

Habitat preference and dive behavior of non-breeding emperor penguins in the eastern Ross Sea, Antarctica

Kimberly T. Goetz^{1,*}, Birgitte I. McDonald², Gerald L. Kooyman³

¹National Institute of Water and Atmospheric Research, 301 Evans Bay Parade, Wellington 6021, New Zealand

²Moss Landing Marine Laboratories, 8272 Moss Landing Road, Moss Landing, CA 95039, USA

³Center for Marine Biotechnology and Biomedicine, Scholander Hall, Scripps Institution of Oceanography, 9500 Gilman Drive no. 0204, La Jolla, CA 92093, USA

ABSTRACT: Emperor penguins *Aptenodytes forsteri* are important predators in the Ross Sea ecosystem, yet little is known about their movement and foraging behavior outside the breeding season or within different demographic groups. In early March 2013, we instrumented 20 non-breeding emperor penguins in the eastern Ross Sea with satellite-linked recorders and analyzed their habitat preference and dive behavior. Track length ranged from 273 km to nearly 9000 km and dive data were obtained for over 96 000 dives (mean maximum depth: 90.2 ± 77.8 (SD) m, mean dive duration: 4.6 ± 2.3 min), 17 of which exceeded the previous duration record of 27.6 min. Overall, emperor penguins preferred areas north of Cape Colbeck that were beyond the shelf break and received more sunlight. In these areas, penguins performed dives that were deeper, longer, faster, and more pelagic than dives located near the colony. Birds exhibited various movement and foraging strategies ('shelf' and 'gyre'; benthic and pelagic). The occurrence of deeper and longer dives during the day ($n = 28\,318$) and at twilight ($n = 60\,171$) than at night ($n = 7582$), especially at high latitudes, is consistent with emperor penguins being visual predators. Observed differences in both movement and dive behavior as a function of light may indicate a change in prey preference across space and time. Our study offers novel insight into the habitat preferences and dive behavior for a previously unstudied demographic group, at a time when emperor penguins experience the most severe environmental conditions of their annual life cycle.

KEY WORDS: Emperor penguin · Tracking · Molt · Habitat suitability · Diving · Light · Foraging · Ross Sea

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INTRODUCTION

Quantifying the movement and habitat preferences of marine vertebrates is challenging because their underwater behavior cannot be easily observed and their movement is 4-dimensional, varying over space and time. The advent of bio-logging technology and the increased accessibility of remotely sensed data have revolutionized our understanding of ecology and the interplay between an animal's behavior and its environment (Guisan & Zimmer-

mann 2000, Costa et al. 2010, 2012). Furthermore, the integration of Global Positioning System (GPS) and Advanced Research and Global Observation Satellite (ARGOS) technologies into animal-borne devices has allowed increased knowledge of habitat use, especially for Antarctic species (Burns & Kooyman 2001, McConnell et al. 2002, Fauchald & Tveraa 2003).

Among marine vertebrates, seabirds are frequently the subject of movement and habitat use studies. Foraging seabirds are known to target areas where oceanic features, such as sea surface temperature

and bottom topography, increase primary productivity (Croxall & Wood 2002, Wakefield et al. 2009, 2011, Deppe et al. 2014, Scales et al. 2016). These features aggregate prey and allow predators to forage more efficiently (Keiper et al. 2005, Bailleul et al. 2007, Hyrenbach et al. 2007). Optimal foraging theory predicts that organisms maximize fitness by behaving in ways that increase their ability to capture and consume prey (MacArthur & Pianka 1966). Therefore, predators should adjust their movement and dive behavior according to prey density and availability.

Foraging ability is influenced by factors such as physiology and population demographics. Southern Ocean seabirds, such as emperor penguin *Aptenodytes forsteri*, Adélie penguin *Pygoscelis adeliae*, snow petrel *Pagodroma nivea*, Antarctic petrel *Thalassoica antarctica*, and Antarctic fulmar *Fulmarus glacialis*, are primarily confined to the Southern Ocean pack ice during the breeding season (Ainley et al. 1992, Delord et al. 2016, Tarroux et al. 2016). In addition, because breeding seabirds are central place foragers, their foraging trips are constrained spatially and temporally as they must return to the colony to provision their offspring (Ropert-Coudert et al. 2004). Although non-breeding seabirds are relieved of such constraints, they must still forage successfully to reproduce in the future (Phillips et al. 2005). However, little information exists on the movement and dive behavior for this demographic group.

Adult seabirds occasionally skip breeding but the reasons for this are unclear. Ainley (1978) speculated that the reason for non-breeding among mature Adélie penguins was different between sexes. For females, non-breeding was due to tardy arrival at the breeding colony related to poor nutritional reserves, while, for males, non-breeding was thought to result from high competition for breeding females. Similarly, a study on king penguins *Aptenodytes patagonicus* found that early breeders were more likely to succeed than late breeders and that breeders that failed one year were likely to attempt early breeding the next year (Heezik et al. 1994). In addition, non-breeding status was more likely to occur after a successful breeding outcome than a failed one (Heezik et al. 1994).

Despite being one of the most well studied seabird species, most research on emperor penguin movement and dive behavior has occurred during the breeding season from austral autumn through spring (Wilson 1907, Stonehouse 1953, Prevost 1961). Little is known about emperor penguin behavior after adult birds leave the breeding colonies in mid-December to mid-January to prepare for the molt

(Kooyman et al. 2004, Wienecke et al. 2004, Zimmer et al. 2007). Molting locations are known for <10% of emperor penguin colonies, and movement from these sites after the molt is unknown (Kooyman et al. 2000).

Due to compromised thermoregulatory capabilities during the 1 mo molt, emperor penguins must remain out of the water while they replace all their feathers (Groscolas 1978, Groscolas & Cherel 1992, Williams 1995). As a result, emperor penguins reach their poorest annual body condition during this time. Penguins in the western Ross Sea travel great distances (>1000 km) to reach perennially consistent pack ice in the eastern Ross Sea (Kooyman et al. 2000). These areas are thought to provide more secure habitat throughout the molting process than any other accessible region (Kooyman et al. 2004). After this physiologically and energetically vulnerable time, survival and reproductive success hinges on the ability of penguins to find suitable foraging habitat, often when light is limited.

Emperor penguins are thought to be visual hunters, diving primarily during the day (Kirkwood & Robertson 1997, Zimmer et al. 2007, 2008). Over the course of a year, birds at the southernmost colonies are exposed to a large range of light conditions (0 to 24 h of sunlight) due to their high latitude environment (Zimmer et al. 2008). Light conditions are even more limited underwater and maximum dive depth of penguins has been previously related to light availability in which deeper dives occurred during the day (Kirkwood & Robertson 1997, Zimmer et al. 2008). To date, movement and dive behavior in relation to foraging patterns and light levels has not been examined in detail for emperor penguins at the southernmost colonies of the Ross Sea.

While the environmental drivers of emperor penguin distribution and dive behavior after the molt are not known, sea-ice is thought to provide important habitat for resting (Kirkwood & Robertson 1997, Kooyman et al. 2000, 2004). However, in the western Ross Sea, sea-ice is retreating and advancing >1 mo later and earlier, respectively (Stammerjohn et al. 2012), and it is unknown how these changes might impact emperor penguin survival. To determine how this species will respond to changing climatic conditions, we must first gain insight into their present behavior for all parts of their life cycle and across all demographic groups.

We used tracking and diving data collected from 20 non-breeding emperor penguins after their annual molt. These penguins, tagged in this study, were assumed to be non-breeders for 2 reasons: (1) we arrived at the Cape Colbeck colony nearly 1 mo after

reproductive birds should have completed the molt and commenced foraging (Kooyman et al. 2004, Gearheart et al. 2014), and (2) all individual birds failed to return to a colony during the breeding season. This study therefore provides the first qualitative and quantitative description of movement, habitat preference, and dive behavior for non-breeding birds after their annual molt and fills an important knowledge gap in the life history of emperor penguins in the Ross Sea region.

Our study had 2 objectives: (1) to determine the preferred habitat of non-breeding emperor penguins after their annual molt based on a suite of variables including sea-ice concentration, bathymetric depth, bathymetric slope, distance from the southern boundary of the Antarctic Circumpolar Current, distance from the continental shelf break, distance from the southeast Pacific Basin, and sun zenith angle; and (2) to understand the movement and dive behavior of non-breeding emperor penguins in relation to movement strategy and light levels. We hypothesized that the distribution of emperor penguins will be driven by sea-ice concentration and sun zenith angle. In addition, because emperor penguins are likely visual predators (Kooyman & Kooyman 1995, Kirkwood &

Robertson 1997, Zimmer et al. 2008), we hypothesize that dives will be more frequent, deeper, and longer during the day than during twilight or night.

