Responding to climate change: Adélie Penguins confront astronomical and ocean boundaries

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Abstract. Long-distance migration enables many organisms to take advantage of lucrative breeding and feeding opportunities during summer at high latitudes and then to move to lower, more temperate latitudes for the remainder of the year. The latitudinal range of the Adélie Penguin (*Pygoscelis adeliae*) spans ~22°. Penguins from northern colonies may not migrate, but due to the high latitude of Ross Island colonies, these penguins almost certainly undertake the longest migrations for the species. Previous work has suggested that Adélies require both pack ice and some ambient light at all times of year. Over a three-year period, which included winters of both extensive and reduced sea ice, we investigated characteristics of migratory routes and wintering locations of Adélie Penguins from two colonies of very different size on Ross Island, Ross Sea, the southernmost colonies for any penguin. We acquired data from 3–16 geolocation sensor tags (GLS) affixed to penguins each year at both Cape Royds and Cape Crozier in 2003–2005. Migrations averaged 12 760 km, with the longest being 17 600 km, and were in part facilitated by pack ice movement. Trip distances varied annually, but not by colony. Penguins rarely traveled north of the main sea-ice pack, and used areas with high sea-ice concentration, ranging from 75% to 85%, about 500 km inward from the ice edge. They also used locations where there was some twilight (2–7 h with sun <6° below the horizon). We report the present Adélie Penguin migration pattern and conjecture on how it probably has changed over the past ~12 000 years, as the West Antarctic Ice Sheet withdrew southward across the Ross Sea, a situation that no other Adélie Penguin population has had to confront. As sea ice extent in the Ross Sea sector decreases in the near future, as predicted by climate models, we can expect further changes in the migration patterns of the Ross Sea penguins.

Key words: Adélie Penguin; Antarctica; climate change; geolocation sensor; migration; Pygoscelis adeliae; *Ross Sea; sea ice; wintering ecology.*

Introduction

Long-distance migration enables many organisms to take advantage of lucrative breeding and feeding opportunities during summer at high latitudes and then to move to lower, more temperate latitudes for the remainder of the year (cf. Cockell et al. 2000, Alerstam et al. 2003), a situation complicated for northern terrestrial species in the past million years by the ebb and flow of continental ice sheets (Greenberg and Marra 2005). Marine species that undertake polar-temperate long-distance migrations include seabirds (e.g., Phillips et al. 2005), seals (e.g., McConnell and Fedak 1996), and

whales (e.g., Clapham and Mattila 1990), but the history of change in their migration has been little investigated. The glaciological history of Antarctica, however, has been intensively studied. Because of the unique cold and dry conditions, which preserve subfossil deposits, the appearance and disappearance of Adélie Penguin (*Pygoscelis adeliae*) colonies, as glaciers and sea ice have come and gone, is well understood (Emslie et al. 1998, 2003, 2007; see also Thatje et al. 2008). What we know little of, however, is how the penguins respond in real time to the seasonal flux in sea ice, an important detail in understanding the Holocene history of this species. Environmental changes now occurring, especially in the winter, are affecting seabird numbers and demography (Barbraud and Weimerskirch 2003). Of particular interest is how Antarctic seabirds cope with two challenges: variability in the location of their

TABLE 1. Winter locations (June–July), arrival date, hours of twilight, distance to pack ice edge, and pack ice concentration for Adélie Penguins (*Pygoscelis adeliae*) from the Cape Crozier and Cape Royds colonies, Ross Island, Antarctica.

Year	*n*	Latitude	Longitude	Arrival date (week of year)	Twilight hours	Distance to pack ice edge (km)	Ice concentration (%)
2003	11 (77)	−66.54 ± 0.57	180.43 ± 2.90	23.0 ± 0.0	6.14 ± 0.11	341.66 ± 24.56	74.12 ± 2.37
2004	13 (78)	−68.52 ± 0.41	177.76 ± 3.32	25.3 ± 0.4	5.20 ± 0.11	525.12 ± 16.26	81.13 ± 0.68
2005	17 (98)	−69.96 ± 0.59	185.44 ± 2.38	24.5 ± 0.3	4.11 ± 0.20	631.13 ± 22.57	81.56 ± 0.55

Notes: Sample sizes (*n*) are the number of individuals, with number of positions in parentheses. Values are means ± SE.

foraging habitat (the sea ice ecosystem) and in the amount of light available to them for foraging and navigating.

The Adélie Penguin is one of the southernmost breeding birds in the world, its overall breeding range extending over ~22° of latitude (56–78° S; Woehler 1993). Adélies are pack-ice obligates while at sea (Ainley et al. 1983, 1984, 1994), previously documented as preferring about 70% ice cover (Cline et al. 1969). Southern Adélies are known to depart their breeding grounds in February, thus avoiding a long, dark, ice-covered, and extremely cold winter. In the northern portion of their range, penguins visit colonies year round (Parmelee et al. 1977). Only in those northern areas have the species' winter movements previously been investigated (Fraser and Trivelpiece 1996, Clarke et al. 2003).

