Migratory movements and winter diving activity of Adélie penguins in East Antarctica

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ABSTRACT: Seabirds breeding on the Antarctic continent must cope with extreme changes in sea ice cover and day length throughout the year. Adélie penguins are expected to adjust their migratory movements and diving activity to seasonal changes in foraging conditions, but their winter diving activities have not been examined previously. Here, we tracked 18 and 5 Adélie penguins by using geolocators with and without depth sensors, from a colony in East Antarctica over 2 winter seasons. After breeding, all but one penguin migrated westward from March to April, then moved northward from May to August as the sea ice edge extended to the north, then moved southeastward, returning towards the breeding colony. Migratory movements followed sea ice movements and the seasonal extension in this region, which is influenced by the west-flowing Antarctic Slope Current and wind. Penguins dived deeper during winter, reaching a maximum depth of 129 m. The birds dived mostly between civil dawn and dusk, and tended to stay on ice overnight. Diving effort (total time spent underwater per day) did not decline with sea ice concentrations, suggesting that penguins found open water to dive even with >90% sea ice cover. Diving effort was lowest around the winter solstice, but was relatively high before and after the annual moult, and also before the start of breeding when birds presumably needed to accumulate body reserves. Our results highlight how the migratory movement and winter diving activity of Adélie penguins are closely associated with the seasonal polar environment.

KEY WORDS: Migration · Southern Ocean · Sea ice · Diving behaviour · Foraging · Bio-logging · Seabird

INTRODUCTION

Many seabirds undertake long-distance seasonal migrations to avoid adverse winter conditions and to utilize favorable foraging conditions on the wintering grounds (Alerstam et al. 2003, Shaffer et al. 2006, Egevang et al. 2010, Watanabe 2016). During migration, flying seabirds are able to follow spatial and seasonal changes in biological productivities due to their ability to move long distances in a timely manner (Shaffer et al. 2006, Takahashi et al. 2015). This ability to track spatial and seasonal resource availability will be important in buffering some seabird species from the potential effects of environmental changes on their populations (cf. Lack 1968, Gilroy et al. 2016).

Seabird species breeding on the Antarctic continent must cope with one of the most extreme seasonal environments on Earth (Brierley & Thomas 2002). In summer, Antarctic seabirds exploit enhanced biological productivity near their breeding colonies, usually in ice-free or pack-ice areas during long daylight hours (Knox 2007, Fauchald et al. 2017). In winter, some flying seabird species migrate remarkable distances to ice-free oceanic areas (>5000 km from their breeding colony), presumably to avoid deteriorating foraging conditions during the Antarctic winter (Ashmole 1971, Weimerskirch et al. 2015, Delord et al. 2016). However, this is not the case for penguins breeding on the Antarctic continent or on Subantarctic islands, as they have relatively limited migration ranges (<3000 km), possibly due to their flightlessness (Ballard et al. 2010, Thiebot et al. 2013). Therefore, penguins may be subject to deteriorating winter foraging conditions, such as reduced prey availability, limited daylight hours, and rapidly expanding sea ice cover, and necessarily may need to adjust their seasonal movements and diving behaviour in concert with the highly seasonal polar environment.

Adélie penguins breed on the continental coast and islands around Antarctica for 4 mo in summer, and stay within the sea ice regions of the Southern Ocean for the rest of the year (Ainley 2002). Their migratory movements have been studied recently in the Antarctic Peninsula and Scotia Sea regions (Dunn et al. 2011, Hinke et al. 2015), in the Ross Sea (Ballard et al. 2010), and in East Antarctica (Clarke et al. 2003). These studies suggest that penguin migratory movements generally follow the direction of regional sea ice movement. However, the study in East Antarctica (referring to 30–150° E in this paper; cf. Southwell et al. 2017) reported only partial migratory tracks of 3 post-breeding adults and 6 fledglings from 2 colonies in the Mawson region (Clarke et al. 2003). No such study has been made elsewhere in the Indian Ocean sector of Antarctica, thus, how general the movement pattern described by Clarke et al. (2013) might be, remains unknown. Information about migratory routes are often used to model the effects of winter sea ice conditions on population dynamics (Emmerson & Southwell 2011, Dugger et al. 2014), therefore further studies in East Antarctic regions are needed to understand the regional variations in migratory patterns of Adélie penguins. Moreover, no previous studies have examined the diving activities of Adélie penguins during migration. Such information would be important to assess the effects of shortening day length and expanding sea ice cover

on the foraging behaviour of Adélie penguins during the Antarctic winter.

Therefore, in this study, we used geolocators with depth sensors to examine the migratory movements and winter diving activity of Adélie penguins breeding at a colony in East Antarctica about 20 longitude degrees west of the Mawson region study. We sought to document seasonal patterns of migration routes, diving effort and dive depth of Adélie penguins, and examine how environmental factors such as sea ice concentrations and day length affect their movement and behaviour during migration.

MATERIALS AND METHODS

Geolocator deployment and recovery

The study was conducted at the Hukuro Cove colony (69.21° S, 39.63° E), located in Lützow-Holm Bay, East Antarctica. Two types of geolocators were used: LAT 2500 geolocators with depth sensors and BAS Mk series (Mk5 and Mk15) geolocator without depth sensors (see below for further details of the tags). Geolocators (9 LAT2500, 4 Mk5, 4 Mk15) were attached to 17 Adélie penguins for winter deployments in January 2011, using flexible leg bands (procedure described in detail in Ratcliffe et al. 2014). Geolocators were first deployed on 2 birds that experienced breeding failure in early January, and then on 15 chick-rearing birds in late January. In January 2012, geolocators (all LAT2500) were deployed on 20 chick-rearing birds. Overall, 26 out of 37 birds (70%) were recaptured in the following austral summers of 2011–2012 and 2012–2013. Data were not available from 3 recaptured birds due to detachment of the geolocator from the leg band (1 bird) and malfunction of recovered geolocators (2 birds). In the end, we obtained both location and depth data for 16 birds (with LAT geolocators), movement data only for 5 birds (with Mk geolocators), and diving data only for 2 birds (with LAT geolocators, location data failed). The movement and diving data stopped before return to the breeding colony for 3 birds (data stopped on 6 August, 19 September and 14 October).

The total mass of the geolocators including the ring was 5.5 to 6.6 g (0.62% of the mean departure body mass of tracked birds). Birds were sexed based on external measurements (Kerry et al. 1992), which was later confirmed with the patterns of nest attendance during pre-laying and incubation periods recorded by the geolocators, for those birds where these data were available.