MATERIALS AND METHODS

Animal capture and instrumentation

In early March 2013, we captured and tagged 20 post-molt emperor penguins near Cape Colbeck (Fig. 1). Penguins were sighted from the bridge or crow's nest (ice tower) of the R/V 'Nathanial B. Palmer' and were approached by foot, snow machine, or inflatable boat depending on the location of the bird and ice conditions. Each penguin was manually captured and a hood was placed over the head to calm the bird. A harness was attached and each penguin was weighed using a Pesola spring scale. We recorded mass to the nearest 0.5 kg, after which we quickly attached either a SPLASH tag ($n = 16$) (Wildlife Computers model SPLASH10-283B; $109 \times 32 \times 26$ mm, $L \times W \times H$; 99 g) or a SPOT tag ($n = 4$) (Wildlife Computers model SPOT-293A; $72 \times 54 \times 24$ mm; 119 g).

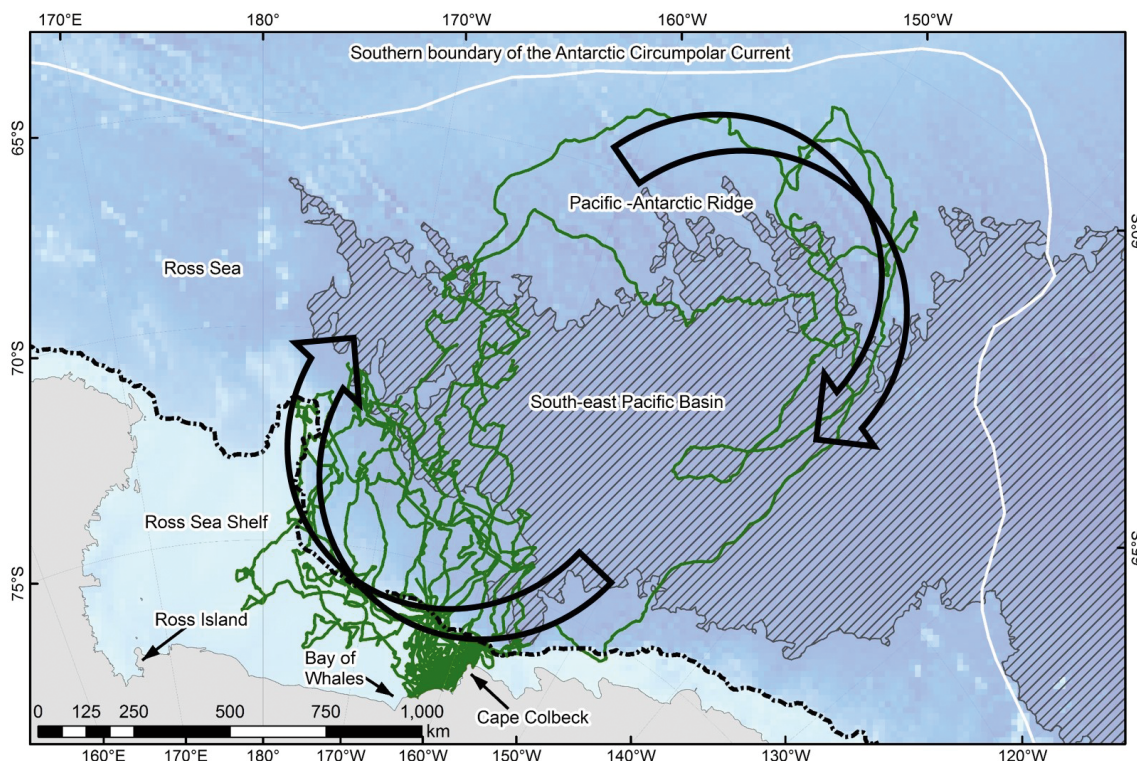


Fig. 1. Tracks of 20 non-breeding emperor penguins *Aptenodytes forsteri* after their annual molt in 2013. The dashed black line indicates the continental shelf break (1000 m isobath), the white line represents the southern boundary of the Antarctic Circumpolar Current, the hatched lines depict the south-east Pacific Basin, and the arrows indicate the direction and approximate location of the Ross Gyre

Instruments were attached using a combination of Loctite super glue, epoxy, and stainless steel cable ties. Briefly, we created a firm platform for tag attachment using a small amount of Loctite 401 super glue on a few feathers located on the dorsal mid back of each penguin. Two to 3 stainless steel cable ties were pushed through the feathers and under the stiff platform that was created after the glue set (<1 min). Finally, we smeared a thin layer of 5 min Loctite epoxy on the bottom of each tag before placing it on the platform and secured it with stainless steel cable ties using a Panduit cable tie gun. This method of attachment was selected based on previous success with this technique in extreme cold. After the epoxy set (~10 min), we plucked a few contour feathers from each bird. DNA from feathers was used to determine sex (analysis performed by Tom Hart, Department of Zoology, University of Oxford). The entire procedure, from capture to release, lasted approximately 15 min. All procedures were approved under the UCSD Animal Subjects Committee Protocol (S10113) and US Antarctic Treaty Permit (2013-006).

Both SPOT and SPLASH tags were duty cycled to transmit every 3 h (0, 3, 6, 9, 12, 15, 18, and 21 h) of each day. During the 1 h transmission period, tags attempted to transmit every 45 s when at the surface and transitioned to every 90 s when dry for 20 consecutive minutes. Transmissions paused when SPLASH and SPOT tag sensors were dry for >9 and 12 h, respectively. During extended dry periods, SPOT tags transmitted every eighth day to indicate position. Maximum transmissions per day were 200 for SPOT and 250 for SPLASH tags. While both types of tags transmitted positional data, only SPOT tags transmitted hourly percent of time when tags were dry and only SPLASH tags collected depth data (sampled at 1 Hz) and transmitted summarized dive data (dive and surface duration, maximum depth, and dive shape). To be classified as a dive, maximum dive depth had to be >5 m and dive duration >1 min. This duration was selected to maximize the attainment of foraging dive data, while taking account of the amount of data that the tags could transmit daily.

Tracking and diving data

We downloaded the raw data for both SPOT and SPLASH tags from ARGOS and decoded the file using a DAP processor (Wildlife Computers). A horizontal speed filter of 30 km h⁻¹ was applied to the data to remove erroneous points (McConnell et al. 1992). Emperor penguin positions were interpolated

every 90 min using a forward looking particle filtering model (Tremblay et al. 2009), which accounts for the errors associated with each ARGOS location class. Dive locations were determined by linking dive time with time along the trackline, and linearly interpolating to the nearest minute.

Using the Geospatial Modelling Environment (MGET, Version 07.2.1), we created 200 correlated random walks (CRW) for each animal by making random draws from the distribution of angles and step lengths between subsequent points along each track (Beyer 2015). Each CRW had the same number of steps as the corresponding penguin track for comparison. Because CRWs often result in overly truncated tracks due to the random selection of turn angles, we selected the 2 CRWs for each animal that had travelled the furthest distance from the tagging location to represent the possible behavior of each animal, unbiased by environmental drivers. For this analysis, points along an animal's track were categorized as 'present' (where an animal was tracked) while those along each CRW were categorized as 'pseudo-absent' (where an animal could have been, based on movement parameters).

Emperor penguin tracks that lasted >100 d were classified into 2 movement strategies, 'shelf' and 'gyre', and dives associated with each strategy were examined. For all tracking and diving locations, we used the 'sun_position' function (Sultan 2004) in MATLAB (MATLAB R2013 2000) to calculate sun zenith angle, i.e. the sun's position in degrees from vertical where 0° represents the sun being directly overhead and 90° represents the sun at the horizon. This function uses an implementation of the algorithm presented in Reda & Andreas (2003) to calculate zenith based on time and position. Using the standard definition of civil twilight which occurs when the sun is 6° below the horizon, we used sun zenith angles to classify dives as 'day' (zenith < 84°), 'twilight' (84° < zenith < 96°), or 'night' (zenith > 96°).

Environmental data

We used daily Advanced Microwave Scanning Radiometer (AMSR2) sea-ice concentration data with a 6.25 km resolution from the University of Bremen (www.iup.uni-bremen.de/seaice/amsr/, accessed Jan 2014). Because daily sea-ice concentration values were stored in byte format (0 to 200), we used the 'Spatial Analyst' extension in ArcGIS 10.3.1 (ESRI 2015) to convert ice concentration data to percent ice cover.

