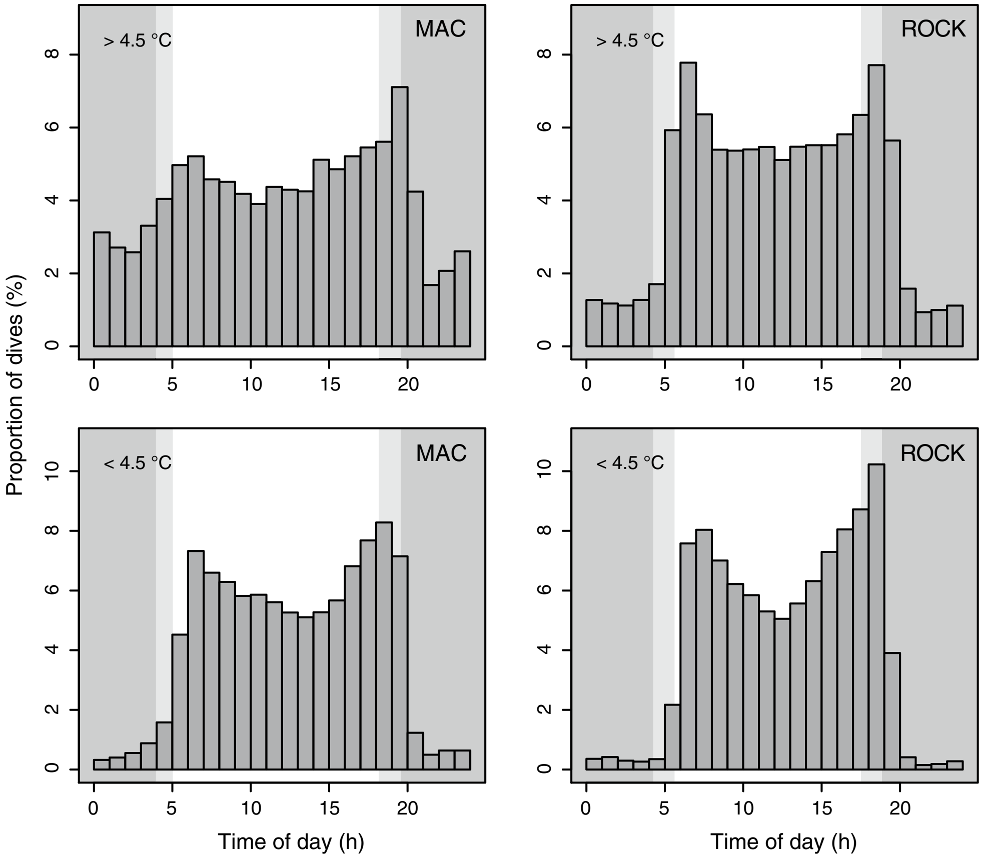


Fig. 7 Proportion of dives (%) performed by macaroni (MAC) and eastern rockhopper (ROCK) penguins in relation to time of day and sea surface temperature (> and <4.5 °C) during the 2014 pre-moult foraging trip. *Dark* and *light shaded bars* represent night-time and nautical twilight periods, respectively, determined for the mean location of core foraging areas at the midpoint of the trip

thermocline during an estimated 6.7 % ($n = 29{,}330$) and 0.6 % ($n = 68{,}186$) of dives >10 m, respectively (Fig. 8). The presence of sub-mesoscale filaments did not influence the diving behaviour of macaroni penguins ($\mathrm{LME}_{\mathrm{dives}>10\mathrm{m}}$, $t_{81} = -1.0$, $P = 0.3$; $\mathrm{LME}_{\mathrm{depth}}$, $t_{81} = 0.3$, $P = 0.8$; $\mathrm{LME}_{\mathrm{duration}}$, $t_{81} = -1.6$, $P = 0.1$; $\mathrm{LME}_{\mathrm{underwater}}$, $t_{81} = -0.3$, $P = 0.8$), but during days when filaments were present eastern rockhopper penguins performed 26 ± 13 (10 %) more foraging dives (>10 m; LME, $t_{136} = 1.2$, $P = 0.048$) at an average of 4.3 ± 1.9 m shallower (LME, $t_{136} = -2.3$, $P = 0.03$) and spent 1.3 ± 0.4 h (18 %) more time underwater (LME, $t_{136} = 3.1$, $P = 0.002$). Dive durations of eastern rockhopper penguins, however, did not differ significantly in relation to filaments (LME, $t_{136} = 1.7$, $P = 0.1$).