In the southernmost part of this species' range, its habitat has been in constant flux through recent millennia and likely will remain so into the near future. The West Antarctic Ice Sheet (WAIS) withdrew southward across the Ross Sea to its present position only since the time of the first Egyptian pharaohs (~6000 yr BP; Emslie et al. 2003, 2007). As it withdrew, new breeding habitat was sequentially exposed from 72° S (northern portion of the Ross Sea) during the Last Glacial Maximum (LGM) to almost 78° S at present (Ainley 2002). Although the ocean was productive in the outermost Ross Sea during the LGM (Thatje et al. 2008), as it is now throughout (Arrigo et al. 1998, 2008), only by migrating could Adélies take advantage of the new breeding opportunities. Providing a challenge, though, are the shortening duration of favorable climate conditions for breeding with increasingly higher latitude, as well as the shortening amount of daylight, since Adélies are visual predators (Wilson et al. 1993) and require daylight for navigation (Emlen and Penney 1964, Penney and Emlen 1967). The southern Ross Sea is well south of the Antarctic Circle and, therefore, dark during half of the year. On the other hand, the seasonal schedule of sea ice advance, extent, and retreat is changing noticeably (Parkinson 2002, Zwally et al. 2002, Stammerjohn et al. 2008, Turner et al. 2009), a critical development for this ice-obligate species (Emslie et al. 1998). Investigating the migratory strategy of Adélie Penguins can therefore reveal insights into how they have met the challenges of receding and otherwise changing ice sheets, as well as into how they are likely to

respond to future changes in their sea ice environment (Ainley et al. 2010).

Here we report results of the first use of GLS (geolocation sensor) tags to track the year-round movements of Adélie Penguins. We sought to document the general pattern (distance, direction, speed, location) of movement, and we hypothesized that Adélies select wintering locations based on two criteria: (1) sea ice present but not so consolidated as to prevent access to the ocean, and (2) light sufficient to see well enough to forage. We believe that these two factors are important in the evolution of migratory patterns in this species (see Fraser and Trivelpiece 1996). We also predicted that penguins originating from two different colonies, Capes Royds and Crozier, would use different wintering locations, with potentially different arrival times and ice and light characteristics, because onset of breeding (as well as autumn departure) differs by as much as a week and population trends at these two colonies have followed disparate trajectories, with over-winter survival being an important determinant of population trends (Ainley et al. 1983, Trathan et al. 1996, Wilson et al. 2001). Annual survival rates at the smaller colony (Cape Royds; 2500 pairs) appear to be consistently lower than those at the larger colony (Cape Crozier; 150 000 pairs) (K. Dugger, D. Ainley, and G. Ballard, *unpublished data*).

MATERIALS AND METHODS

At the end of the Adélie Penguin breeding seasons (end of January) of 2003/2004, 2004/2005, and 2005/2006, we attached GLS tags to 10–20 penguins at each of two colonies on Ross Island: Cape Crozier and Cape Royds (98 total tags, 41 retrieved functioning; Table 1; see also Appendix A). We chose these two colonies because they are markedly different in size, which has implications for several aspects of this species' breeding biology (Ainley et al. 2004). Moreover, the penguins at Royds nest 7–10 d later than those at Crozier and thus have a different annual phenology.

We selected only birds that were feeding large, crèched chicks and appeared in good physical condition in late January and early February. We did this to increase the probability that we would be able to find these birds the following spring, at which time we caught them again to remove the archival tags. Birds were sexed by cloacal exam (at Crozier) in 2003 and by size, behavior, and timing of colony attendance in all other years and

locations (Ainley and Emison 1972, Ainley et al. 1983, Kerry et al. 1992).

Encased within the epoxy block of each 9-g GLS tag (MK3 tag; Afanasyev 2004) were a battery (rated for a 3-yr life), a light sensor, a clock, and a microchip for data storage. Each device was fastened to a white Darvic plastic band (A. C. Hughes, Middlesex, UK) using a Panduit stainless steel cable tie (Panduit, Tinley Park, Illinois, USA). The plastic band (with tag attached) was placed on the left leg of the penguins. We chose a white band to match the color of the leg feathers because penguins will attempt to remove anything affixed to them that is any color other than black or white (Wilson and Wilson 1989). This method of attachment required <5 min of handling per individual.

The nests of tagged birds were flagged, with positions recorded by GPS in order to facilitate tag retrieval. We searched for individuals with tags each spring by frequently scanning all birds within 5–10 m of nest markers. Tags were removed upon detection; all data pertaining to the bird's breeding status and condition were recorded if they could be determined, and the tag's archives were immediately downloaded. When recaptured, most birds were breeding, and had minimal feather wear around the tag area and some callusing on the leg. Five individuals had more severe callusing, and one individual limped prior to tag removal, we think because the band was attached too loosely (the bird subsequently recovered completely). Tag attrition was a function of normal over-winter penguin mortality (estimated range 4–27% annual mortality for 1996–2002 at Cape Crozier; Dugger et al. 2006), tag loss, tag and band loss or tag malfunction. It is also possible that the tags increased adult mortality, although we have no direct evidence of this. We retrieved 65% of the tags within one year, and 68% after two or more years (data from these tags not reported in this study). We believe that some individuals were missed because GLS tags were inconspicuous and emigration rates were higher than normal (Shepherd et al. 2005); at least two birds were missed for one year and one bird, from Royds, for two years, where temporary emigration owing to a large grounded iceberg was especially high (K. Dugger, D. Ainley, P. Lyver, K. Barton, and G. Ballard, *unpublished data*). Annual variability in survival and effects of marking penguins remain under study (Dugger et al. 2006; K. Dugger, D. Ainley, and G. Ballard, *unpublished data*).