Polar Front positions were downloaded from the on-line GIS database (<http://gis.ccamlr.org>) of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). We extracted the southern boundary of the Antarctic Circumpolar Current, digitized from Orsi et al. (1995), and created a spatial grid of calculated distances from this boundary.

To examine the importance of bathymetric depth, we used ETOPO-1, a 1 arc-minute global relief model of the earth's surface (Amante & Eakins 2009) (www.ngdc.noaa.gov/mgg/global/, accessed Apr 2013). The southeast Pacific Basin was defined as waters > 4000 m deep with low bathymetric slope. Using this feature, we created a continuous grid representing distance from this feature. Bathymetric slope was created by quantifying the degree change from one depth value to the next. We defined the continental shelf break as the 1000 m bathymetric contour (Knox 2007) and used the 'Spatial Analyst' extension to create a continuous grid representing distance from the shelf break.

We divided the study area into 6.25 km² cells based on the resolution of the sea-ice data. Pseudo-absence points were removed from the dataset if they occurred in cells where an animal was present. We extracted values for all environmental parameters at the midpoint of each cell that contained presence or pseudo-absence data. Finally, we subsampled the data to include only one point per day for each track to avoid oversampling. In this case, we choose all presence and pseudo-absence points that occurred between 24:00 and 01:00 h GMT, a time when the sun is at the highest position in the sky for each location.

Statistical analyses

Habitat preference

We considered a set of 7 continuous environmental parameters to model the habitat preference of non-breeding emperor penguins after their annual molt: sea-ice concentration, bathymetric depth, bathymetric slope, distance from the southern boundary of the Antarctic Circumpolar Current, distance from the south-east Pacific Basin, distance from the continental shelf break, and sun zenith angle (Table 1). We ran a correlation matrix on all variables to test for covariate dependency using the Spearman

method. Since highly correlated variables contribute equally to the model, the covariate that was thought to be least meaningful was removed.

Boosted regression tree (BRT) models were used to determine the main environmental influences on emperor penguin distribution. BRT models use 2 algorithms: (1) classification and regression trees, and (2) boosting to combine a collection of models (Elith et al. 2008). Within the statistical software R 3.2.2 (R Development Core Team 2013), we used the 'gbm.step' function in the 'dismo' package (Hijmans et al. 2017) and evaluation functions in the 'gbm' package (Ridgeway et al. 2017) to fit a BRT model to our data. A binomial error distribution of the Bernoulli family was used to predict the probability of emperor penguin occurrence. A learning rate of 0.2 was used to determine the contribution of each successive tree to the final model as it proceeds through multiple iterations. Due to the large dataset, a 'tree complexity' of 5 was used to allow multiple interactions between variables. Finally, 0.5 was specified for 'bag fraction', meaning that half the data was chosen randomly as a training dataset for each iteration of the model fit. Initially, 50 trees were fit using recursive partitioning of the data after which residuals from the initial fit were fit with another 50 trees, and so forth, until the model deviance was minimized.

Due to the nature of animal movement data, we expected spatial autocorrelation in our data despite spatial and temporal subsampling. Spatial autocorrelation in the model residuals (calculated in relation to nearest neighbors) was tested by calculating the Moran's *I* statistic using the 'moran.test' function within the R package 'spdep' (Bivand et al. 2013,

Table 1. Median and range values of environmental variables considered in habitat preference models for non-breeding emperor penguins *Aptenodytes forsteri* after their annual molt in 2013

Variable	Description	Median and range
ICECON	Ice concentration (%)	99.0 (0.0–100.0)
ETOPO	Water depth (m)	1814.0 (13.0–4846.0)
SLOPE	Bathymetric slope (degrees)	0.9 (0.0–10.2)
DACC	Distance (km) from the southern boundary of the Antarctic Circumpolar Current	1203.7 (89.5–1507.3)
DSEPB	Distance (km) from the south-east Pacific Basin demarked by the 4000 m isobath	125.0 (0.0–711.6)
DSHELF	Distance (km) from the continental shelf break defined as the 1000 m isobath	89.5 (0.0–1481.8)
ZENITH	Sun angle, degrees from vertical where 0–84° represents day, 84–96° represents twilight and >96° represents night	89.2 (45.9–105.5)

Bivand & Piras 2015). Moran's I generally varies from -1 to $+1$ (from strong negative to strong positive spatial autocorrelation), with zero indicating no spatial autocorrelation (Legendre & Fortin 1989). We found low but significant autocorrelation in the residuals (Moran's $I = 0.37$, $p < 0.001$). Because spatial autocorrelation can lead to erroneous model results (Dormann 2007), we created a residual auto-covariate term (RAC) that was included as an explanatory variable in the model (BRT + RAC model) following methods presented in Crase et al. (2012) and then recalculated the Moran's I statistic.

We used the relative influence produced by the BRT model (ranging from 0 to 100%) to assess the importance of each explanatory variable and used partial dependence plots to visualize model fit (Elith et al. 2008). Relative influence is calculated by summing the contribution, or branch length, of each variable in the BRT. Backwards elimination of variables was implemented to drop any terms that provided no evidence of model improvement. Finally, the percent deviance explained and the area under the receiver operator characteristic curve (AUC) were used to assess model performance. AUC values range from 0.5, for models with no discrimination ability, to 1.0 for models with perfect discrimination ability (Pearce & Ferrier 2000). Models with AUC values > 0.7 are considered 'useful' and those with AUC values > 0.9 are considered 'very good' because sensitivity is high relative to the false positive rate (Swets 1988).

Dive behavior

Dive data were reviewed to check for onboard processing errors and presented as mean \pm standard deviation. Dives > 32.2 min were discontinuous from the remainder of the data (< 32.2 min) and were much greater than the previously published maximum dive duration of 27.6 min (Sato et al. 2011). As a result, these 12 dives (range 35.1 to 53.7 min) were removed from our analysis as we suspect that the algorithm on the tag may have combined more than one dive. For each dive, we estimated dive speed (m s^{-1}) by dividing maximum dive depth (m) by dive duration (s). In addition, we extracted bathymetric depth at each dive location and subtracted this value from the maximum dive depth. This difference was then divided by the bathymetric depth and multiplied by 100 to produce a value that represented the percentage within the water column (PWC). In cases where the maximum dive depth was deeper than the bathymetric depth, the

bathymetric depth was changed to the dive depth. PWC values of 100% represent dives that occurred at the same depth as the ocean bottom. Dives with PWC values between 80 and 100% were considered 'benthic' and all other dives were classified as 'pelagic'.

The 'ggplot2' package (Wickham 2009) and 'stat_density2d' function in R were used to produce a scatterplot of maximum dive depth (m) versus dive duration (min) with 25, 50, 75, and 90% kernel density contours. In addition, we used the 'geom_density' function to display the density profile of dive duration and maximum dive depth along each respective axis of the scatterplot.

To investigate the spatial distribution of dive data, we used the 'Point Statistics' tool within the 'Spatial Statistics' toolbox in ArcGIS 10.3.1. Using a 50 km neighborhood (the maximum daily displacement of transiting penguins), we produced spatial grids depicting mean (1) maximum dive depth (m), (2) dive duration (min), (3) dive speed (m s^{-1}), and (4) PWC (%). Finally, we used the 'Hotspot Analysis' tool to identify statistically significant spatial clusters of high values (hot spots) and low values (cold spots) of the 4 parameters above using the Getis-Ord statistic (G_i^*). A 'zone of indifference' setting was used to reduce edge effects. The results from the hotspot analysis were transformed into a smooth surface using a mean neighborhood analysis on the z-scores and were rescaled to values between -1 and 1 to accurately reflect hotspots (red) and low spots (blue).

We examined dives in relation to light level by calculating the sun zenith angle and subsequently classifying each dive as 'day' (zenith $< 84^\circ$), 'twilight' ($84^\circ < \text{zenith} < 96^\circ$), or 'night' (zenith $> 96^\circ$). We used the 'geom_density' function within the 'ggplot2' package in R to produce separate kernel density plots of dive duration and maximum dive depth by light category and movement strategy. Mann-Whitney U -tests, a non-parametric version of the t -test, were used to examine the statistical differences between light categories as well as differences between movement strategies. p -values < 0.05 were considered significant.