Discussion

The consistent movement of both macaroni and eastern rockhopper penguins to distant foraging areas south of the Prince Edward Islands during the pre-moult foraging trip is in accordance with ship-based observations made south of the islands in April 2008 where a peak abundance of crested penguin sightings (mostly macaroni penguins) was noted at 50–52°S (Ryan 2009). The long-distance dispersal of macaroni penguins *Eudyptes chrysolophus* during the pre-moult period was first, and rather accurately, inferred by Brown (1987) who used speed meters to estimate that two individuals travelled 700–1200 km from Marion Island. Such large-scale dispersal of macaroni penguins during the pre-moult period has since been reported at South Georgia (54.0°S, 38.03°W; Green et al. 2009b; Waluda et al. 2010; Horswill 2015), Crozet (46.4°S, 51.8°E) and Kerguelen Islands (Thiebot et al. 2014) and Bouvetøya (54.4°S, 3.8°E; Lowther et al. 2014) (Table 5). However, ours is the first study to document the dispersal of eastern rockhopper penguins during the pre-moult period.

Marine habitats and association with sub-mesoscale and mesoscale features

Given that both species in this study travelled such large distances to forage in cooler waters (~3.5 °C) south of the APF, and assuming that penguins adopt foraging strategies

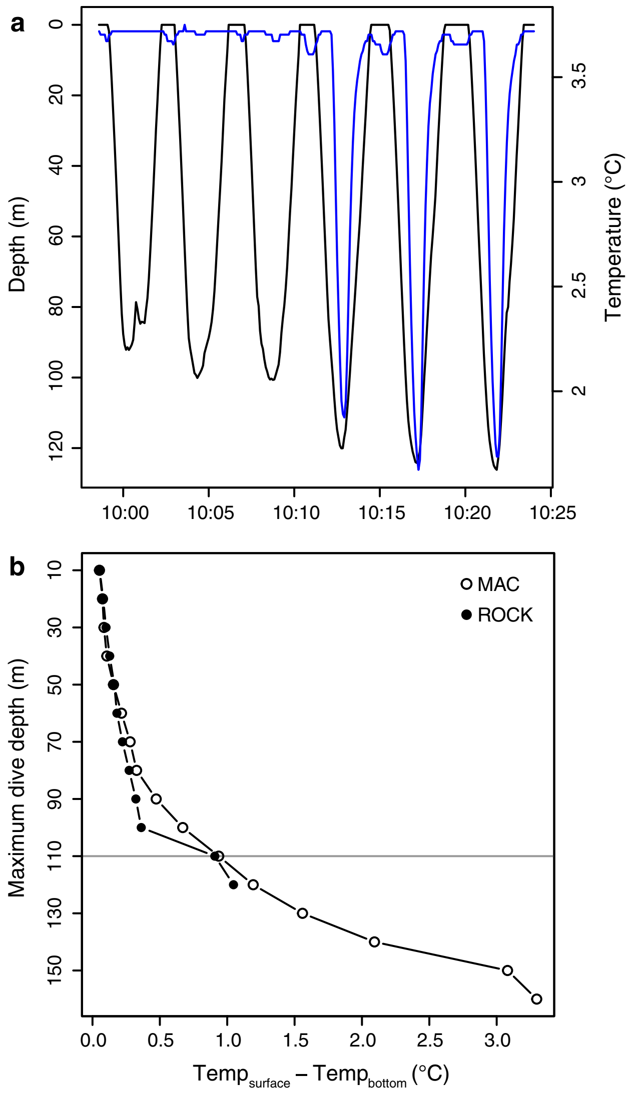


Fig. 8 Depth profiles of a macaroni penguin during the pre-moult trip showing the sharp decline in water temperature when the thermocline was encountered ~110 m (**a**), and the temperature differences between surface and bottom waters encountered by macaroni and eastern rockhopper (ROCK) penguins in relation to depth (**b**) showing the approximate position of the thermocline (*grey line*)