Geolocation data analysis

LAT2500 geolocators (8 × 36 mm, 3.6 g; Lotek Wireless) recorded daily locations by on-board processing of light data via a template-fit algorithm (Ekstrom 2007). The daily locations available from the algorithm were analyzed as follows. First, aberrant positions (e.g. positions in the Northern Hemisphere) and positions during vernal and autumnal equinox periods were removed (see Fig. S1A,B in the Supplement at www.int-res.com/articles/suppl/m589p227_supp.pdf). Second, biases in the latitude data were corrected, because latitudes derived from the template-fit algorithm of LAT geolocators were reported to have biases (Hinke et al. 2015). The extent of latitude biases was reported to vary within a year (16 to 727 km), so latitude data were corrected based on the estimated weekly biases provided in Hinke et al. (2015). Longitude data were not corrected, because the biases reported for longitude data were relatively small (<60 km). Third, generalized additive models (GAMs) were fitted to the bias-corrected latitude data (Fig. S1C) and the non-corrected longitude data (Fig. S1D), following Mosbech et al. (2012) and Orben et al. (2015). We determined that the GAM approach was warranted, because latitude data derived from geolocations shows a higher degree of error than longitude data, and the GAM approach allowed us to predict latitudinal and longitudinal locations separately. GAM output for latitude and longitude were used to infer penguin movement directions and monthly mean positions (Fig. S1E).

Mk5 and Mk15 geolocators (18 × 18 × 6.5 mm, 3.5 g for Mk5; 17.5 × 16 × 6 mm, 2.5 g for Mk15; British Antarctic Survey) measured light levels every 1 min and recorded the maximum value after each 10 min period. Sunrise and sunset times were estimated from the thresholds in the light curves. Latitude was derived from day length and longitude from time of local midday with respect to Greenwich Mean Time and day of the year, using BAS Trans-Edit and Locator software. We fitted a GAM to latitude and longitude data from Mk geolocators, as we did for LAT geolocators.

Depth and wet–dry state data analysis

Two parameters were calculated in order to estimate diving behaviour: (1) time spent diving (>1 m depth) per day, as an index of daily dive effort, and (2) mean and maximum dive depth, as an index of water column use. An additional parameter was calculated as an index of daily haul-out behaviour: (3) time out of the water per day based on the wet–dry state of the logger. We examined the effect of daylight hours and sea ice concentrations experienced by penguins on the time spent diving and mean dive depth (see 'Environmental parameters').

LAT2500 geolocators were set to record depth and wet–dry state every 120 s throughout the recording period. The sampling interval of 120 s was not sufficient to identify individual dives, but would enable us to infer daily diving effort and seasonal patterns of depth use. To test this, we used another data set obtained during the chick-rearing period and compared daily dive parameters recorded at a 1 s sampling interval with those resampled for a 120 s sampling interval (Fig. S2A in the Supplement). To infer maximum dive depth from the 120 s sampling interval, we detected the inflection point of depth (where the recorded depth switched from descending to ascending), and used this as an index of maximum dive depth (Fig. S2A). The mean daily depths of inflection points were positively correlated with mean daily dive depth obtained from 1 s sampling intervals ($r^2 = 0.73$; $F_{1,17} = 50.67$, p < 0.001; Fig. S2B). Time spent diving per day calculated from 120 s recording intervals showed a close match with that calculated from 1 s recording intervals ($r^2 = 0.99$; $F_{1,17} = 2170.95$, p < 0.001; Fig. S2C).

Environmental parameters

To characterize the seasonal patterns in sea ice extent, we computed monthly averaged sea ice concentrations for each month from daily sea ice concentration data obtained from the US National Snow and Ice Data Centre (http://nsidc.org). The data set used was the NASA Bootstrap SMMR-SSM/I combined dataset (spatial resolution: 25 × 25 km). Using this data set, mean sea ice concentrations were calculated within a radius of 150 km from monthly averaged penguin locations determined from geolocation; 150 km was chosen to broadly reflect the positional uncertainty of geolocation estimates (flying seabirds: Phillips et al. 2004; diving fur seals: Staniland et al. 2012). Monthly averaged sea ice concentrations were also calculated for the area of 0 to 40° E longitude and 60 to 70° S latitude (see Fig. 1A), to compare seasonal patterns in regional sea ice conditions between 2011 and 2012.

Sunrise, sunset, civil dawn and civil dusk times were estimated from daily bird locations (GAM outputs) using the 'Maptool' package in R v.3.3.1 (R

Core Team 2016). Hours of daylight were calculated as the time between civil dawn and civil dusk, as twilight hours can plausibly be used for foraging during winter for Adélie penguins (Ballard et al. 2010).

Statistics

One-way ANOVA was used to compare migratory parameters between our 2 study years and between sexes. Birds from both sexes were pooled when comparing study years, and birds from both years were pooled when comparing sexes, due to our relatively small sample size. Generalized linear mixed models (GLMMs) were fitted to examine the relationships between penguin diving activity (response variables: time spent diving per day and mean daily dive depth) and environmental factors (explanatory variables: daylight hours, sea ice concentrations). The models using penalized quasi-likelihood were fitted for parameter estimation (R package 'MASS', function 'glmmPQL'; Venables & Ripley 2010), to account for temporal autocorrelations of the variables in the model (Bolker et al. 2009, Heerah et al. 2017). Gamma error distributions with log-link functions were used to account for the positive, continuous, right-skewed nature of the response variables. Variance inflation factor (VIF) (Zuur et al. 2010) was used to check for co-linearity in explanatory variables; some variables, such as 'month' or 'day of the year', were subsequently omitted as explanatory variables due to the high VIF values (>4.2). Explanatory variables were standardized via centering and scaling after being transformed (log-transformation for mean daily dive depth; arcsine transformation for sea ice concentration values, after conversion to values between 0 and 1 for sea ice concentration values of 0 to 100%), to facilitate comparison of slope coefficients and normality of explanatory variables. Mean (±SE) values are shown, unless otherwise stated.