RESULTS

Data summary

The average body mass of the 20 non-breeding emperor penguins was 31.5 ± 3.1 kg, mean \pm SD. Satellite tags recorded 12 to 323 d of individual emperor penguin movement data, with tracks ranging from

~270 km to nearly 9000 km in length. In addition, the 16 SPLASH tags recorded maximum dive depth and duration for over 96 000 dives with individual mean maximum dive depths ranging from 53.4 to 119.6 m and dive durations ranging from 3.7 to 5.5 min. Details on sex, mass, tag duration, total track length, mean maximum dive depth and duration per individual bird are given in Table S1 in the Supplement at www.int-res.com/articles/suppl/m593p155_supp.pdf. After the tags were attached, 14 of the 20 emperor pen-

guins traveled south towards the Bay of Whales, the southern-most point of open ocean in the Ross Sea ($78^{\circ}30'S$, $164^{\circ}20'W$), where they foraged close to the continent for 2 to 3 wk before beginning a 4 mo migration north or northeast as the ice extent expanded (Figs. 1 & 2).

In early August, 4 of the 7 emperor penguins with transmitting tags started transiting towards the colony while 2 birds, both females, continued to forage < 200 km from the ice edge until early October before

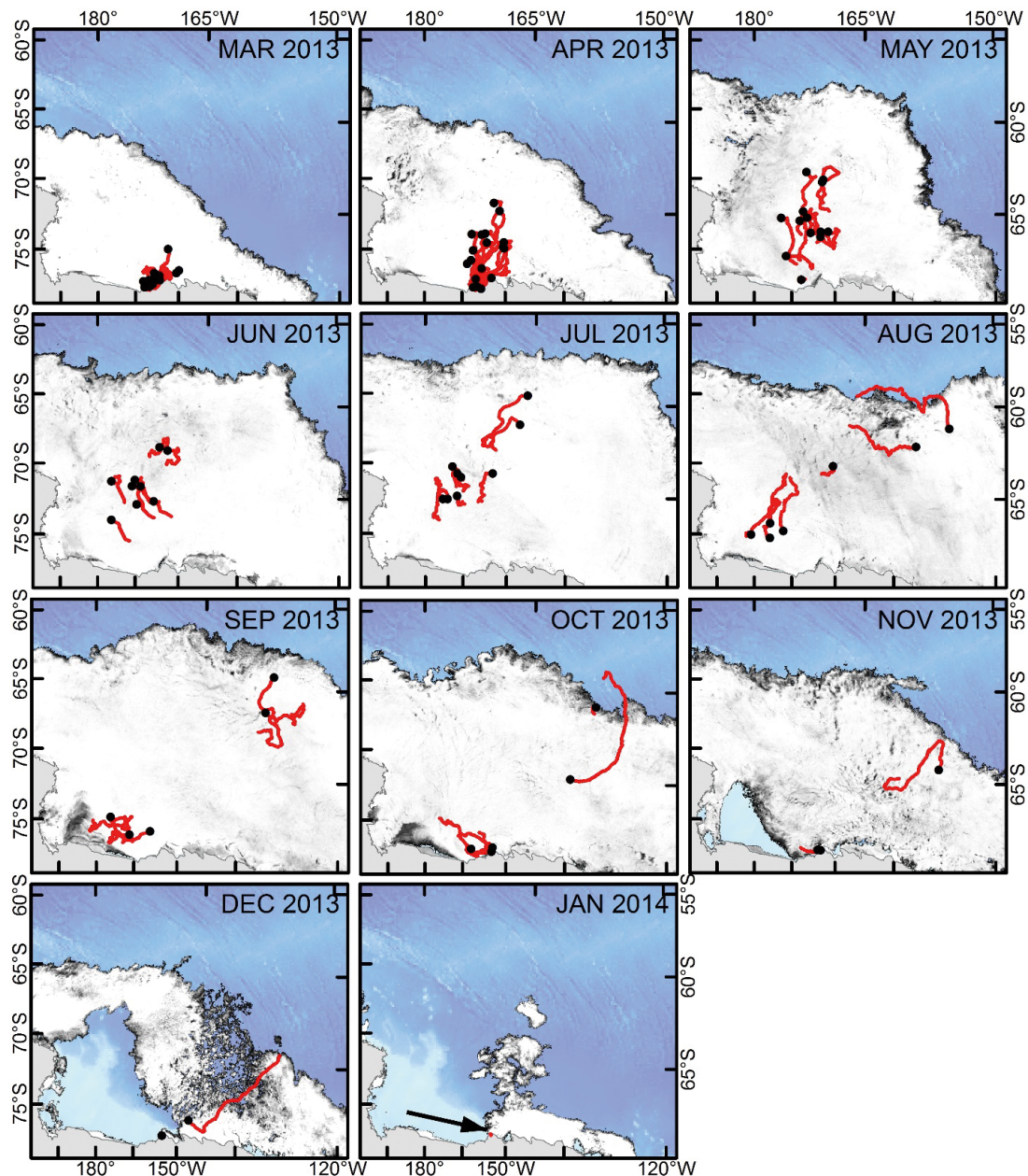


Fig. 2. Monthly tracks (red lines) of 20 non-breeding emperor penguins *Aptenodytes forsteri* after their annual molt in 2013. Ice concentration is shown for the last day of each month and black dots indicate the location of individual birds at that time. The black arrow on the January 2014 panel indicates the location of data points

heading south (Fig. 2). Birds with tags that transmitted >100 d ($n = 9$) appeared to be engaging in one of 2 movement strategies. 'Shelf' animals ($n = 6$) traveled along the edge of the southeast Pacific Basin and along the shelf break, often in a counter-clockwise direction, while 'gyre' animals ($n = 3$) traveled north from Cape Colbeck in the same clockwise direction as the Ross Gyre (Fig. 3). Three penguins appeared to return to Cape Colbeck between late October 2013 and January the following year, after the breeding season had ended.

Habitat preference

After running a correlation matrix, we found that distance from the shelf was highly correlated with (1) distance from the southeast Pacific Basin, (2) distance from the southern boundary of the Antarctic Circumpolar Current and (3) bathymetric depth (Fig. S1 in the Supplement). To simplify the model, of these 4 variables, only distance from the shelf break was retained in the analysis. In examining the remaining 3 variables, we found little variation in bathymetric slope ($0.8 \pm 1.2^\circ$, mean \pm SD) and sea-ice concentra-

tion within the pack ice ($88.8 \pm 26.3\%$) so we removed them from further analyses.

The 2 variables included in the habitat model, distance from the shelf break and zenith, were important predictors of emperor penguin distribution both before and after the inclusion of the RAC term used to account for spatial autocorrelation. The BRT + RAC model reached an optimal number of trees at 2150 and accounted for 73.2% of the mean total deviance. Dropping terms did not improve model performance and the AUC value for the model was 0.98, indicating good model performance.

Overall, the sun zenith angle and distance from the shelf break made a similar relative contribution to the BRT + RAC model. After the inclusion of the RAC term, the relative influence of the 2 variables decreased, from 54.0 to 16.7% and from 46.0 to 18.3% for distance from the shelf break and sun zenith angle, respectively. This indicates that the RAC term, with a relative influence of 65.1%, was important in accounting for spatial autocorrelation in the model. This result is further supported by a change in the Moran's I value from 0.37 to 0.16 before and after the inclusion of the RAC term. Emperor penguins preferred areas where the sun zenith angle was $<90^\circ$