Light data collected by GLS tags were analyzed using MultiTrace software (Jensen Software Systems, Laboe, Germany). The GLS tags measured visible light every 60 s and recorded the maximum reading every 10 min. By recording light level, day length could be estimated for each day of deployment. The midpoint of a local day (light period) was taken as noon; the midpoint of a local night (dark period) was taken as midnight. The local time of noon and midnight were compared against GMT (Greenwich Mean Time) to determine longitude; day length on a given date was used to determine latitude (Hill 1994).

Fast-moving animals may cover large distances in an east–west direction during a 24-h period. Under such scenarios, the calculated day length may be more or less than 24 h and calculations of latitude must be compensated accordingly. This correction factor enables the compensation algorithm to take into account whether travel occurred mainly during the day or night. Penguins travel relatively slowly (compared with flying birds, for example), and in the absence of any evidence to suggest otherwise, we applied the default correction factor of 0.5 (i.e., equally likely to travel during light or dark). Given the inaccuracy of latitude estimation during equinoxes (Hill 1994), we excluded the period around the equinoxes when location estimates were clearly affected (~1 week before and 3 weeks after the autumnal equinox, 3 weeks before and 2 weeks after the vernal equinox). Any locations derived from light curves with obvious interruptions or interference around the times of sunset or sunrise (probably as a result of diving or of changes in orientation, or intermittent shading of the sensor by snow, ice, or feathers) were noted during processing and subsequently excluded if obviously anomalous (Hill 1994).

To reduce the position error inherent in GLS data (Phillips et al. 2004), penguin positions (two per day, one at noon and one at midnight) were smoothed using a 5-day moving average weighted by location and number of neighbors. We chose this 5-day period because we felt that fewer days resulted in overconfidence of positions and more than 5 days underutilized the detail available in the data. Weekly means of these positions for each individual were used for all analyses.

Data were filtered to remove any locations that required unrealistic swim speeds between estimated positions (>2.3 m/s sustained over a 12-h period; Clark and Bemis 1979, Brown 1987). The great-circle distance between consecutive fixes was used in all velocity calculations. We were unable to obtain any positions until the time of first sunset, which in the southern Ross Sea is 20 February, by which time all penguins had already departed Ross Island.

We deployed three static GLS tags to overwinter at Cape Crozier (77° S) and three at Cape Hallett (72° S) in 2004, to be used as a reference. These data were processed as just outlined, and results were compared with device locations determined precisely by GPS. Potential consistency in errors (great-circle distances) among devices and among days was examined, with midday fixes only used in the comparisons to reduce the problem of lack of serial independence. Results from the analyses of the static devices were used to help parameterize some of the inputs to MultiTrace and to verify the importance of eliminating data near the equinoxes, as described previously.

To assess the overall validity of the positions that we report for penguins, we analyzed the known error in the

data from static devices after processing these data in the same way we had processed the data from tags deployed on penguins. Thus, the position data from the Cape Hallett reference devices were evaluated to estimate mean error in penguin data using a mixed-effects model with tag identification included as a random effect and week as a main effect. We chose to use only Cape Hallett data for this analysis because its latitude more closely approximated the average positions of the penguins in the analysis. Results of these analyses showed that weekly mean errors ($\pm$SE) were lowest in June and July (33.0 $\pm$ 0.3 km) and highest in February and October (99.2 $\pm$ 0.4 km). The overall mean error was estimated to be 58.6 $\pm$ 0.8 km. Such accuracy may be surprising (cf. Phillips et al. 2004), but two factors combine to explain why this level of accuracy was achieved. First, error rates are known to be highest near the equinoxes, and these positions were removed from our data. Second, the use of a mixed-effects model would smooth estimates and further reduce error.

To compensate for the gap in GLS data due to the absence of darkness in the first portion of each deployment, we also tracked the late-summer (late January to late February, 2004–2006) movements of 10 individuals using 20–26 g satellite tags (SPOT4 and SPLASH; Wildlife Computers, Redmond, Washington, USA; note that these individuals did not also have GLS tags) affixed to the back feathers of breeders (for attachment methods, see Wilson and Wilson 1989, Ballard et al. 2001). Tags were set to transmit every 45 s for the first eight successive transmissions and then switch to once every 90 s thereafter, with up to 1440 transmissions allowed per day. Tags were programmed to turn off after being dry for 6 h in order to conserve batteries. All transmissions were received and processed within the ARGOS system (CLS Corporation, Ramonville Saint-Agne, France). Data from these tags were available until the transmitters were lost (due to molting), died (due to low battery voltage), or stopped transmitting (after being dry for >6 h and not re-immersed). Positions with ARGOS accuracy code Z were deleted, all others (i.e., A, B, 0, 1, 2, 3) were included only if they were within an appropriate distance, given penguin swimming speed (<2.3 m/s) and time between positions from at least two other locations with code of 1, 2, or 3 (i.e., ≤1000 m error), with no more than 12 h allowed between positions.