RESULTS

Migratory movement

Most Adélie penguins from Lützow-Holm Bay followed an approximately clockwise migration route over the 8.5 mo long non-

breeding period (Fig. 1B, see also Fig. S1E in the Supplement), showing a similar movement pattern in both study years (Fig. 2). After mid-February, all penguins moved westward (except one bird that moved eastward in 2012) from the Lützow-Holm Bay region (Fig. 2). Penguins remained out of the water for an average of 17.2 d in March (likely to moult; see 'Diving activity') near the equinox period when it was not possible to estimate latitude from light-based geolocation. However, penguins continued to move westward during this period (longitude data unaffected by equinox). The 2 birds that failed breeding early in 2011 reached 24° E and 27° E, respectively, in mid-February, while birds that continued to rear chicks until late January were still near Lützow-Holm Bay (40° E), suggesting that the failed breeders started migration earlier. In 2011 and 2012, penguins reached the mean westernmost longitude of 6.7 ±
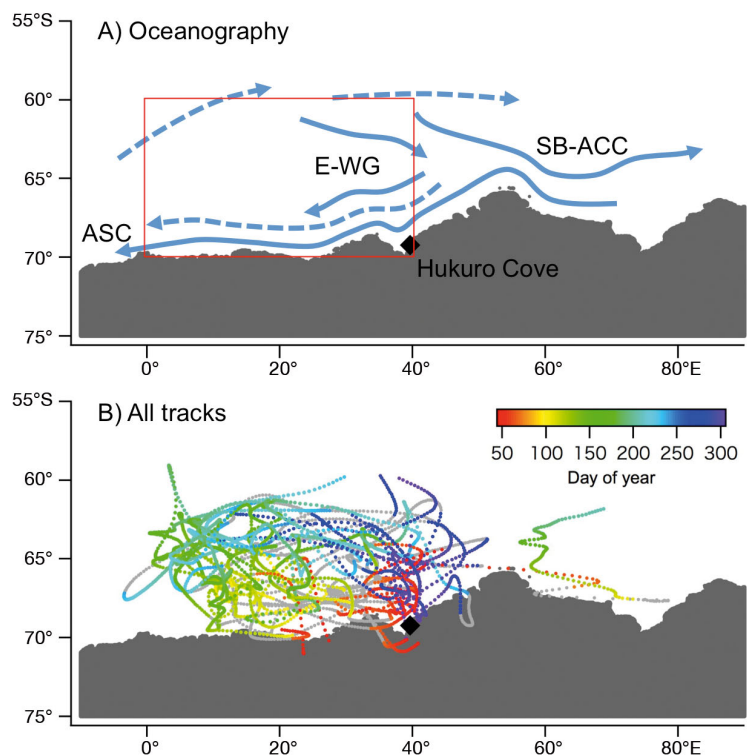

Fig. 1. (A) General oceanography of the study region, showing major ocean currents and sea ice movement directions, based on Kimura (2004) and Williams et al. (2010). Solid blue line: direction of major currents (ASC: Antarctic Slope Current; E-WG: Eastern Weddell Gyre; SB-ACC: Southern Boundary of Antarctic Circumpolar Current); dashed blue line: sea ice movement directions. Red box: the area of 0 to 40° E longitude and 60 to 70° S latitude, where mean sea ice concentrations are calculated for Fig. 4. The Antarctic continent (dark grey) and the location of Hukuro Cove breeding colony (black diamond) are also shown. (B) Daily estimated locations of all tracked Adélie penguins in 2011 and 2012. Colour code shows the day of each study year; grey indicates locations during equinox periods
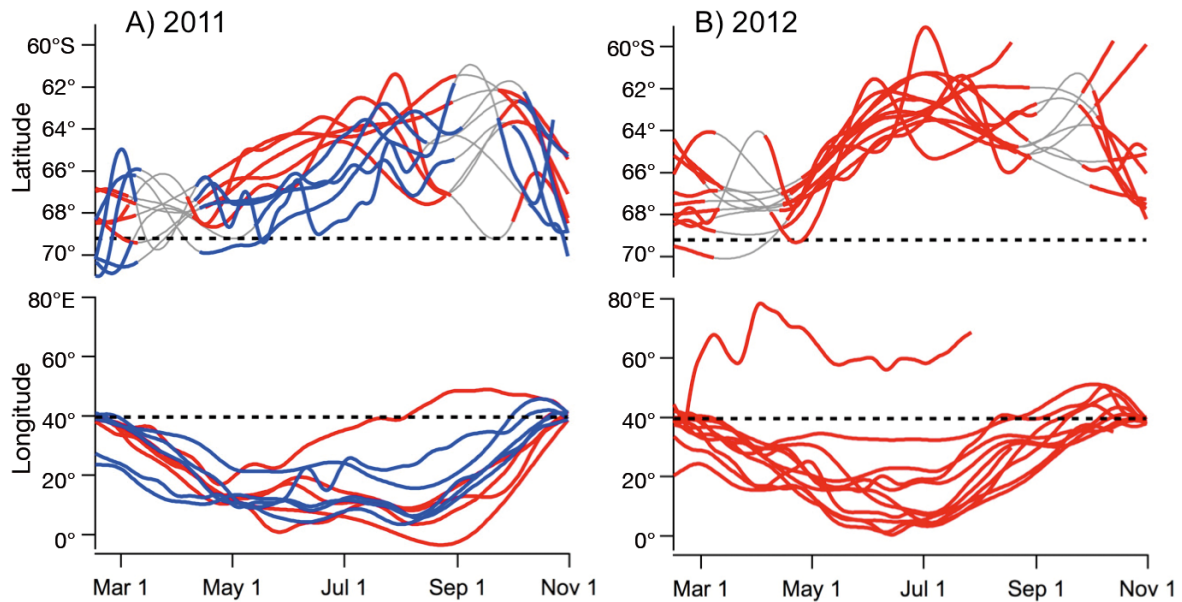
Fig. 2. Latitudinal and longitudinal movements of Adélie penguins estimated from generalized additive model (GAM) smoothing of geolocator data during the non-breeding period of (A) 2011 (n = 10 birds) and (B) 2012 (n = 11 birds). Latitude and longitude for the Hukuro Cove breeding colony are shown as dashed lines. Note that similar results were obtained from different types of geolocators (red lines: Lotek; blue lines: Mk) in 2011. Only Lotek geolocators were used in 2012. Latitude estimates during the equinox period are shown as grey lines. All penguins except one bird (Bird 2337) in 2012 moved westward from the breeding colony

2.0° E and 10.6 ± 3.1° E on 12 July 2011 (±14 d) and 4 June 2012 (±10 d), respectively. The patterns in latitudinal movements were more difficult to interpret due to large errors in geolocation (see Fig. S1C), but penguins from both years generally moved north from April–May to August–September as the sea ice edge extended to the north (Figs. 2 & 3). They reached the mean northernmost latitude of 62.4 ± 0.3° S and 61.2 ± 0.5° S on 6 September 2011 (±9 d) and 29 July 2012 (±17 d), respectively. None of these migratory parameters differed significantly between years or sexes (ANOVA, p > 0.056). They moved southeastward during September and October and returned to the Lützow-Holm Bay region in late October–November. They reached the breeding colony or the fast ice attached to the land near the breeding colony (based on depth and wet/dry records) on 31 October 2011 (±0.9 d) and 24 October 2012 (±1.4 d), with a significant difference between years (ANOVA, $F_{1,17}$ = 10.6, p < 0.01), but not between sexes (ANOVA, $F_{1,17}$ = 0.18, p = 0.68).