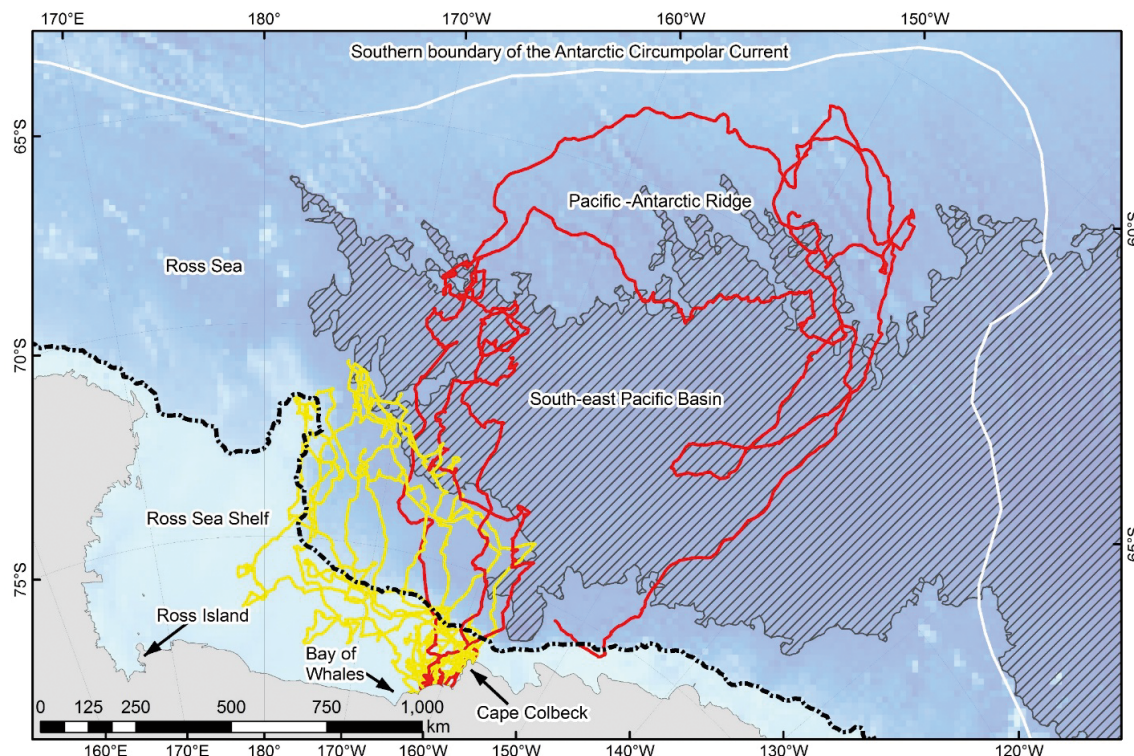


Fig. 3. Tracks of non-breeding emperor penguins *Aptenodytes forsteri* after their annual molt in 2013. Tracks were limited to tags that transmitted over 100 d ($n = 9$) and are color-coded by presumed strategy (yellow = 'shelf', $n = 6$; red = 'gyre', $n = 3$). The dashed black line indicates the continental shelf break (1000 m isobath), the white line represents the southern boundary of the Antarctic Circumpolar Current, and the hatched lines depict the southeast Pacific Basin

(daylight or twilight) and showed a preference for locations that were beyond the shelf break (Fig. 4).

Dive behavior

Mean maximum dive depth and duration were 90.2 ± 77.8 m (range 5 to 460 m, $n = 96\,071$) and 4.6 ± 2.3 min (range 1.0 to 32.2 min) (Fig. 5, Table S1). Although there was a large range of depths and durations, 90% of the dives ($n = 67\,281$) were 7.0 to 275.5 m in depth (99.9 ± 62.6 m) and 1.1 to 8.5 min in duration (5.0 ± 1.6 min) (Fig. 5). Moreover, 25% of the dives ($n = 19\,028$) were <43 m deep (22.0 ± 8.3 m) and <3.6 min in duration (2.4 ± 0.6 min). For all emperor penguins, approximately 33 and 6% of the dives exceeded the measured (5.6 min) (Ponganis et al. 1997) and behavioral (8 min) (Kooyman & Kooyman 1995) aerobic dive limit (ADL), the point beyond which animals rely on anaerobic metabolism. In addition, 11 penguins performed dives ($n = 17$) that exceeded the previous duration record of 27.6 min (Sato et al. 2011); these ranged from 27.6 to 32.2 min.

The mean maximum dive depth, duration, and dive speed of emperor penguin dives were deeper (>165.4 m), longer (>6.6 min) and faster (>0.5 m s⁻¹) at the farthest extent of their foraging range than at other locations (Fig. 6A,C,E). Deep, long, and fast

dives were also significantly clustered in these areas, as well as in areas near the shelf break (Fig. 6B,D,F). Even though deeper, longer and faster dives also occurred near-shore, they had less influence on the result due to spatial averaging across a large number of dives. Significant clusters of shallow, short, and slow dives were found on the shelf and beyond the shelf break where emperor penguins dives were <85.0 m deep, <4.5 min in duration, and at speeds of <0.3 m s⁻¹ (Fig. 6A–F). Penguins proximate to the Bay of Whales exhibited different dive behavior, in which deep, short, and fast dives were significantly clustered as opposed to other areas over the shelf (Fig. 6B,D,F).

Dives performed on the shelf had higher mean PWC values and were significantly clustered (Fig. 6G,H). Benthic dives occurred only on the shelf, while pelagic dives occurred both on and off the shelf. All penguins instrumented with SPLASH tags performed benthic dives ($n = 2\,232$) proximate to Cape Colbeck, while only 3 birds and 1 individual performed benthic dives near the shelf break to the east and to the west of Cape Colbeck, respectively (Fig. S2 in the Supplement). Benthic dives comprised $<5\%$ of all dives, and 92% of these dives occurred in March and April. The mean maximum dive depth and available bathymetric depth for all benthic dives was 237.5 ± 63.2 m and 252.5 ± 64.8 m, respectively.

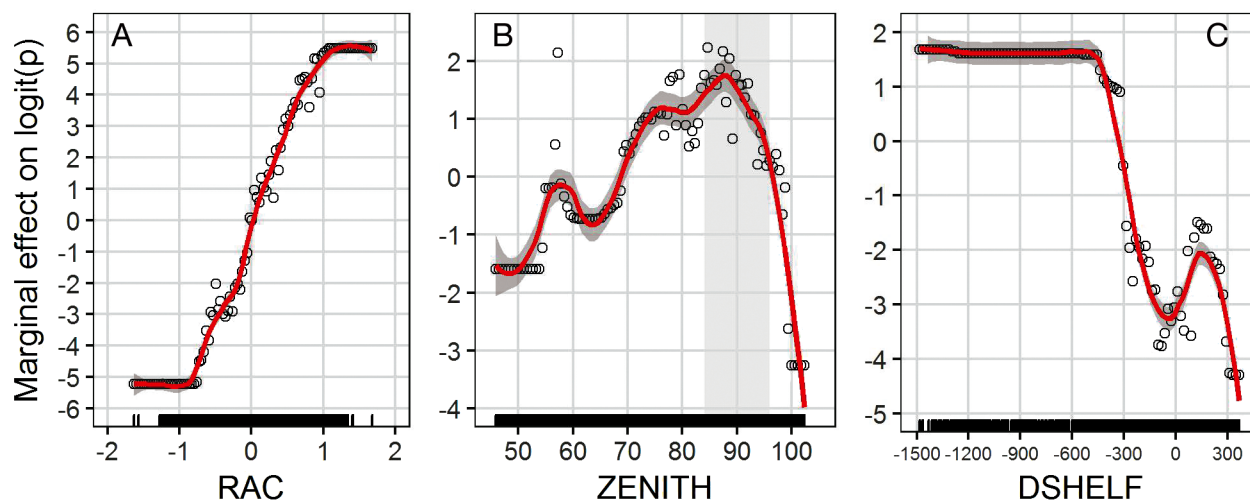


Fig. 4. Partial dependence plots for 3 variables used in a boosted regression tree model to determine the habitat preference of non-breeding emperor penguins *Aptenodytes forsteri* after their annual molt in 2013: (A) a residual auto-covariate (RAC) term to account for spatial auto correlation in the data; (B) sun angle from vertical (ZENITH, degrees); (C) distance from the shelf break (DSHELF, m). Occurrence is indicated on the y-axis on a logit scale with a zero mean over the data distribution. Values over zero on the y-axis have a positive influence on emperor penguin occurrence. The distribution of the full dataset across each chosen variable is shown as 'rugs' on the x-axes. Black open circles indicate the model fit and the red lines represent smoothed response curves with 95% confidence intervals shown in grey. Vertical shading on the partial dependence plot for ZENITH represents the sun zenith angles that occur at twilight, with values on the x-axis to the left and right of the shading representing day and night, respectively. Negative values for DSHELF indicate distances beyond the shelf break. See Table 1 for explanations of variables