We calculated the potential wintering area of Adélie Penguins from Ross Island by creating a polygon containing all GLS-derived penguin positions for all winters using the following boundaries: the Antarctic coastline, the eastern and westernmost longitudes, and the northernmost latitude in the retrieved positions (Fig. 1). Thus, the potential wintering polygon included any place where a penguin might be found during the nonbreeding period based on empirical results from this study. We were not attempting to define the precise area (e.g., by using kernel analysis) used by penguins. Our interest was in estimating the area of potential use (for the study period), and we do not expect that our study included the full range of possible wintering locations for these penguins. For each penguin position and for 30 random locations for each week, we calculated the mean ice concentration within 100 km, the distance to the large-scale ice edge (as defined by the 15% ice concentration contour), the number of hours of light (twilight and daylight), and the distance to the latitude of 24-h darkness. Weekly time of sunrise and sunset and civil twilight (sun <6° below the horizon) for each 15' latitude were obtained from the U.S. Naval Observatory website (data *available online*).[8]

Mean weekly sea ice concentrations and distance to the large-scale ice edge (as defined by the 15% ice concentration contour) were derived from the Special Sensor Microwave Imager (SSM/I) on board the F13 satellite of the Defense Meteorological Satellite Program (DMSP). Data were collected daily and mapped to a resolution of 25×25 km grid cell size (Cavalieri et al. 2006). Calculation of ice concentration was possible due to the strong contrast between microwave emissions of ice and water. Daily ice motion vector data for 2003 were obtained from the website of the Polar Remote Sensing Group of the Jet Propulsion Laboratory, California Institute of Technology (*available online*).[9] We created monthly averages of daily ice flow rates and bearings to evaluate variability in these parameters in the context of penguin movements in a descriptive sense. To assess direct effects of ice movement (speed and direction) on penguin movements, we used weekly mean values for all grid cells within 100 km of weekly mean penguin positions. To assess the effect of ice speed on penguin speed (km/d), we used a mixed-effects generalized linear model with penguin identity (ID) included as a random effect and week of year as a fixed (categorical) effect, predicting that the effect of ice speed on penguin speed would vary by week (after removing the 5% of penguin weekly speeds that were calculated to be >97 km/d, which we assume to be due to location errors). Separately, we assessed the correlation between ice movement direction and penguin movement direction using the circcorr package in STATA (Cox 1998).

Using two-tailed t tests, we compared distance to ice edge (negative for south, positive for north), mean ice concentration values, and distance to locations with at least two hours of twilight per day for actual wintering positions ($n = 253$; Table 1) with 30 randomly selected locations for each week ($n = 630$) within the potential wintering area. To inspect the difference in mean ice concentrations between penguin locations and random locations, we calculated the univariate kernel density for each type of location using the Epanechnikov kernel function (STATA: kdensity).