that maximise net energy gain (MacArthur and Pianka 1966), it is likely that prey must be more available (or at least predictable) and/or more energy-rich than in PFZ waters nearer the Prince Edward Islands. Satellite-derived surface chlorophyll-a concentrations revealed the higher productivity of Antarctic Zone (AAZ) waters relative to Polar Frontal Zone (PFZ) waters typically observed during the austral summer (Sokolov and Rintoul 2007). As blooms are known to extend for hundreds of kms downstream of topographical features (Sokolov and Rintoul 2007), elevated primary productivity at the south-west Indian Ridge (SWIR; Fig. 3) may considerably enrich AAZ waters south of the islands. Total macrozooplankton and fish biomass are generally higher south of the APF compared to PFZ waters (Pakhomov et al. 1994; Pakhomov and Froneman 2000). As macaroni and eastern rockhopper penguins feed primarily on euphausiids during breeding (Crawford et al. 2003a, b), and isotope data from other localities suggest a primarily crustacean-based diet for both species during the pre-moult period (Jaeger and Cherel 2011; Thiebot et al. 2014), differences in PFZ and AAZ euphausiid communities may be a factor causing penguins to travel such large distances to AAZ waters. Euphausiid communities in PFZ waters are generally dominated by sub-Antarctic species (*Euphausia vallentini*, *E. longirostris, Nematoscelis megalops, Thysanoessa* spp.), whereas those in AAZ waters are typically Antarctic species (*E. triacantha*, *E. frigida*) (Pakhomov et al. 1994; Pakhomov and Froneman 2000; Ansorge et al. 2009); however, eddies are known to entrain species across the APF (Bernard et al. 2007; Ansorge et al. 2009). Penguins were unlikely targeting the Antarctic krill *E. superba* as this species rarely occurs north of 60° in this region of the Southern Ocean (Atkinson et al. 2008). Additionally, the increased abundance of myctophids in AAZ waters may provide penguins with an energy-rich supplement to euphausiids, as suggested by many studies focusing on the diet of post-breeding crested penguins in the Southern Indian Ocean (Cherel et al. 2007; Thiebot et al. 2012, 2014).

The region immediately upstream of the penguins' core foraging areas is characterised by extremely high mesoscale activity associated with the persistent generation of eddies over the SWIR (Durgadoo et al. 2011; Frenger 2013). These eddies typically move east, passing south of the Prince Edward Islands, or move south/south-east and dissipate over the Enderby Basin (Durgadoo et al. 2011; Ansorge et al. 2015). Eddies and associated filaments are important foraging areas for many top predators throughout the Southern Ocean (Nel et al. 2001; Cotté et al. 2007; Bost et al. 2009; Cotté et al. 2015; Massie et al. 2015) as they support elevated aggregations of macrozooplankton and micronekton (Ansorge et al. 2009). Maps of SLA and FSLE revealed a consistent eddy field in the lee of the SWIR during the study period (Fig. S7–S11), supporting the concept of an eddy conglomeration in this region (Ansorge and Lutjeharms 2005). Movements of penguins appeared to be influenced by the structure of the mesoscale environment, with penguins avoiding extreme eddies (>0.3 m) and waters characterised by high EKE. Such avoidance may benefit penguins by reducing the energetic cost of swimming against currents (Bon et al. 2015). Association of penguins with well-defined eddies was only apparent for a few individuals; however, most penguins targeted waters characterised by weak positive SLA and relatively low EKE downstream of and/or within convergence zones between

Table 5 Characteristics of the pre-moult foraging trip of macaroni penguins from different breeding localities

Locality	Year	*N*	Technique	Departure date	Duration (days)	Maximum range (km)	Direction	Distance to 3.5 °C isotherm (km)*	Distance to core AAZ (km)*	References
Marion (47°S)	1985	2	Speed meter	–	–	945 ± 332	–	738	–	Brown (1987)
	2012	5	GPS	19-Feb ± 1	35 ± 7	1018 ± 166	S	657	724	This study
	2013	6	GPS	16-Feb ± 2	29 ± 3	780 ± 60	S	606	677	
	2014	9	GPS	18-Feb ± 1	38 ± 7	873 ± 104	S	681	734	
Crozet (47°S)	2009	9	GLS	14-Feb ± 4	50 ± 7	824 ± 343	S, SE	796	810	Thiebot et al. (2014)
Kerguelen (49°S)	2011	13	GLS	17-Feb ± 1	42 ± 4	941 ± 271	SE	667	813	Thiebot et al. (2014)
South Georgia (54°S)	1976	29	–	–	13 ± 1	–	–	–	–	Williams and Croxall (1991)
	2002	17	BGL	20-Feb ± 4	21 ± 1	634 ± 115	N, NW, W	142	378	Green et al. (2009b)
	2003	15	BGL	21-Feb ± 4	18 ± 1	697 ± 88	N, NW	175	384	
	2004	4	PTT	19-Feb	18 ± 7	489 ± 80	N, NW, W	175	435	Waluda et al. (2010)
	2012	4	GPS	24-Feb ± 1	17 ± 1	357 ± 40	NW	154	374	Horswill (2015)
Bouvetøya (54°S)	2008	3	PTT	1-Mar ± 0	20[a]	444 ± 111	N, NW	437	411	Lowther et al. (2014)