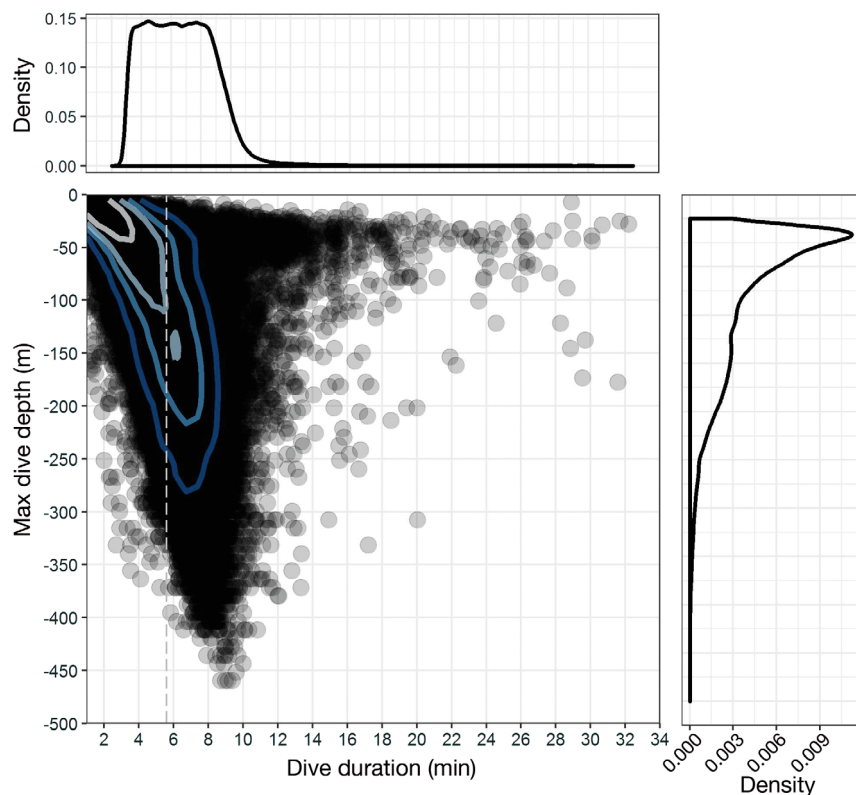


Fig. 5. Scatterplot of maximum dive depth and duration for all dives (circles) from 16 non-breeding emperor penguins *Aptenodytes forsteri* instrumented with SPLASH satellite tags after their annual molt in 2013. The grey dashed line indicates the calculated 5.6 min aerobic dive limit (Ponganis et al. 1997). Lighter to darker lines signify the 25, 50, 75 and 90% data contours. Density plots of dive duration and maximum dive depth are shown on the top and right side of the scatterplot, respectively

When examining the number of dives h^{-1} , corrected for the number of hours in each light category (day, twilight, or night), dive rate was significantly higher during daylight and twilight hours than at night ($U_{\text{day_night}} = 1 \times 10^6$, $p < 0.001$; $U_{\text{twi_night}} = 7.6 \times 10^4$, $p < 0.001$) (Fig. 7A). On average, non-breeding emperor penguins performed 5.5 ± 3.2 dives h^{-1} and 5.6 ± 2.9 dives h^{-1} during the day and twilight, respectively, compared to 0.4 ± 0.7 dives h^{-1} at night. Although there was a trend towards shallower and shorter dives from day to night, there was no detectable difference in maximum dive depth and duration between the 3 light categories (Fig. 7B,C). Emperor penguins preferred to dive during daylight ($n = 28318$) and twilight ($n = 60171$) hours than at night ($n = 7582$); this was most apparent from the hourly percent of time dry (recorded by the SPOT tags) which showed that birds preferred to be on the ice during the night and in the water when some level of light was available (Fig. S3 in the Supplement).

Of the 9 emperor penguins assigned a movement strategy, 8 animals had associated dive data ($n = 73199$); dives from the 5 'shelf' animals ($n = 38797$) were typically 1 to 2 min in duration and <50 m deep, while dives from the 3 'gyre' animals ($n = 34402$) were usually 6 to 7 min in duration and approximately 150 m deep (Fig. 8). Maximum dive depth and duration were significantly different ($p < 0.001$) between 'shelf' and 'gyre' strategies during the day and twilight (depth: $U_{\text{day}} = 7.0 \times 10^7$, $U_{\text{twilight}} = 3.2 \times 10^8$; duration: $U_{\text{day}} = 7.0 \times 10^7$, $U_{\text{twilight}} = 3.0 \times 10^8$). However, during the night, only maximum dive depth was significantly different between the 2 movement strategies (depth: $U_{\text{night}} = 4.6 \times 10^6$, $p < 0.001$; duration: $U_{\text{night}} = 4.1 \times 10^6$, $p = 0.06$).

DISCUSSION

Previously, movement and habitat associations of emperor penguins were known primarily during the breeding season. The only information outside this season is based on data from 3 tags attached to emperor penguins in the eastern Ross Sea which transmitted for >2 mo (Kooyman et al. 2004). Two birds traveled west towards western Ross Sea colonies and one, presumably a non-breeding bird, traveled north and was still well within the pack ice in early June when birds are typically at breeding colonies.

This is the first study to focus exclusively on the movement, habitat preference, and dive behavior of non-breeding emperor penguins after their annual molt. While we are confident that the emperor penguins tagged in our study were non-breeders, the reasons why these birds did not breed is unknown. The body mass of non-breeding penguins tagged in this study (31.5 ± 3.1 kg, mean \pm SD) was more similar to breeding emperor penguins prior to their annual molt (32.1 ± 4.5 kg) than to that after the molt (20.3 ± 2.7 kg) (Kooyman et al. 2000). This indicates that non-breeding birds completed the molt and recouped a substantial amount of body mass in the vicinity of Cape Colbeck prior to our arrival in mid-March.

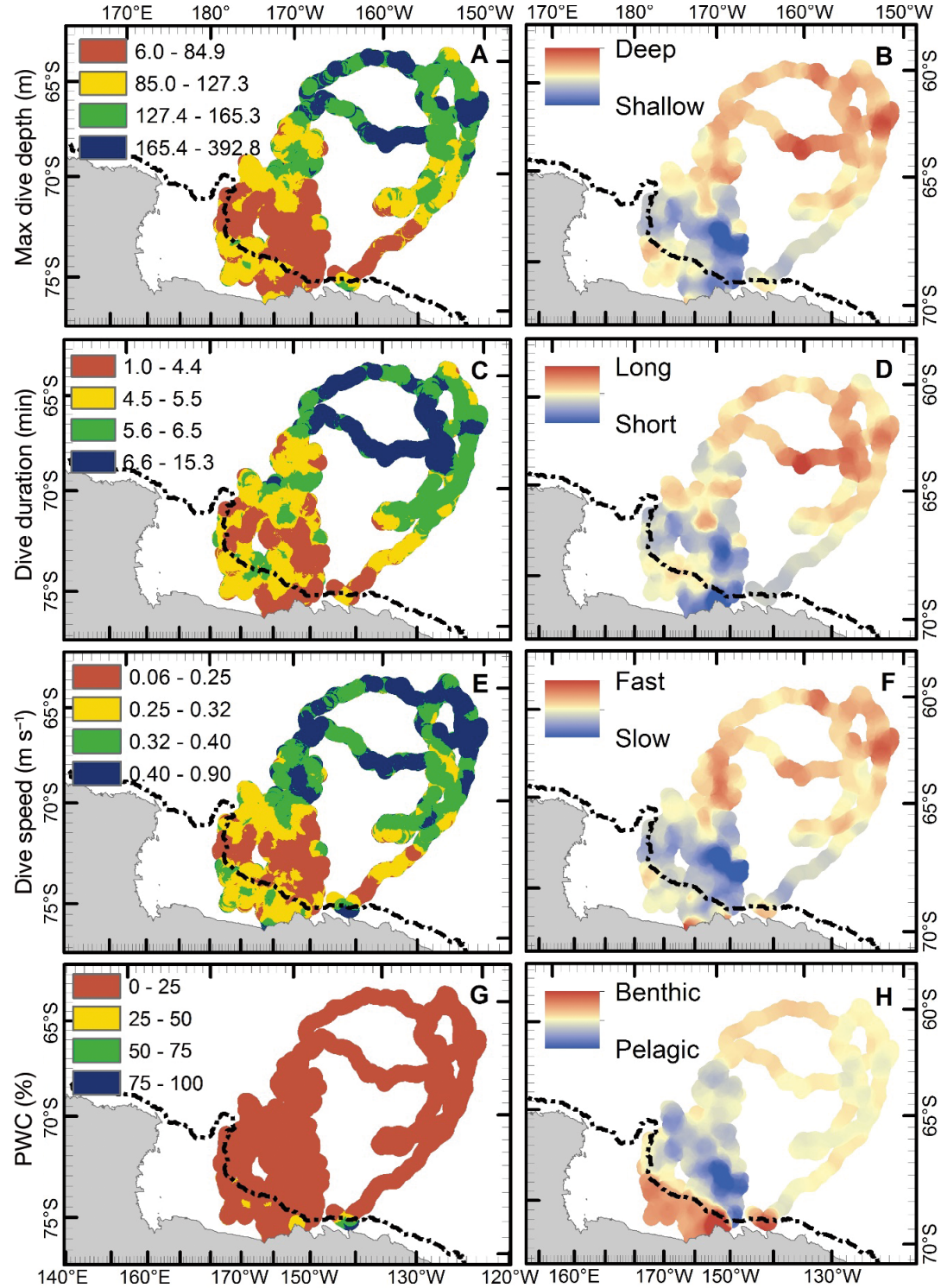


Fig. 6. Spatial mean (left panels) and hotspot analysis (Getis-Ord Gi* statistic, right panels) of (A,B) maximum dive depth (m), (C,D) dive duration (min), (E,F) dive speed (m s⁻¹), and (G,H) maximum dive depth relative to bathymetric depth, shown as percent of the water column (PWC, %) for 16 non-breeding emperor penguins *Aptenodytes forsteri* instrumented with SPLASH satellite tags after their annual molt in 2013. For spatial means, the keys on panels A, C, & E depict 4 classes based on natural breaks in the data, while the key on panel G is divided into 4 equal intervals. For hotspot analysis, red areas indicate statistically significant clustering of deep, long, fast or benthic dives while blue areas indicate statistically significant clusters of shallow, short, slow or pelagic dives, unbiased by the number of birds present. The black dashed line represents the continental shelf break, defined as the 1000 m isobath