The maximum distance from the colony during the non-breeding period did not differ between years (1485 ± 83 vs. 1489 ± 137 km for 10 and 9 birds in 2011 and 2012, respectively; ANOVA, $F_{1,17}$ = 0.001, p = 0.98) or between sexes (1472 ± 133 vs. 1493 ±

96 km for 6 female and 13 male birds, respectively; ANOVA, $F_{1,17}$ = 0.02, p = 0.90). The mean date of the maximum distance reached from the colony did not differ between years (12 July 2011 ± 12 d vs. 6 July 2012 ± 11 d; ANOVA, $F_{1,17}$ = 0.07, p = 0.80) or between sexes (2 July ± 11 d for females vs. 14 July ± 12 d for males; ANOVA, $F_{1,17}$ = 0.38, p = 0.55).

Sea ice conditions experienced by penguins differed in different winter months (Figs. 3 & S3). Mean sea ice concentrations within 150 km of the mean monthly penguin locations were lowest in March and gradually increased, reaching >90% in July in both years. Sea ice concentrations experienced by penguins did not differ between the 2 study years (Fig. 4). Monthly mean sea ice concentrations in the area of 0 to 40° E longitude and 60 to 70° S latitude increased rapidly from April to July, and did not differ between 2011 and 2012, suggesting that seasonal sea ice conditions were similar between the 2 study years (Fig. 4). Between February and April, sea ice concentrations around the penguins were higher than that of mean sea ice concentrations in the area of 0 to 40° E longitude and 60 to 70° S latitude (Fig. 4), suggesting that penguins tended to remain in the areas of higher sea ice cover, possibly because of the need for stable ice floes for their annual moult.
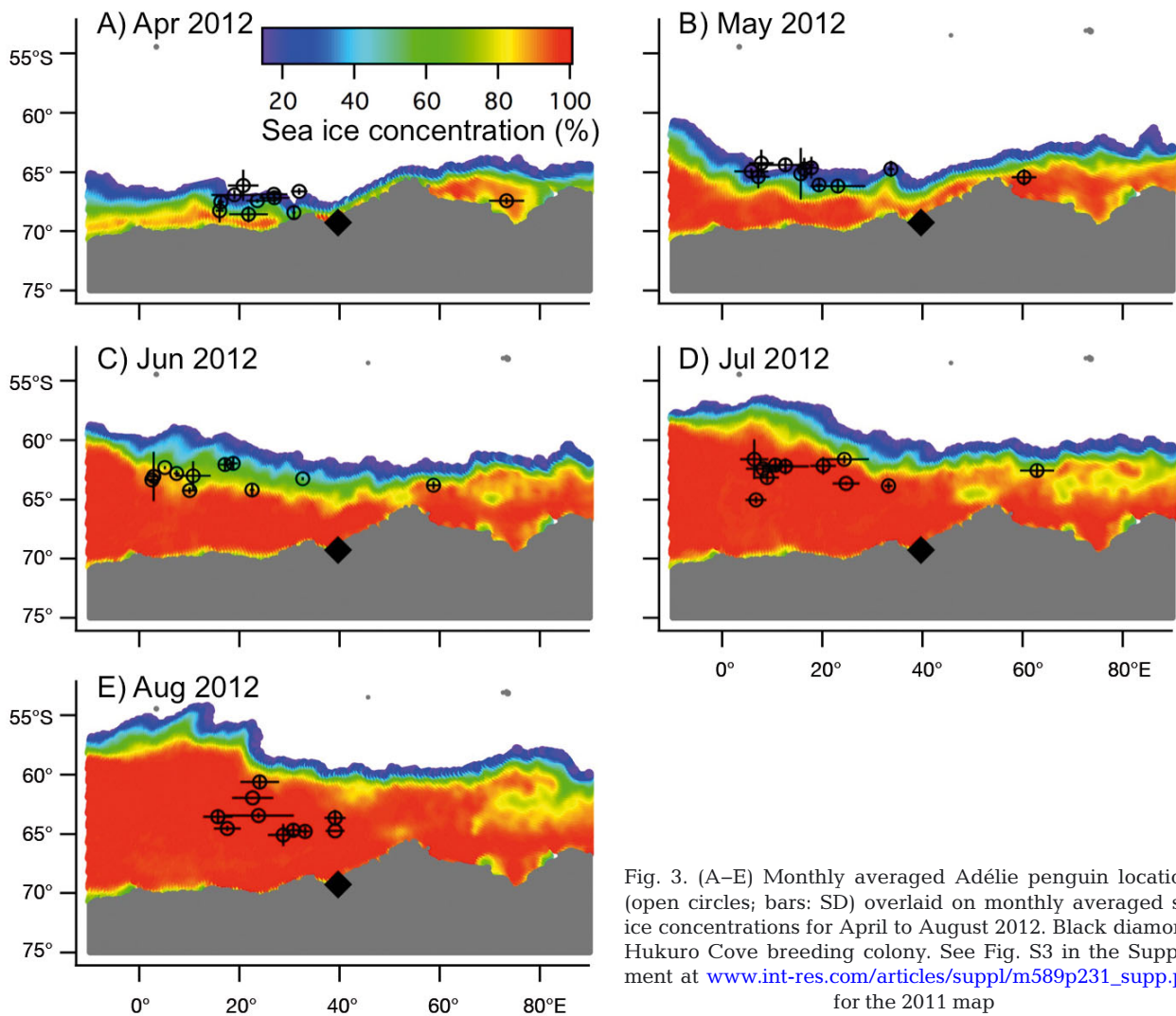
Fig. 3. (A–E) Monthly averaged Adélie penguin locations (open circles; bars: SD) overlaid on monthly averaged sea ice concentrations for April to August 2012. Black diamond: Hukuro Cove breeding colony. See Fig. S3 in the Supplement at www.int-res.com/articles/suppl/m589p231_supp.pdf for the 2011 map
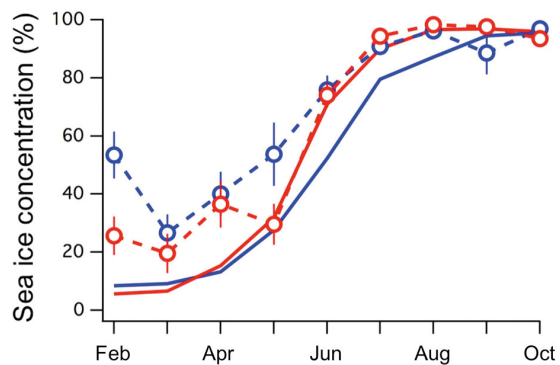