GPS global positioning system, *GLS* geolocation, *BGL* behavioural geolocation, *PTT* platform terminal transmitter, * on March 1

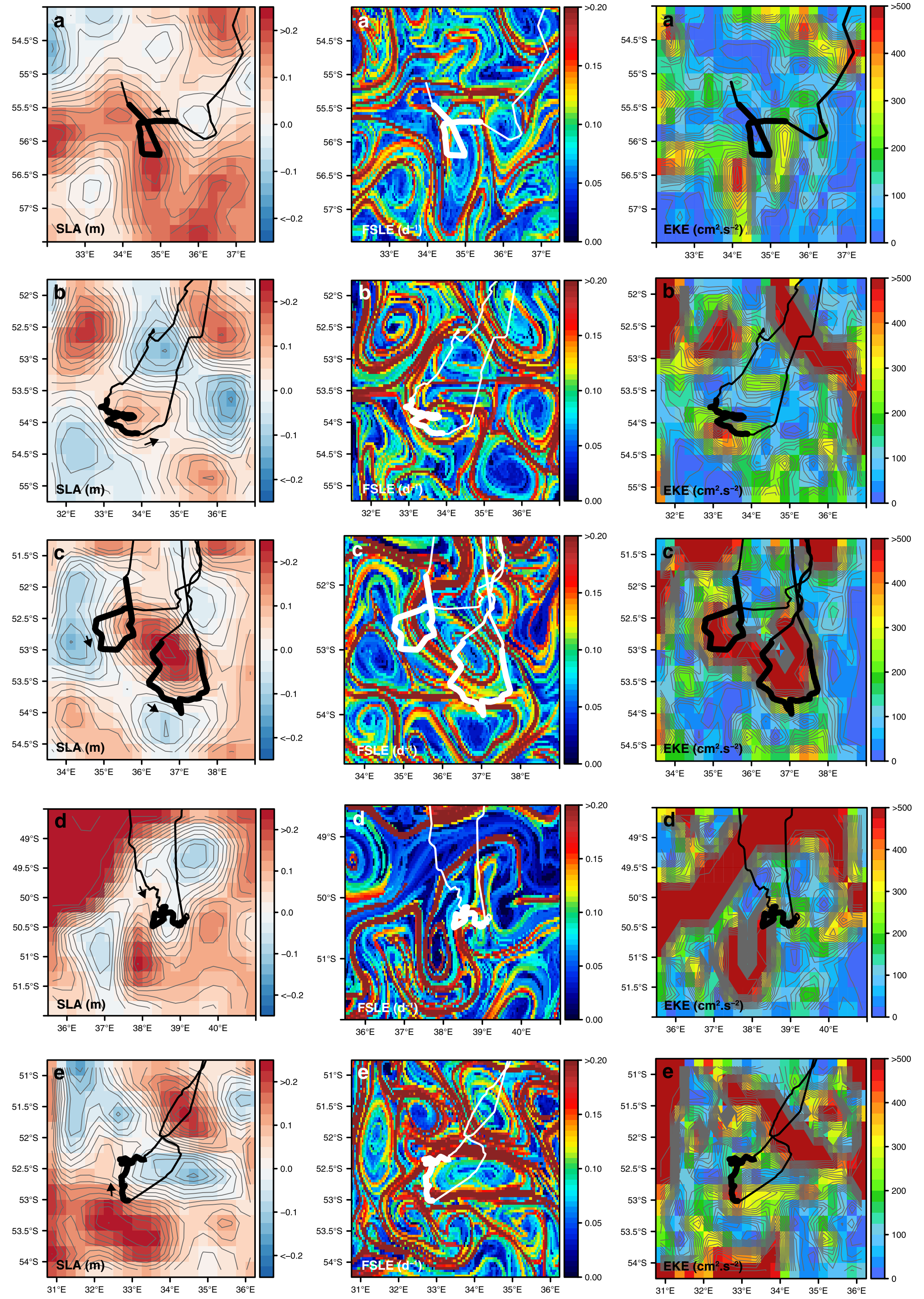
[a] Data only available for one individual