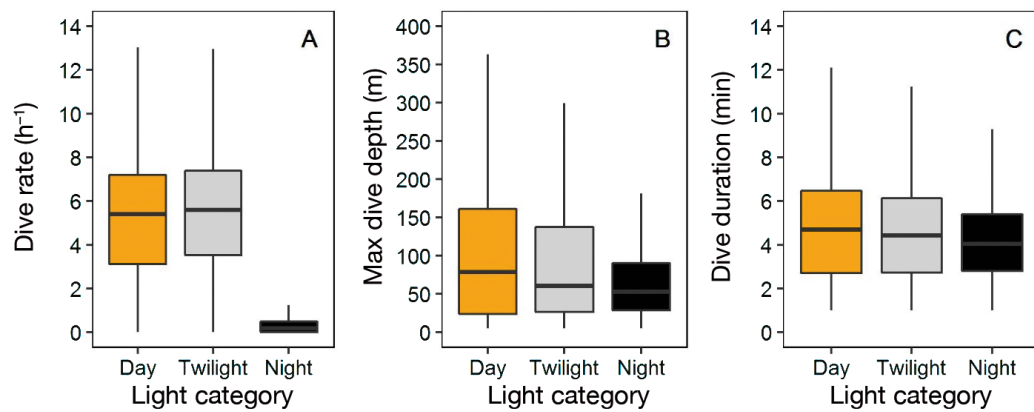


Fig. 7. Dive characteristics by light category for 16 non-breeding emperor penguins *Aptenodytes forsteri* instrumented with SPLASH satellite tags after their annual molt in 2013: (A) dive rate (dives h^{-1}); (B) maximum dive depth (m); (C) dive duration (min). 'Day' (between sunrise and sunset) is shown in orange, 'twilight' (after sunset or before sunrise when the sun is $\leq 6^\circ$ below the horizon) in grey, and 'night' (when the sun is $> 6^\circ$ below the horizon) in black. The middle line within the box represents the median value, the lower and upper boundaries of the box represent the first and third quartiles of the data, and whiskers (top and bottom lines) represent the highest and lowest value within $1.5 \times$ the inter quartile range. For display purposes, outliers are not shown

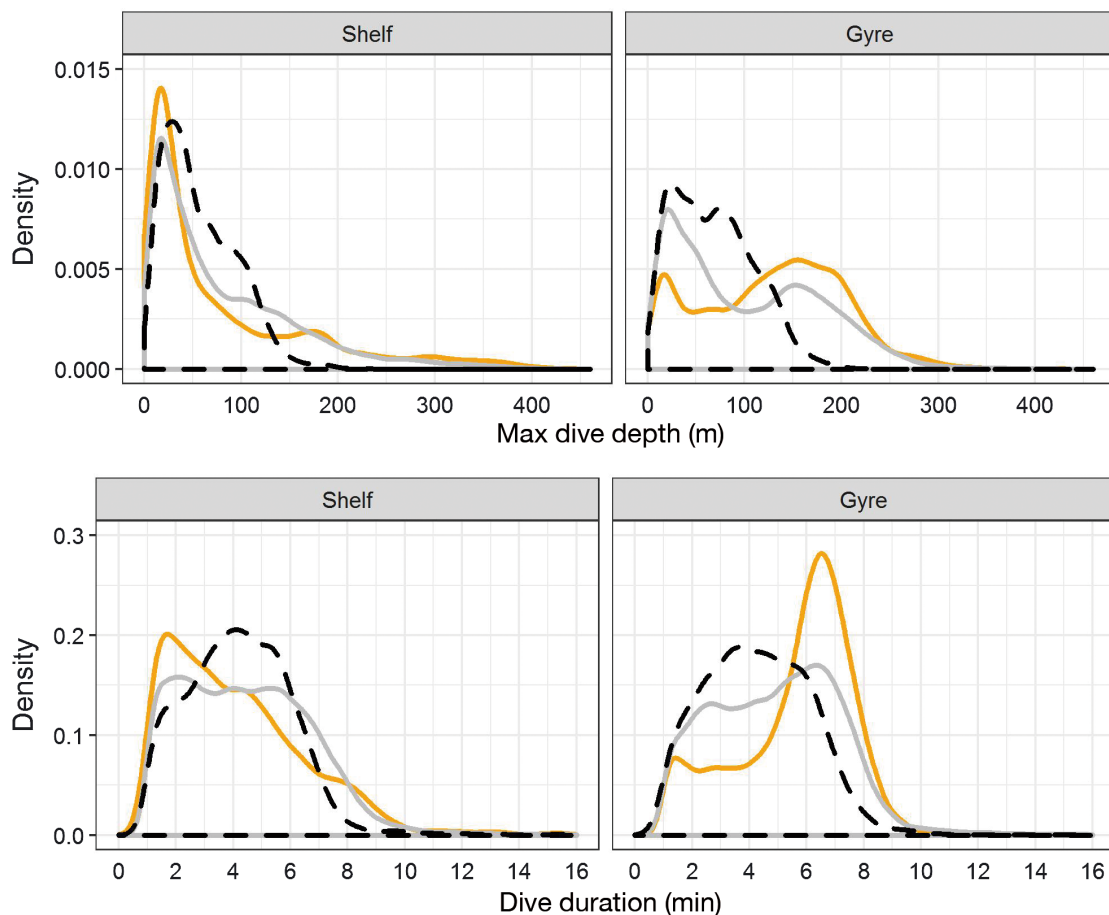


Fig. 8. Kernel density plots of maximum dive depth and duration relative to light levels and strategy ('shelf', $n = 38\,797$; 'gyre', $n = 34\,402$) for emperor penguins *Aptenodytes forsteri* instrumented with SPLASH tags after their annual molt in 2013. Only results for birds that transmitted for > 100 d ($n = 9$) are shown. Data for 'day' are shown as orange lines ($n = 20\,443$), for 'twilight' as grey lines ($n = 46\,839$), and for 'night' as black dashed lines ($n = 5\,917$) (see Fig. 6 legend for definitions). For display purposes, dive duration is limited to 16 min, though the line continued at near-zero levels to a maximum dive duration of 32.2 min

Habitat preference

Post-molt emperor penguins showed a strong preference for areas located beyond the continental shelf break, defined as the 1000 m isobath. These areas are also characterized by deeper water. While transiting south towards Cape Colbeck, 4 of the 7 birds with transmitting tags traveled almost exclusively along the shelf break. Areas proximate to the shelf break are often characterized by high productivity associated with bottom topography (McConnell et al. 1992, Croll et al. 1998, Charrassin et al. 2002). The Antarctic Slope Front is an oceanographic feature near the shelf break that has a strong influence on biological processes (Jacobs 1991).

The continental shelf acts as a southern boundary to the Ross Gyre which circulates around the southeast Pacific Basin (Rickard et al. 2010). This deep-reaching gyre is bounded by the Pacific-Antarctic Ridge to the north and entrains circumpolar deep water to make it available for mixing with shelf and slope waters (Carter et al. 2008). The northward deflection of the Ross Gyre likely causes prey species to become trapped against the protruding shelf (Sala et al. 2002, Rickard et al. 2010). This process was observed by Marr (1962) who showed that the overall distribution of Antarctic krill *Euphausia superba* was highest on the west side of the gyre. The linkage between prey species and gyre systems may explain why some penguins foraged primarily along the shelf break, i.e. along the southern boundary of the Ross Gyre.

Emperor penguins are known to move north as ice extent increases and remain within the pack ice where water can be accessed through cracks and leads (Kirkwood & Robertson 1997). During our study, all penguins remained within the pack ice and did not travel into open water. From early March, sea-ice continues to grow in the Ross Sea, expanding northwards until reaching its full extent in September (Zwally et al. 2002, Comiso et al. 2011). When the penguins left Cape Colbeck after their annual molt, the sea-ice edge was already located well north of the colony and sea-ice concentration was high with little variation in areas where penguins were tracked. Fine-scale features such as cracks found within the pack ice were not detectable in the satellite data but were most likely adequate for accessing water.