Fig. 4. Monthly averaged sea ice concentrations in the vicinity (<150 km) of penguin locations (open circles with dashed lines) and in the area of 0 to 40° E longitude and 60 to 70° S latitude (solid lines). Blue and red colours indicate data from 2011 and 2012, respectively

Diving activity

Time spent diving per day varied during the non-breeding period (Fig. 5). Penguins did not dive and remained out of the water all day for 17.2 ± 0.4 d (n = 23 birds) in March, when they presumably carried out their annual moult (cf. Dunn et al. 2011). The presumed moult began on 9 March 2011 (± 2.8 d) and 7 March 2012 (± 1.3 d). The 2 birds that failed breeding early in 2011 started their moult about 2 wk earlier (19 and 25 February 2011, respectively) than other birds (9 to 18 March 2011). Penguins tended to spend more time per day diving in late February–early March, in April–May, and in September–October, which correspond to before and after the annual moult, and before arrival at the breeding colony (Fig. 5). In contrast, they spent less time diving around the winter
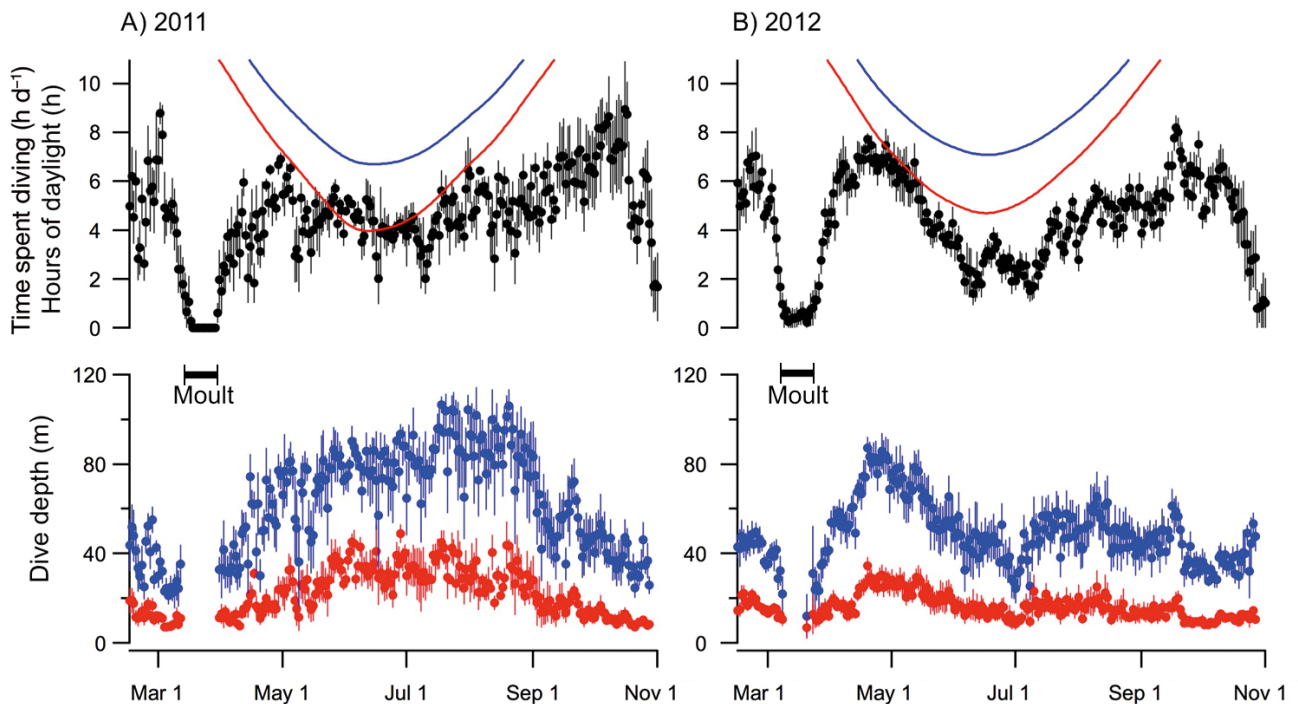
Fig. 5. Seasonal changes in the diving behaviour of Adélie penguins during the non-breeding period of (A) 2011 (n = 5 birds) and (B) 2012 (n = 11 birds). Time spent diving (black dots), mean (red dots) and maximum (blue dots) dive depths per day are shown as average values across individual birds with standard errors (vertical bars). Mean hours of daylight (red line) and daylight + twilight (blue line) experienced by penguins were calculated based on the penguins' daily position data and over-laid on the time spent diving. The average period of moult is indicated by a black horizontal bar for each year. Breeding period starts in November
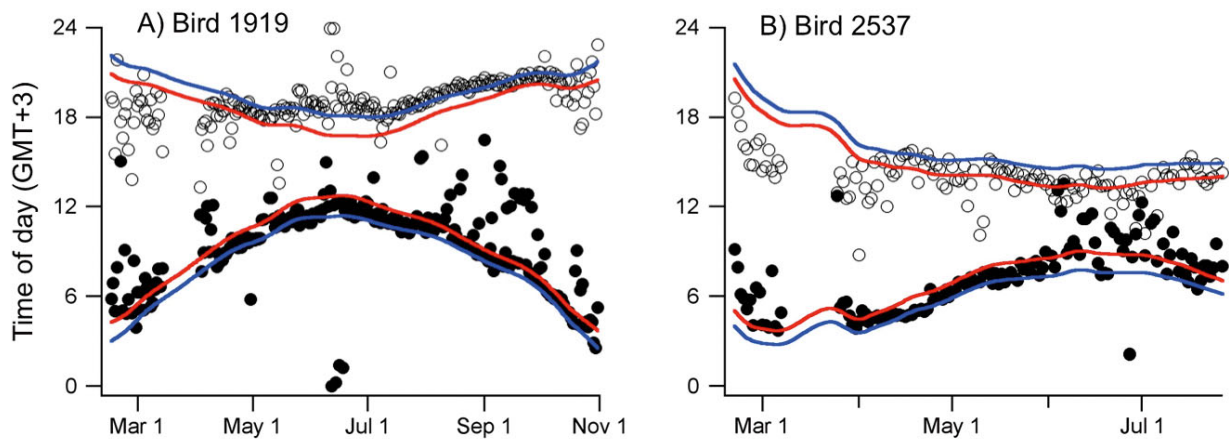