eddies (Fig. 9; Fig. S7–S11). Importantly, all penguins exhibited strong associations with sub-mesoscale filaments (Table 4; Fig. 9) that are often associated with eddy edges (Lapeyre and Klein 2006). Recent evidence highlights the importance of such features for macaroni penguins during the pre-moult period at Bouvetøya (Lowther et al. 2014) and the incubation period at the Crozet Islands (Bon et al. 2015). The edges of warm eddies have shallower thermoclines and mixed layers than the core (Ansorge et al. 2009), and sub-mesoscale filaments are associated with reduced vertical mixing and increased water column stability (Lévy et al. 2012), which may force prey into surface waters more accessible to penguins. It is possible that the dissipation of eddies over the Enderby Basin acts as an important mechanism for the lateral advection of prey into the region which are then retained along sub-mesoscale filaments and in neighbouring waters characterised by relatively lower EKE. Indeed, it is suggested that krill abundance is highest in waters of moderate EKE where upwelling is maintained, but krill are less likely to be advected (Santora et al. 2012). If this is the case, macaroni and eastern rockhopper penguins would be able to forage more efficiently in such areas that aggregate preferred prey and/or make them more accessible. Further investigations into these fine-scale foraging strategies are, however, needed to elucidate such mechanisms.

Fig. 9 Movements of macaroni (**a**, **b**) and eastern rockhopper penguins (**c**, **d**, **e**) in relation to maps of sea level anomaly (SLA), finite-size Lyapunov exponent (FSLE) and eddy kinetic energy (EKE). *Thicker line* represents 3 days prior to and after the date of mapped environmental variables; 17 March 2012 (**a**), 4 March 2013 (**b**), 22 March 2013 (**c**), 17 March 2013 (**d**) and 17 March 2014 (**e**). *Arrows* indicate direction of movement

Inter-annual variation

Due to the highly dynamic and complex nature of Southern Ocean ecosystems, the limited period during which this study was undertaken, and rather small sample sizes, it was difficult to identify specific environmental drivers of inter-annual variation in foraging trip characteristics. Positions of the APF and SACCF, and cooler isotherms (2–4 °C), south of the islands varied marginally between years (Fig. 1; see also Fig. S6), with the core AAZ and 3.5 °C isotherm located slightly nearer (~80 km) the islands in 2013. This difference appears insufficient to account for the inter-annual variation in maximum foraging ranges, suggesting the influence of other factors. Perhaps the most distinct difference between years was the early disintegration of the summer bloom in 2014, resulting in decreased surface chlorophyll-a concentrations both within core foraging areas and upstream at the SWIR. This may explain why both species spent significantly more time at sea in


a
SLA (m)
54.5°S
55°S
55.5°S
56°S
56.5°S
57°S
33°E
34°E
35°E
36°E
37°E
>0.2
0.1
0.0
−0.1
<−0.2
a
FSLE (d⁻¹)
>0.20
0.15
0.10
0.05
0.00
a
EKE (cm².s⁻²)
>500
400
300
200
100
0
b
SLA (m)
52°S
52.5°S
53°S
53.5°S
54°S
54.5°S
55°S
32°E
33°E
34°E
35°E
36°E
b
FSLE (d⁻¹)
b
EKE (cm².s⁻²)
c
SLA (m)
51.5°S
52°S
52.5°S
53°S
53.5°S
54°S
54.5°S
34°E
35°E
36°E
37°E
38°E
c
FSLE (d⁻¹)
c
EKE (cm².s⁻²)
d
SLA (m)
49°S
49.5°S
50°S
50.5°S
51°S
51.5°S
36°E
37°E
38°E
39°E
40°E
d
FSLE (d⁻¹)
d
EKE (cm².s⁻²)
e
SLA (m)
51°S
51.5°S
52°S
52.5°S
53°S
53.5°S
54°S
31°E
32°E
33°E
34°E
35°E
36°E
e
FSLE (d⁻¹)
e
EKE (cm².s⁻²)

2014 compared to 2013, but does not account for the longer trips performed by macaroni penguins in 2012. Reduced primary productivity is likely to reduce prey availability, forcing penguins to spend more time searching for and/or pursuing prey. Reasons for the decreased productivity are unclear, but as mesoscale processes are key drivers of primary productivity (Kahru et al. 2007; Frenger 2013), such conditions may be linked to the structure of the mesoscale environment. Mesoscale activity in this region is largely determined by the interaction of the ACC with the SWIR (Durgadoo et al. 2011), and thus, fluctuations in the positions of major frontal boundaries associated with the ACC may indirectly influence primary productivity. The mesoscale environment was most distinctly different in 2013 due to a corridor of extreme eddies upstream of the Prince Edward Islands (Fig. S8, S10) which might have resulted from the close proximity of the APF and SACCF over the SWIR (Ansorge et al. 2009). Continued monitoring is required in order to better understand how environmental conditions drive inter-annual variation in pre-moult foraging trip characteristics.