In addition to sea-ice, the northward movement of emperor penguins at high latitudes is driven by increased light levels which influence the foraging abilities of visual predators (White et al. 2007, Zimmer et al. 2008). Because emperor penguins tagged in our study did not breed, there was no incentive to return

to the colony until the days grew longer and the sea-ice retreated. It is important to note that 2013 was an anomalous ice year in which the maximum sea-ice extent in the southern hemisphere was over 2 standard deviations above the 1979–2012 mean (Reid et al. 2015). In addition, due to strong winds and lower than normal sea surface temperatures, the Ross Sea never reached its climatological mean minimum ice extent during the previous summer. While we are uncertain about how the increased sea-ice extent may have altered the behavior of non-breeding emperor penguins after their annual molt, Barbraud & Weimerskirch (2001) found that sea-ice extent had 2 opposing effects on the demographic parameters of emperor penguins in Terre Adélie during the breeding season. Increased sea-ice extent negatively affected hatching success by increasing distance between the colony and foraging areas, but positively affected adult survival by increasing food availability. In other words, increased sea-ice extent favored higher survival rate among adults at the expense of lower fecundity (Barbraud & Weimerskirch 2001). Therefore, emperor penguins in our study may have been reproductively mature but chose not to return to the breeding colony. Instead, these birds may have favored increased survival over the possibility of wasting energetic investment in raising offspring in sub-optimal or poor environmental conditions.

Mature emperor penguins breed nearly every year and the proportion of the breeding population has been estimated at 80% of the total population (Barbraud & Weimerskirch 2001). However, there is no information about the proportion of mature emperor penguins that skip breeding or fail to breed each year. Due to the lack of demographic information on non-breeding birds and the anomalous sea-ice extent in 2013, the behavior of birds tagged in this study may not be representative of emperor penguin behavior in other years. While we acknowledge that tag attachment can have measurable negative effects (Elliott et al. 2012, Vandenabeele et al. 2012), due to the small size and streamlined nature of the tags used in our study we do not believe breeding behavior was impacted.

Dive behavior

Emperor penguins tagged in this study dived beyond their calculated and behavioral aerobic dive limit on 33 and 6% of their dives, respectively. In addition, dive durations of non-breeding emperor penguins exceeded the previous record of 27.6 min, from

a study with >20 000 dives by breeding birds foraging during the spring and summer (Sato et al. 2011). Because SPLASH tags only transmit summary data for each dive, it is sometimes difficult to know if these long dives were an artifact of faulty on-board processing. However, 17 dives, ranging from 27.6 to 32.2 min, had realistic dive durations, depths and surface intervals, suggesting these results were not spurious. These dives represent only a small percentage of the total number of dives recorded (<0.0002%) and their duration could be due to the difficulty of finding breathing holes in dynamic pack ice during low light conditions. Extreme environmental conditions are a natural phenomenon and result in birds losing their breathing holes from time to time. In such situations, penguins must rely on exceptional adaptations to hypoxemia (Ponganis et al. 2007, Williams et al. 2012).

Movement strategy appeared to influence emperor penguin foraging behavior during daylight and twilight: 'shelf' birds performed shorter and shallower dives compared to 'gyre' animals. The spatial patterns in maximum dive depth, duration, and speed were likely driven by the behavior of emperor penguins' prey species. Penguins dived at a significantly higher rate and dived deeper and longer during the day and twilight than at night. These findings support our initial hypothesis that birds would dive more during the day and agree with results from previous studies that examined the association between dive behavior and light levels (Kooyman & Kooyman 1995, Kirkwood & Robertson 1997, Zimmer et al. 2008). The preference of emperor penguins for increased light levels may be the result of (1) a reliance on vision for hunting, (2) the need to keep track of ice holes when light is limited, (3) the diel nature of emperor penguin prey species, or (4) a predator avoidance strategy.

Implications for diet

Emperor penguins are known to primarily consume krill and nototheniid fish, particularly Antarctic silverfish *Pleurogramma antarctica* (Green 1986, Pütz 1995, Cherel & Kooyman 1998, Kooyman et al. 2004, La Mesa et al. 2004). High abundances of *P. antarctica* are known to occur on the Ross Sea shelf (Eastman 1985, Donnelly et al. 2004, La Mesa et al. 2004, O'Driscoll et al. 2011). In addition, crystal krill *Euphausia crystallophias* generally occurs in low densities over the shelf while the larger *E. superba* primarily occurs in off-shelf waters (Sala et al. 2002). However, biological samples collected at 19 stations

on the Ross Sea shelf (Brooks et al. 2018) revealed that *E. superba* was present, and in high abundance, in the Bay of Whales when birds tagged during this study were nearby. Because biological samples are rarely collected in the Bay of Whales, we do not know if this finding is anomalous. However, it is possible that *E. superba* was transported onto the eastern shelf and into the Bay of Whales along the Little America Trough (Ashford et al. 2012).

During the day, *E. superba* are patchily distributed both vertically and horizontally at depths from 20 to 120 m (Kalinowski & Witek 1980, Everson 1982), while adult *P. antarctica* are distributed over the shelf and proximate to the continental shelf-break at depths from 100 to 400 m (O'Driscoll et al. 2011). The dive behavior associated with the 2 movement strategies in combination with the known dive depths of their primary prey items suggests that non-breeding emperor penguins classified as 'shelf' animals primarily forage on krill at depths <50 m while 'gyre' animals mostly consume krill at shallower depths and fish and squid in waters >150 m deep off the shelf. Results from our study support Klages (1989), who found that penguins have different feeding strategies depending on whether they are consuming primarily krill or fish and squid; in general, shallow diving was associated with foraging on krill while deep diving was associated with foraging on fish and squid. Prey switching has also been observed in thick-billed murre *Uria lomvia*, which performed deeper dives as a result of switching from krill to fish and squid during late winter (Orben et al. 2015), which coincides with the timing of this study.

Although rare (<5% of all on-shelf dives), the occurrence of benthic diving primarily around Cape Colbeck may also indicate switching from benthic or benthic-pelagic prey in March and April to mostly pelagic prey later in the year as birds traveled farther from the colony. During the breeding season, benthic diving is thought to be a strategy towards feeding on predictable prey during a critical stage of their life cycle (Rodary et al. 2000). This strategy may also prove profitable after the molt when birds are at their worst physiological condition and may explain the unexpected presence of emperor penguins at Cape Colbeck at the time of our arrival.

CONCLUSIONS

Prior to this study, habitat associations and diving behavior were known for emperor penguins primarily during the breeding season. Understanding be-

havior throughout their entire annual life cycle, especially when birds are not restrained by chick-rearing duties, is critical to predict how emperor penguins might respond to environmental variation and perturbations. By documenting the movement, habitat preference, and dive behavior of non-breeding emperor penguins, this study begins to fill a knowledge gap in our understanding of an understudied demographic group, corresponding to the part of their annual life cycle when birds experience the harshest physiological and environmental conditions.

Results from this study support our hypothesis that sun zenith angle influenced both presence and dive behavior of non-breeding emperor penguins. Because emperor penguins are thought to be visual predators, the occurrence of more frequent, longer, and deeper dives during daylight and twilight was expected. Unfortunately, due to the combination of an anomalously high maximum sea-ice extent, the low resolution of the sea-ice satellite data, and the lack of variation in sea-ice concentration, our study was not able to determine if the distribution of non-breeding emperor penguins was driven by sea-ice concentration. Furthermore, without additional research, we cannot determine whether the behavior of birds tagged in our study was typical for non-breeding emperor penguins or whether their non-breeding status was due to anomalous sea-ice conditions.

The spatial-temporal variation in movement and dive behavior exhibited by birds during this study may indicate that non-breeding emperor penguins can adapt their behavior if their preferred foraging areas become inaccessible. The observed differences in both movement strategies ('shelf' and 'gyre') and dive behavior (benthic and pelagic) suggest that emperor penguins alter their prey preference over space and time. Benthic dives occurred primarily around Cape Colbeck during March and April, after which nearly all dives were pelagic regardless of location, suggesting that benthic or benthic-pelagic prey are important for recouping body condition after the molt. As sea-ice conditions continue to change, (Stammerjohn et al. 2012) there may come a time when emperor penguins can no longer access preferred foraging areas farthest from their colonies based on physiological limitations alone.

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