Fig. 6. Start (filled circles) and finish (open circles) time of diving activity for 2 Adélie penguins for each day during the non-breeding period. Time of day is shown as the time at the Hukuro Cove colony (GMT + 3 h). Red lines: sunrise and sunset times (sun above and below horizon); blue lines: civil dawn and dusk times (sun at 6° below horizon), calculated from the smoothed penguin locations obtained by from geolocators (see Fig. 2). (A) Bird 1919 moved west from the colony, and (B) bird 2537 was the only bird that moved east from the colony. Note that the timing of diving activities reflected the differences in longitudinal locations of the 2 penguins

solstice when they experienced the shortest daylight hours, especially in 2012 (Fig. 5). In fact, penguins tended to start diving between civil dawn and sunrise, and to end daily diving activity around civil dusk

(Fig. 6). Wet–dry records showed that penguins remained out of the water, presumably staying on sea ice for 15.21 ± 0.38 and 15.19 ± 0.39 h d^{-1}, respectively, during April–September of 2011 (n = 5 birds) and

Table 1. Generalized linear mixed effect model (GLMM) examining the relationships between time spent diving (h d⁻¹) by Adélie penguins, daylight hours, sea ice concentration, mean daily dive depth and study year. GLMM fitted with an autocorrelation term (corAR1) included. Explanatory variables were standardized to facilitate comparison of slope values. Model: Time spent diving ~ daylight hours + sea ice concentration + mean daily dive depth + factor(year)

Fixed effects	Value	SE	df	t	p
Intercept	1.4809	0.0583	3014	25.398	<0.001
Daylight hours	0.2658	0.013	3014	20.454	<0.001
Sea ice concentration	−0.0567	0.0131	3014	−4.319	<0.001
Mean daily dive depth	0.3053	0.0092	3014	33.048	<0.001
Factor(year)2012	0.0526	0.0706	14	0.745	0.468
Random effects	Intercept	Residual			
~ 1| Bird SD	0.1211	0.3918			

terns differed between years (Fig. 5). In 2011, mean and maximum dive depths were relatively shallow in April, getting deeper as the season progressed until June–August. In 2012, mean and maximum dive depths were deepest in late-April to early May, getting shallower thereafter. Mean and maximum daily depths were relatively shallow in September and October in both years. Mean daily dive depth showed weak negative relationships with both daylight hours and sea ice concentrations (Table 2, Fig. S4), probably reflecting the shallow daily dive depths during September and October when daylight hours were longer and sea ice concentrations were higher.

2012 (n = 13 birds), and were usually doing so after dusk and before dawn. Penguins spent more time diving per day when they experienced more daylight hours (time between civil dawn and civil dusk) (Table 1, Fig. 7). Sea ice concentration had little effect on time spent diving (Fig. 7), although there was a weak negative relationship (Table 1).

Penguins dived to a maximum depth of 129 ± 4 m (2011; n = 5 birds) and 124 ± 5 m (2012; n = 13 birds) during the non-breeding period. Mean and maximum daily dive depth varied as the season progressed, but the seasonal pat-

Table 2. Generalized linear mixed effect model (GLMM) examining relationships between mean daily dive depth (m) of Adélie penguins, daylight hours, sea ice concentration and study year. GLMM fitted with an autocorrelation term (corAR1) included. Explanatory variables were standardized to facilitate the comparison of slope values. Model: Mean daily dive depth ~ daylight hours + sea ice concentration + factor(year)

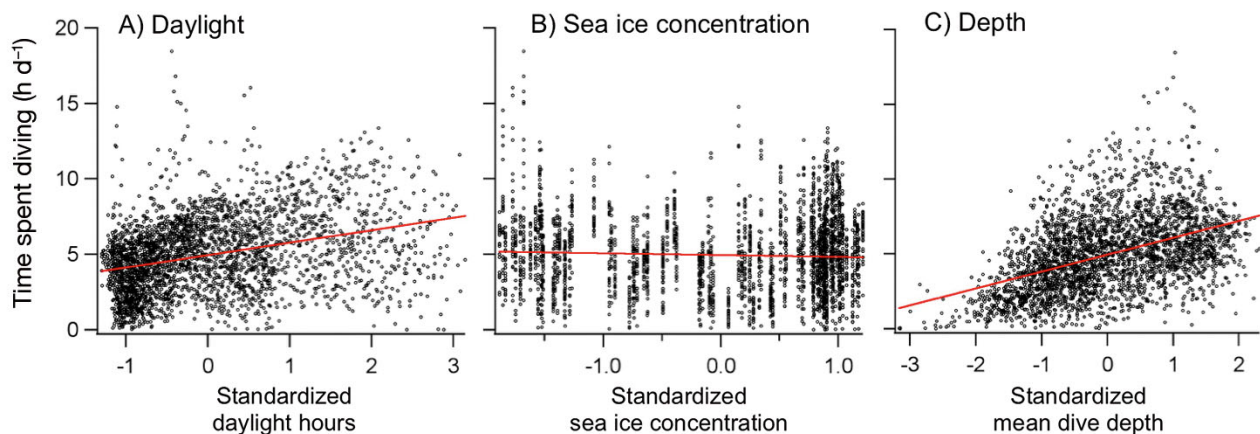| Fixed effects	Value	SE	df	t	p
Intercept	3.1068	0.1182	3015	26.274	<0.001
Daylight hours	−0.1825	0.0317	3015	−5.752	<0.001
Sea ice concentration	−0.1014	0.0311	3015	−3.262	0.0011
Factor(year)2012	−0.3826	0.1432	14	−2.671	0.0183
Random effects	Intercept	Residual			
~ 1| Bird SD	0.2351	0.7148			

Fig. 7. Effects of (A) daylight hours (daylight + twilight hours), (B) sea ice concentration and (C) mean dive depth on time spent diving by Adélie penguins from April to October. Explanatory variables were standardized after data transformations (log and arcsine transformations for mean dive depth and sea ice concentration, respectively). See Table 1 for modeling results. Least-square regression lines are shown

DISCUSSION

This study examined the migratory movements of Adélie penguins in East Antarctica, a region where relatively little information is available. It also presented the first record of the winter diving behaviour of Adélie penguins. The results presented here contribute to our understanding of how these non-flying, diving seabirds cope with adverse foraging conditions in Antarctic winter.