Diving behaviour

Both species dived actively throughout trips, but exhibited diving behaviour more typical of intensive foraging in cooler waters (<4.5 °C; i.e. more dives >10 m, increased VTD, deeper dives, and steeper descent and ascent rates; Table 4), supporting the importance of these waters as core foraging areas. As macaroni and eastern rockhopper penguins are visual predators that forage predominantly during the day (Tremblay and Cherel 2003; Green et al. 2005), the more frequent night dives in warmer waters were likely associated with travelling. In cooler waters, diving activity of both species was concentrated in the mornings and evenings (Fig. 7). Euphausiids and fish are well known to exhibit diel vertical migration patterns and are probably more accessible to penguins during these periods (Hulley 1990). To our knowledge, this study provides the first evidence of the utilisation of thermoclines by crested penguins (Fig. 8), but such features were insignificant for eastern rockhopper penguins due to their low encounter rate (0.6 % of dives >10 m) as a consequence of a reduced ability to dive to such depths (Fig. 5). Thermoclines are important features for penguins as they structure the vertical habitat of prey (Charrassin and Bost 2001; Ropert-Coudert et al. 2009).

Macaroni penguins in this study exhibited similar diving behaviour to chick-rearing penguins at Marion Island (Pichegru et al. 2011), as also observed for macaroni penguins at South Georgia (Green et al. 2005). However, dive depths and durations of macaroni penguins in this study were greater than those during breeding and pre-moult at South Georgia and more akin to those during the over-wintering period at South Georgia (Green et al. 2005) and incubation period at Kerguelen (Sato et al. 2004). This study is the first to reveal insights into the diving behaviour of eastern rockhopper penguins during the pre-moult period. Dive depths and durations were similar to those during the breeding season at Marion (Whitehead et al. unpubl data) and Crozet Islands (Tremblay and Cherel 2003), but were deeper and longer than those during the breeding season at Macquarie Island (Hull 2000). In comparison with southern rockhopper penguins *E. chrysocome chrysocome* in the south-west Atlantic Ocean, dive depths and durations were greater at Marion Island, perhaps owing to differences in prey distribution and availability (Schiavini and Raya Rey 2004; Pütz et al. 2006; Raya Rey et al. 2009; Ludynia et al. 2013). Interestingly, a male rockhopper penguin in this study performed the deepest dive recorded for this species (122.3 m).

Comparison between species

Macaroni and eastern rockhopper penguins exhibited similar habitat preferences and at-sea distributions during the pre-moult foraging trip (Fig. 3), but spatiotemporal overlap is considerably reduced by the 2- to 3-week difference in departure dates (Table 1; Fig. 4), linked to differences in the onset of breeding (Brown 1987). This phenological difference may have evolved to reduce interspecific competition during the breeding season when foraging pressure near the islands is high, but it also appears to reduce potential interspecific competition during the pre-moult foraging period, and possibly during the initial and final weeks of the winter trip (Thiebot et al. 2012). Royal and eastern rockhopper penguins and Adélie *Pygoscelis adeliae* and chinstrap *P.antarctica* penguins also exhibit allochrony throughout their annual cycle (Trivelpiece et al. 1987; Hull 2000). This time shift appears to be a vital aspect of segregation during the pre-moult period as it allows eastern rockhopper penguins to exploit similar habitats to macaroni penguins whilst minimising potential competition. Contrastingly, these two species exhibit markedly different habitat preferences during the winter period (Thiebot et al. 2013). Comparisons of diving behaviour revealed a large overlap in their use of the water column (Fig. 5); however, macaroni penguins dived more frequently to depths > 80 m (Table 4) and thus encountered thermoclines more often. This suggests that the size or type of prey taken during the pre-moult period might differ slightly between species, and prompts further investigations into potential dietary differences; however, isotopic studies at other localities suggest that macaroni and eastern rockhopper penguins forage at a similar trophic level during the pre-moult period (Cherel et al. 2007; Thiebot et al. 2014). If the same prey are targeted, it is important to consider