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[8] ⟨http://aa.usno.navy.mil/data/docs/RS_OneDay.php⟩
[9] ⟨http://rkwok.jpl.nasa.gov/icemotion/download_MV.html⟩
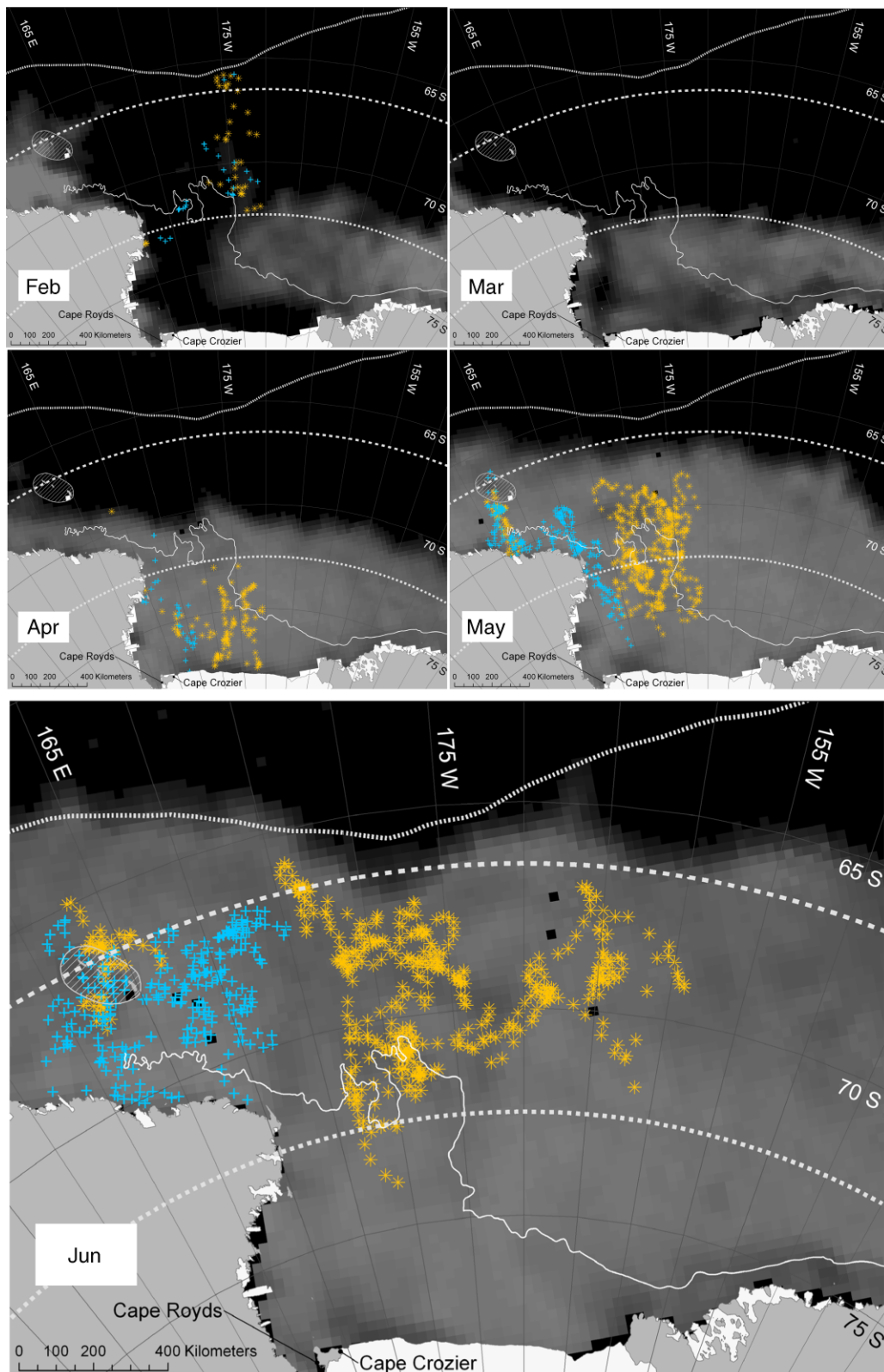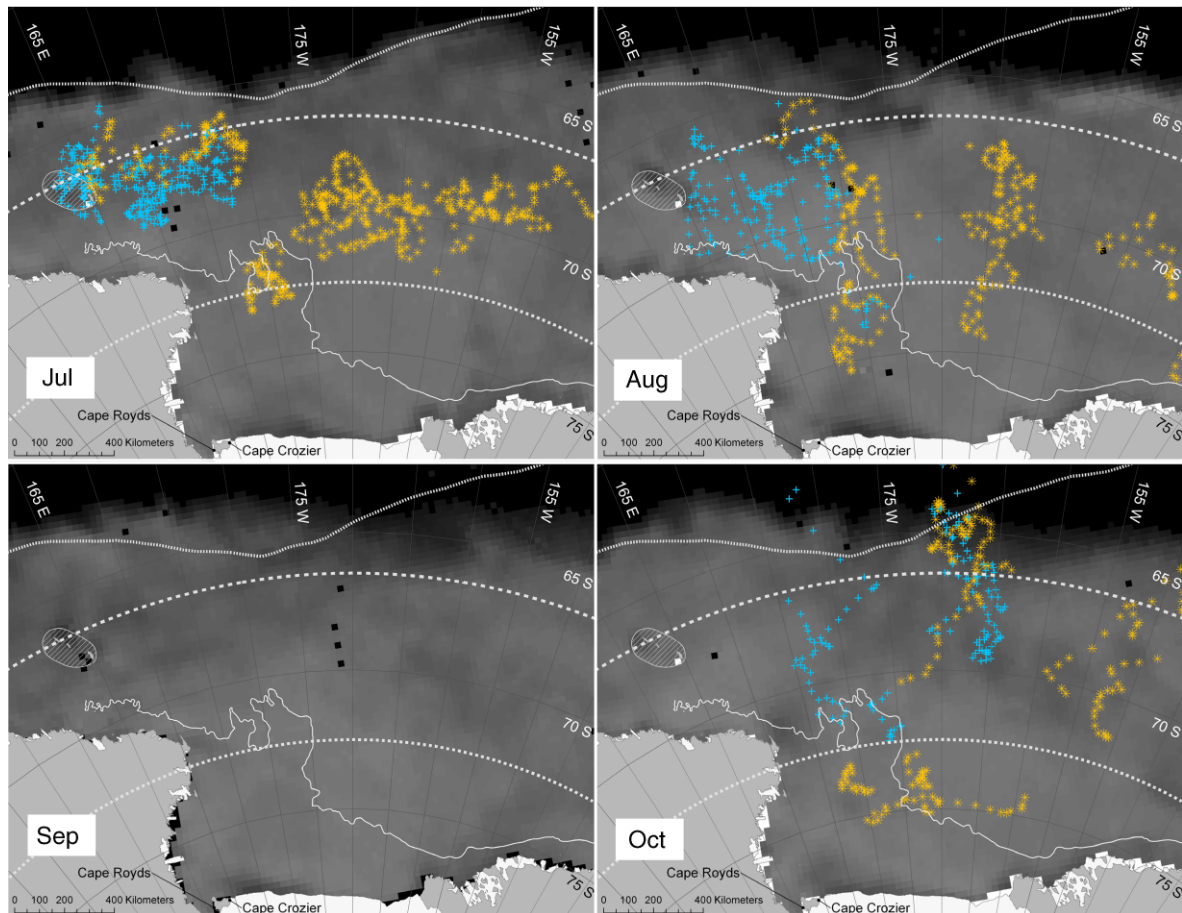
(Fig. continues on next page)