Migratory movement

Adélie penguins from an East Antarctic colony moved in a complex pattern, with most birds showing similar movement directions. Here, we discuss their migratory patterns in relation to (1) sea ice movement and extension, (2) seasonal and latitudinal changes in day length and light availability and (3) regional prey availability.

First, seasonal movement patterns of the penguins followed the sea ice movement and extension in this region of the Southern Ocean. Between February and May, penguins generally moved westward, similar to the direction of sea ice movement which is strongly affected both by the Antarctic Slope Current and by wind (Fig. 1A; Kimura 2004, Kwok et al. 2017). The longitudinal positions of penguins moved westward from 33.8 to 27.6° E during the moult in March (Fig. 2), suggesting that moulting penguins, which usually do not move much (cf. Dunn et al. 2011), drifted on ice floes. From May through August, penguins moved northward as sea ice extended rapidly to the north. The eastern Weddell Sea region (0 to 30° E), where our penguins wintered, shows the greatest northerly ice extension around Antarctica (Kimura & Wakatsuchi 2011), which was reflected in the rapid increases in sea ice concentrations around the penguins in winter (Fig. 4). This northward movement may be necessary if penguins are to maintain access to water in the expanding sea ice. From August to October, penguins moved eastward and southward, returning towards the breeding colony. Sea ice moves eastward at a latitude of 60 to 65° S in this region (Fig. 1A; Kimura 2004, Kwok et al. 2017), which probably contributes to the penguins' movement in a similar direction. These results suggest that the migratory movements of penguins generally follow the regional ocean currents and sea ice movements. This appears to be the case for Adélie penguins in other regions of the Southern Ocean (Clarke et al. 2003, Ballard et al. 2010, Dunn et al. 2011).

Clarke et al. (2003) showed westward movements of 3 post-moult adults and 6 fledglings from the Mawson region, suggesting the influence of the west-flowing Antarctic Slope Current. Interestingly, birds from Lützow-Holm Bay and Mawson region and had similar longitudinal shifts to their wintering areas (20 to 30° to the west), suggesting the important influence of the Antarctic Slope Current in shaping similar penguin migration patterns across East Antarctica. It should be noted, however, that penguins are still able to move against the ocean current, as shown by one bird (Bird 2337) that apparently moved eastward against the west-flowing Antarctic Slope Current (Fig. 2B). Outward migration with oceanographic currents appears to be common in other species of penguins (e.g. Thiebot et al. 2013) and may benefit penguins by enabling them to conserve energy, especially before or after the energetically demanding moult period (Green et al. 2009).

Second, daylight availability is likely another driver for the latitudinal movement of penguins (Ballard et al. 2010). The daily schedule of diving activity was closely related to the time of civil dawn and dusk (Fig. 6), suggesting the importance of the prevailing light regime on the foraging behaviour of these visual hunters. However, our penguins continued to move north in July and August even after the winter solstice, suggesting that the northward extension of sea ice drove the northern movement of our penguins wintering at relatively low latitudes with enough daylight availability. The situation is different for Adélie penguins wintering at higher latitudes such as those from the Ross Sea, as penguins needed to move north beyond the latitude of zero winter twilight (72.7° S) during June and July (Ballard et al. 2010).

Third, regional differences in prey availability may affect the movement of penguins, but the prey species of Adélie penguins and their regional distributions are poorly known during the Antarctic winter. Crustaceans such as Antarctic krill are thought to be one of their major prey items (Ainley et al. 1992, Cherel 2008). The main wintering destinations of our penguins (62 to 68° S, 0 to 20° E) are not areas of elevated Antarctic krill density, based on a database of krill distribution, KRILLBASE (Fig. 1 of Hill et al. 2013). Further, KRILLBASE shows that krill density was relatively high in the area adjacent to Lützow-Holm Bay (64 to 68° S, 30 to 45° E), suggesting that regional differences in krill density, at least as compiled in the database, cannot explain the migratory movement of Adélie penguins from Lützow-Holm Bay. Myctophid fish and squid might also be important prey during winter (Ainley et al. 1992), but again, no information

is available on the horizontal and vertical distribution of these taxonomic groups in winter. The deeper diving depth observed during winter (Fig. 5) might be related to the penguins feeding on myctophids. Intraspecific competition may be another factor affecting regional prey availability. There are large populations of Adélie penguins breeding in the Mawson region (Southwell et al. 2017) that use the area in front of Lützow-Holm Bay during winter, possibly relying on the high krill densities in this region (Clarke et al. 2003). In contrast, no breeding colonies of Adélie penguins are found between 25°W and 39°E, due to a lack of suitable breeding habitat (Lynch & LaRue 2014, Southwell et al. 2017). This 'gap' in breeding distribution may lead to less competition for foraging habitat for Adélie penguins from Lützow-Holm Bay, located at the edge of the species' breeding distribution in East Antarctica.

Our regional comparisons of migratory distances emphasize the effect of sea ice extension on the migrations of Adélie penguins (Table 3). The maximum distance reached from the breeding colony tended to be further for higher latitude sites (Table 3), suggesting that the costs of migratory movements may increase with latitude. Previous studies showed that post-breeding Adélie penguins from King George Island and Signy Island moved south into the Weddell Sea during the early part of their migration to find suitable ice conditions for moult (Dunn et al. 2011, Hinke et al. 2014, 2015). The ice edge retreats south of these islands during February and March, leading to southward movement of the penguins from these islands. In contrast, Adélie penguins from 2 East Antarctic colonies (Mawson region and Hukuro Cove; Clarke et al. 2003, this study) migrated westward first, then northward, as sea ice extended seasonally. Post-breeding Adélie penguins from the southern Ross Sea, the southern-most breeding locality for this species, migrated northward to gain access to the northern ice edge (Ballard et al. 2010). Therefore, differences in access to the sea ice edge appear to explain the regional differences in migratory patterns of Adélie penguins.