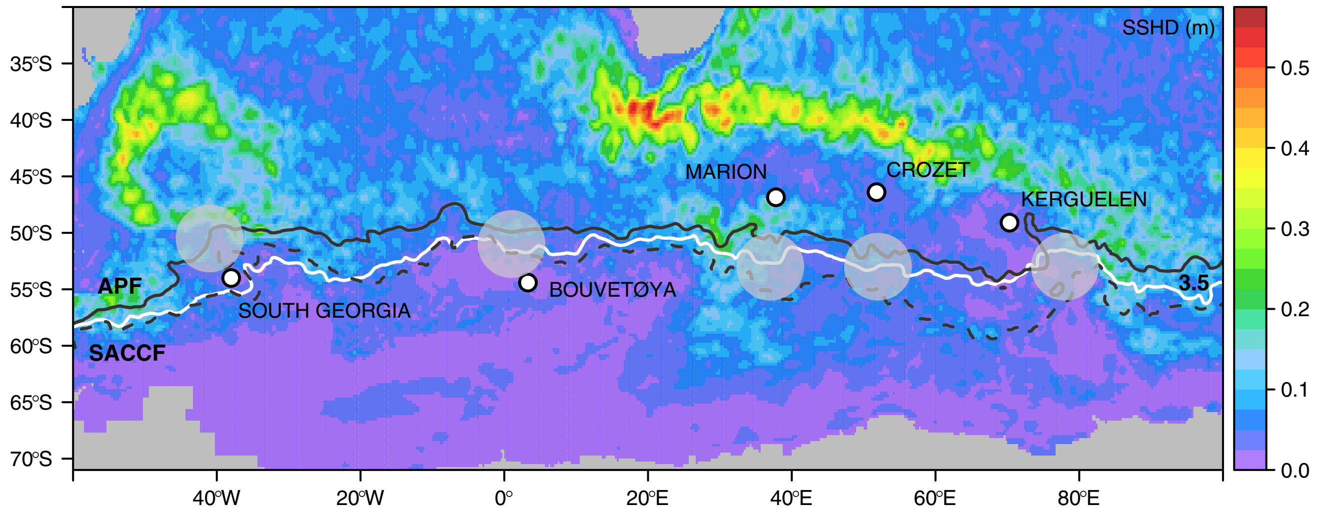


Fig. 10 Macaroni penguin breeding localities (*white circles*) and approximate foraging areas (*grey circles*, see Table 5) during the pre-moult foraging trip. *Colour* represents sea surface height variability (SSHD) across the Atlantic and Indian Ocean sectors of the Southern Ocean at the end of February during 2002–2014 (*source*: Aviso). Mean positions of the 3.5 °C isotherm, Antarctic Polar Front (APF) and Southern Antarctic Circumpolar Current Front (SACCF) are shown

that intense foraging by macaroni penguins at core foraging areas during the 2 weeks leading up to the period when eastern rockhopper penguins are at sea may reduce prey availability unless new prey are advected into the region. Additionally, the greater abundance of macaroni penguins and their increased ability to dive deeper and for longer than eastern rockhopper penguins, as expected from their larger body size and lung capacity, suggests that if foraging areas overlapped and resources were limited, they would likely outcompete eastern rockhopper penguins. Thus, in less productive years when both species spend more time concurrently at sea, such as 2014, the potentially larger spatiotemporal overlap may negatively affect the foraging efficiency of eastern rockhopper penguins. However, inspection of SSTs exploited in 2014 revealed that macaroni penguins foraged in marginally cooler or warmer waters than eastern rockhopper penguins, whilst both species were concurrently at sea (Fig. 4). Further studies with larger sample sizes are, however, needed to determine whether such fine-scale segregation occurs.

Pre-moult habitat and trip characteristics in a circumpolar context

Throughout the range of macaroni penguins, the duration of pre-moult foraging trips varies considerably (Table 5). For instance, macaroni penguins at South Georgia conduct relatively short trips (13–21 days; Williams and Croxall 1991; Green et al. 2009b) compared to birds at Crozet and Kerguelen (50 and 42 days, respectively; Thiebot et al. 2014). SST preferences of penguins in this study were remarkably similar to macaroni penguins at Crozet and Kerguelen that reached waters ~3.5 °C (Thiebot et al. 2014). Thiebot et al. (2014) suggested that the duration of trips was related to the distance from the colony to the 3.5 °C isotherm (~796 km from Crozet and 667 km from Kerguelen). The proximity of the 3.5 °C isotherm to Marion Island (~635–681 km) is similar to Kerguelen and closer than Crozet, and penguin trip durations are appreciably shorter (~33 days). At South Georgia, the 3.5 °C isotherm is generally located to the south of the island during the pre-moult period yet macaroni penguins travel > 350 km north-west of the island to slightly warmer waters (~5 °C; Waluda et al. 2010; Horswill 2015). The inter-island differences in preferred SST at foraging areas suggest that whilst SST may play an important role as an environmental cue to local populations, other processes ultimately determine favourable foraging areas. At a broad scale, macaroni penguins forage predominantly in AAZ waters between the APF and the SACCF (Fig. 10), although behavioural geolocation of penguins from South Georgia suggests they also forage north of the APF in the PFZ (Green et al. 2009b). Both the APF and SACCF are associated with high mesoscale activity and productivity (Strass et al. 2002; Kahru et al. 2007; Frenger 2013), and the shedding of eddies into AAZ waters may provide penguins with a rich mesoscale environment in which to forage. The strong relationships between the distance of the colony to the core AAZ and the duration and maximum range of the pre-moult foraging trip (Fig. 11) further emphasise the global importance of this region for macaroni penguins. To our knowledge, there are no previous