Fig. 1. Adélie Penguin locations and sea ice concentration and distribution for February–October 2004 (for 2003–2005 see Appendix A: Fig. A1). Penguin locations are excluded for March and September due to inaccuracy in GLS (geolocation sensor) positions near equinoxes (see *Materials and methods*). Sea ice concentration was derived from the Special Sensor Microwave Imager on board the F13 satellite of the Defense Meteorological Satellite Program. Black is ocean; light colors represent sea ice (lighter = higher ice concentration). Orange starbursts are Cape Crozier penguins; blue crosses are Cape Royds penguins as determined by GLS tags. The average southern boundary of the Antarctic Circumpolar Current is shown near the top of each image (fine dotted line), along with the Antarctic Circle (more northerly latitude line, bold dotted) and the latitude of zero winter twilight (72.7° S, lower medium dotted line). The Ross Sea shelf break is indicated with a solid white line (2000-m isobath; Davey 2004), and the average location of the Balleny Island polynya is indicated with a gray hatched oval (based on combined winter sea-ice data 2003–2004). The Ross Ice Shelf is at the center of the bottom of each image. Base map layers are from British Antarctic Survey (1998). Small black squares and polygons are missing sea ice data; white squares and polygons are "masked" during the data processing by NSIDC (i.e., no ice values were calculated for those cells because of their proximity to land or ice shelves).

The random locations were assessed so that we could compare characteristics of places that penguins utilized with ones that were available to the penguins but not necessarily occupied. For all analyses of wintering areas, we used positions from 1 June to 31 July. This period corresponds to the peak of winter darkness, and the time for which we had the most consistent position data.

After determining the mean distance from the ice edge for wintering penguins, we calculated the minimum date that penguins reached this distance in each year (necessary only for penguins that did reach this distance); this was a proxy for "wintering-area arrival date." We defined the northward migration period in days as winter-area arrival date minus 5 February (the approximate mean departure date; G. Ballard and D. Ainley, *personal observations*), and northward migration speed is the distance from the colony on the winter arrival date/northward migration period. We used ANOVA to evaluate effects of colony and year on northward migration speed.

We calculated the maximum distance that penguins reached during winter, and the time it took to reach that point and to return from that point (assuming an average arrival date of 1 November; G. Ballard and D. Ainley, *personal observation*) for each individual in each year. We used ANOVA to evaluate effects of colony and year on arrival dates to the maximum wintering distance, and on average speed sustained to reach and return from the maximum wintering distance.

We used mixed-effects general linear models with ID treated as a random effect to evaluate whether latitude, longitude, twilight period, distance to ice edge, and sea-ice concentration varied by colony and year. Twilight hours were squared and ice concentration values were arcsine square-root transformed in order for model residuals to comply with assumptions of normality; other terms met model assumptions without transformation. All statistical tests were conducted using STATA v. 10 (Stata Corporation 2008). We report means ± SE throughout.

RESULTS

General migration patterns

At-sea movements.—The migration of most Adélie Penguins from Cape Crozier roughly followed a clockwise course (Fig. 1; see Appendix B), as follows: (1) in February, birds migrated toward the NNE toward the nearest residual pack ice (eastern Ross Sea), where they began molt (Fig. 2); (2) during molt, resting on an ice floe for 3 weeks, they moved northward and somewhat westward in a pattern consistent with pack ice movement (Appendix C); (3) by late fall and early winter, probably as a result of ice flow, they were located in the pack ice in the vicinity of the continental shelf break; (4) subsequently, they moved farther north, occasionally visiting the Balleny Islands Polynya (an area of open water in the ice pack) but otherwise remaining relatively near the large-scale ice edge, which generally occurs between the Antarctic Circle and the Antarctic Circumpolar Current (ACC) southern boundary; once out of the Ross Sea they became entrained in the Ross Gyre (see Jacobs et al. 2002: Fig. 1), which prevented them from being advected much farther away from Ross Island (Fig. 1; Appendices B and C); (5) by late winter they moved with the ice eastward along the ice edge; and (6) in late September and October they moved south and then west, returning to their breeding colonies. The general pattern of movement for penguins from Cape Royds was north through the various polynyas along the way, finally reaching the large-scale ice edge somewhat west of most of the individuals breeding at Crozier, and then movement east and south against the flow of ice in the spring (Fig. 1; Appendices B and C).