Diving activity

Daily diving effort of Adélie penguins changed seasonally. We discuss these results in relation to (1) availability of daylight, (2) sea ice concentration and (3) seasonal changes in the energy demands of penguins during moult and reproduction.

First, the hours of daylight probably constrain the diving activity of visual predators such as penguins (Wilson et al. 1993, Kirkwood & Robertson 1997, Green et al. 2005). Indeed, our results showed that the time spent diving per day decreased with daylight duration (Fig. 7A), and hours of daylight most severely constrained daily dive time from May to August (Fig. 5). Yet it is still unknown how the availability of light affects the daily dive schedule of penguins, though it is clearly important to their visual ability either to locate prey underwater (Shiomi et al. 2016) or to avoid predation (Ainley & Ballard 2012). Our results suggest that penguins dived deeper when hours of daylight were shorter (Table 2, Fig. S4 in the Supplement), which is counter-intuitive, assuming lower light availability at deeper depths. Underwater light availability will be highly variable depending upon the local sea ice cover, hence *in situ* light measurements together with studies of diving behaviour will be needed to investigate this question further. Such studies should also consider the possibility of feeding on different prey species between summer and winter, and also the vertical diel migration of prey species.

Table 3. Maximum distance reached by Adélie penguins during winter migration, from various breeding colonies around Antarctica

| Colony | Colony location | | Distance from the colony | | No. of birds tracked | Reference |
	Latitude	Longitude	Mean ± SE (km)	Maximum (km)		
Signy	60.7°S	45.6°W	1092 ± 107	2235	12	Dunn et al. (2011)
Admiralty Bay	62.46°S	58.42°W	1070[a]	1070[a]	1[a]	Hinke et al. (2014)
Mawson	67.58°S	62.82°E	1369 ± 175	1653	3	Clarke et al. (2003)
Hukuro Cove	69.21°S	39.63°E	1487 ± 76	2087	19	This study
Ross Sea[b]	77.45°S	169.2°E	1722 ± 66	2552	41	Ballard et al. (2010)

[a]Calculated from the map provided in Fig. 1 of Hinke et al. (2014)
[b]Birds were tracked from both Cape Crozier and Cape Royds; Cape Crozier location is shown

Second, winter sea ice conditions have been suggested as an important factor affecting the foraging behaviour of penguins, acting both directly as a physical barrier to access open water and indirectly via its effect on the availability of ice-associated prey. For Adélie penguins, demographic studies suggest that winter survival has non-linear quadratic relationships with winter sea ice conditions, with lower survival rates when their supposed wintering area has too little or too much ice (between 15 and 80% cover) (Wilson et al. 2001, Ballerini et al. 2009, Emmerson & Southwell 2011). These studies suggest that penguins might have limited access to open water in years of excessive sea ice cover, and might experience reduced availability of ice-associated prey such as krill in years of insufficient sea ice cover. However, our results showed that sea ice concentration had little effect on the daily dive time or dive depth of Adélie penguins (Figs. 7 & S4), even though penguins experienced relatively high (>80%) and low (<20%) sea ice concentrations. This suggests that there was no 'optimal' sea ice concentration in terms of penguin diving effort, and penguins were able to find leads or small areas of open water even under conditions of high sea ice concentration. Penguins moved north as the sea ice cover extended (Fig. 3), which might help them find locations to dive, because sea ice cover would be more susceptible to movement and open leads due to wind stress near ice edge. On the other hand, our results showed that seasonal patterns in dive depths differed considerably between years (Fig. 5), despite similar seasonal trends in sea ice concentrations (Fig. 4). This suggests that the local accessibility of prey under winter sea ice might vary between years despite broadly similar sea ice conditions.

Third, our penguins tended to spend more time diving per day in late February–early March, April–May and September–October, which correspond with the times of pre-moult, post-moult and pre-arrival at the breeding colony, respectively. Before the annual moult, Adélie penguins gain more than 2.2 kg of body mass from the late chick-rearing period (Penney 1967) to attain a body mass of as much as 6.7 kg at the start of moult. After the long fasting period associated with moult, Adélie penguins have lost as much as 40% of their body mass and must immediately resume foraging to recover their body reserves (Penney 1967). The energy demands associated with moult probably drive the increased diving effort in late February and April–May. Penguins also need to accumulate body reserves for reproduction before coming back to the colony in October and November

for courtship, laying and incubation. Body reserves at arrival are related to the propensity for successful breeding in Adélie penguins (Vleck & Vleck 2002). The increased diving effort in September and October would contribute to the accumulation of body reserves upon arrival at the colony. A previous year-round study on macaroni penguin diving behaviour reported similar seasonal patterns, showing elevated diving effort before the annual moult and before the start of reproduction (Green et al. 2005). These results suggest that Adélie penguins adjust their diving effort to seasonal changes in energy demands for both moult and reproduction, even under highly seasonal and variable environmental conditions. Penguins require enough hours of daylight to increase their diving effort, which may be an important factor affecting the annual cycle of moult and reproduction.

CONCLUSIONS

Our results confirm that Adélie penguins have a relatively restricted migratory range (up to 1500 km from the colony) and experience a variety of sea ice conditions during Antarctic winter. This contrasts with some flying seabird species that can move quickly to follow relatively constant sea ice habitat conditions (e.g. Ainley et al. 1993, Divoky et al. 2016, Fauchald et al. 2017). The migratory movements of Adélie penguins generally followed the direction of sea ice movement and northward seasonal extension of sea ice, which might make them susceptible to possible future changes in oceanographic circulation and wind patterns. Dive depth was generally deeper in winter than in summer, and was highly variable between and within years, possibly reflecting the changes in prey type or vertical availability of prey, though further studies on winter diet are needed. Penguins dived mostly between civil dawn and dusk, and stayed on ice during the night or between dives for long intervals, which made them subject to drift with ice. Diving effort was low in mid-winter, when available hours of daylight were short, but was high before and after the annual moult and before the start of reproduction (probably to meet increased energy demands) under longer hours of daylight. Our results highlight how the migratory movement and winter diving activity of Adélie penguins are closely associated with the seasonal polar environment.

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