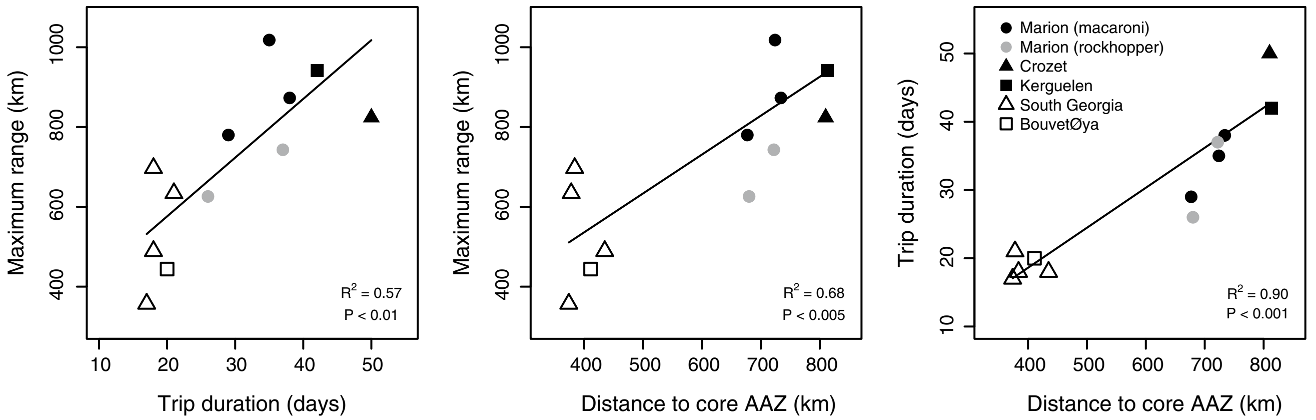


Fig. 11 Linear regressions of pre-moult foraging trip characteristics of macaroni penguins at various breeding localities in relation to their distance to the core Antarctic Zone (AAZ; midpoint of the Antarctic Polar Front and Southern Antarctic Circumpolar Current Front). Eastern rockhopper penguins also included for comparison. Multiple points for localities represent different years

records of foraging ranges or habitats of rockhopper penguins during the pre-moult period; however, trip durations of 9 and 13 days have been reported for eastern rockhopper penguins at Macquarie Island (Hull et al. 2004; 1995 and 1996, respectively; core AAZ ~ 189 and 277 km S, respectively) and 20 to 25 days for southern rockhopper penguins at the Falklands (Strange 1982; core AAZ ~580 km S). Future studies at other localities are required to validate the importance of the core AAZ to both macaroni and rockhopper penguins during the pre-moult period and to determine whether penguins at these localities associate with eddies and/or sub-mesoscale filaments.

Conclusions

At a broad scale, the consistent movement of both macaroni and eastern rockhopper penguins from Marion Island to cooler waters (~3.5 °C) south of the APF in the lee of the SWIR documents for the first time the importance of this region as a predictable foraging area for these penguins after the breeding season. The association of penguins with mesoscale eddies (and sub-mesoscale filaments) further supports the value of such features in sustaining top predator populations at the Prince Edward Islands (Nel et al. 2001; Massie et al. 2015). Both macaroni and eastern (subspecies of southern) rockhopper penguins are listed as vulnerable (BirdLife International 2015) due to recent population declines (30 and 70 % since 1994/95, respectively, at the Prince Edward Islands; Crawford et al. 2009). Changes in the prey environment at pre-moult foraging areas may have implications for adult survival during and after the moult and may thus be an important driver of population dynamics. Given the recent changes documented in the Southern Ocean, such as increasing SST (Gille 2002; Mélice et al. 2003) and the southward shift in major frontal boundaries (Hunt et al. 2001), continued monitoring is necessary in order to determine how penguins might adapt to associated changes in this dynamic region of the Southern Ocean (Péron et al. 2012).

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All procedures performed in this study were in accordance with the ethical standards of the Faculty of Science Animal Ethics Committee (SFAEC), University of Cape Town (2013/V5/NEW).

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