Overall, penguin movement speed was correlated with ice movement speed ($\beta = 5.45 \pm 1.18$ km/d, $Z = 4.60$, $P < 0.0001$; $n = 11$ individuals, 336 positions). We did not detect a correlation between penguin and ice movement direction ($r = 0.028$, $P = 0.76$), although the relationship with speed supports the concept that penguins were generally moving in the same direction as the ice.

Trip length.—Trip length (including all meanders) for all years was $12\,760 \pm 468.9$ km, mean ± SE ($n = 41$, range 8539–17 600 km). Trip lengths varied annually ($F_{2,27} = 29.65$, $P < 0.0001$), but not by colony ($F_{1,27} = 0.08$, $P = 0.78$). In 2003 penguins made longer trips than in 2004 and 2005 ($P < 0.0001$). Maximum great-circle distance that penguins journeyed from home colonies averaged 1722 ± 66.3 km ($n = 41$, range 946–2552 km) and also varied by year ($F_{2,38} = 4.96$; $P = 0.01$) but not by colony ($F_{1,38} = 0.55$, $P = 0.46$).

Traveling speed.—Penguins reached their first wintering locations in mid-to-late June each year (mean date 20 June ± 1.7 d) and reached their maximum distance from colonies in mid-July to early August (mean date 22 July ± 11.9 d). Penguins traveled more rapidly while returning from their maximum wintering distance than they did while reaching this distance (31.71 ± 3.73 km/d [mean ± SE] vs. 15.09 ± 1.99 km/d, respectively; $t = -3.93$, $P = 0.0001$). Travel speeds to and from this distance did not vary by colony or year (for all tests, $P > 0.10$). Penguins were also faster returning from their maximum distance than they were arriving at their first wintering location (10.35 ± 0.40 km/d). Penguins traveled northward to their first wintering locations more swiftly in 2003 than in 2004 or 2005 (12.34 ± 0.60 vs. 9.52 ± 0.41 km/d and 9.21 ± 0.58 km/d, respectively; $F_{2,30} = 11.22$; $P = 0.0003$), but no colony effect was evident ($F_{1,30} = 1.42$; $P = 0.24$).

Wintering areas

Overall mean latitude of wintering positions for Crozier penguins was $68.81° S \pm 0.50°$ ($n = 26$) and for Royds penguins was $68.29° S \pm 0.59°$ ($n = 15$). Mean longitude for Crozier penguins at $175.29° W \pm 1.87°$ was quite disparate from that of Royds penguins, $176.44° E \pm 2.86°$ (note the E–W difference). Latitude was significantly affected by year ($Z = -4.59$, $P < 0.0001$; Table 1) but not by colony $Z = 1.31$, $P = 0.19$), whereas longitude was significantly affected by colony ($Z = -2.76$, $P = 0.006$) but not by year ($Z = 1.73$, $P = 0.08$). Despite the large spatial spread in wintering locations and the relatively smaller sample size from Cape Royds, in all years Royds birds wintered west of Crozier birds ($8.27°$ average difference; Fig. 3).

Arrival week at the first winter location was most commonly between 11 and 17 June and varied among years (week 23 in 2003, week 25 in 2004 and 2005; $F_{2,29} = 15.16$, $P < 0.0001$) but not colonies ($F_{1,26} = 2.88$, $P = 0.10$). Arrival date at the maximum distance from the colony averaged 22 July ± 11.92 d, not consistently varying among colonies or years ($F_{3,38} = 0.56$, $P = 0.64$).

Characteristics of wintering area

Ice extent and concentration.—Ice extent in the combined potential penguin wintering area varied annually, with 2003 having the largest extent in March–June, 2004 being intermediate, and 2005 having the least (Fig. 1; see Appendix B). Maximum ice extent was reached earliest in 2003 and latest in 2005. Ice concentration at random locations in the penguin wintering area was highest in 2003 ($80.9\% \pm 1.3\%$) and lower in 2004 and 2005 ($75.0\% \pm 1.5\%$ and $75.5\% \pm 1.5\%$; $F_{2,627} = 4.87$, $P = 0.008$).
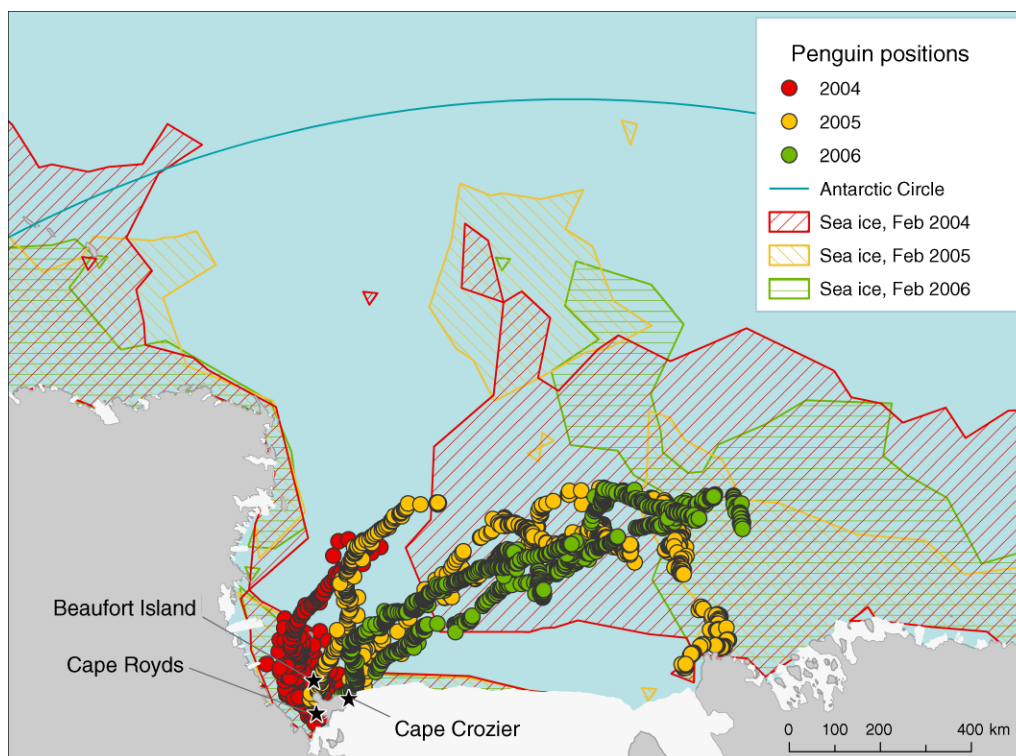
FIG. 2. Adélie Penguin positions in relation to sea ice distribution (indicated for each year by cross-hatched areas) in the post-dispersal/pre-molt period, late January to late February, 2004–2006. Penguins from three colonies (Capes Royds, Crozier, and Beaufort Island, $n = 10$ individuals total) in the southern Ross Sea were tracked using satellite transmitters (platform transmitter terminals, PTTs) until batteries failed or PTTs were molted off with feathers. Each color for penguin locations matches the color for sea ice during February of the same season. The small triangles are simply small amounts of sea ice, coded as for the larger areas. In general, penguins traveled east-northeast or northeast, usually toward the edge of the pack ice upon leaving the colony. Base map layers are from British Antarctic Survey (1998). Sea ice data are from the Special Sensor Microwave Imager on board the F13 satellite of the Defense Meteorological Satellite Program, 1 February, 2004–2006.

Ice concentrations where penguins were located were approximately the same as at random locations, 79.2% $\pm$ 0.8 % vs. 77.1% $\pm$ 0.86% ($P = 0.16$). Penguins were not found in locations with either 100% or 0% ice cover (Fig. 4). The overall kernel density of penguin location by ice concentration implies that penguins preferred ice cover between ~75% and 85%, whereas random locations reached highest density between 80% and 90%.

We did not detect a difference in ice concentration at wintering locations by colony ($n = 253$ positions for 41 individuals, $Z = 1.09$, $P = 0.28$) or by year ($Z = 1.52$, $P = 0.13$; Table 1).

Distance to ice edge (15% ice concentration contour).—Penguins almost never ventured north of the large-scale ice edge (4 of 253 weekly positions = 1.6%), whereas random points were more often located north of the edge (i.e., in open water; 31 of 630 positions = 4.9%). Among positions north of the ice edge, penguins averaged only 17.7 $\pm$ 6.5 km while random points averaged 89.5 $\pm$ 11.5 km ($P = 0.03$). Taking the entire potential wintering area into account, penguins averaged

510.4 $\pm$ 14.6 km south of the ice edge while random points averaged 619.5 $\pm$ 16.4 km ($P = 0.0001$).

Distance to the large-scale ice edge did not vary by colony ($Z = 0.40$, $P = 0.69$), but did vary by year ($Z = -3.96$, $P < 0.0001$; Table 1), with 2003 having the shortest distances and 2005 the longest.

Distance to daylight, amount of light available.— Winter penguin positions averaged 533.8 $\pm$ 18.0 km north of the latitude of zero twilight, 121 km farther north from this line than randomly generated points ($P < 0.0001$; Fig. 4). They averaged 52.6 $\pm$ 18.0 km south of the latitude of zero day length, so sunrise/sunset was not an important determinant of wintering location, whereas the availability of twilight was. Penguins' positions averaged 1.27 $\pm$ 0.10 h of daylight and 5.07 $\pm$ 0.10 h of twilight, compared with 1.41 $\pm$ 0.07 and 4.16 $\pm$ 0.11 h (respectively) for random locations.

The amount of twilight available to wintering penguins varied by year ($Z = -4.72$; $P < 0.0001$) but not by colony ($Z = 1.32$ $P = 0.19$). Penguins experienced 0.94 and 2.03 fewer twilight hours in 2004 and 2005 than in 2003, respectively (Table 1).
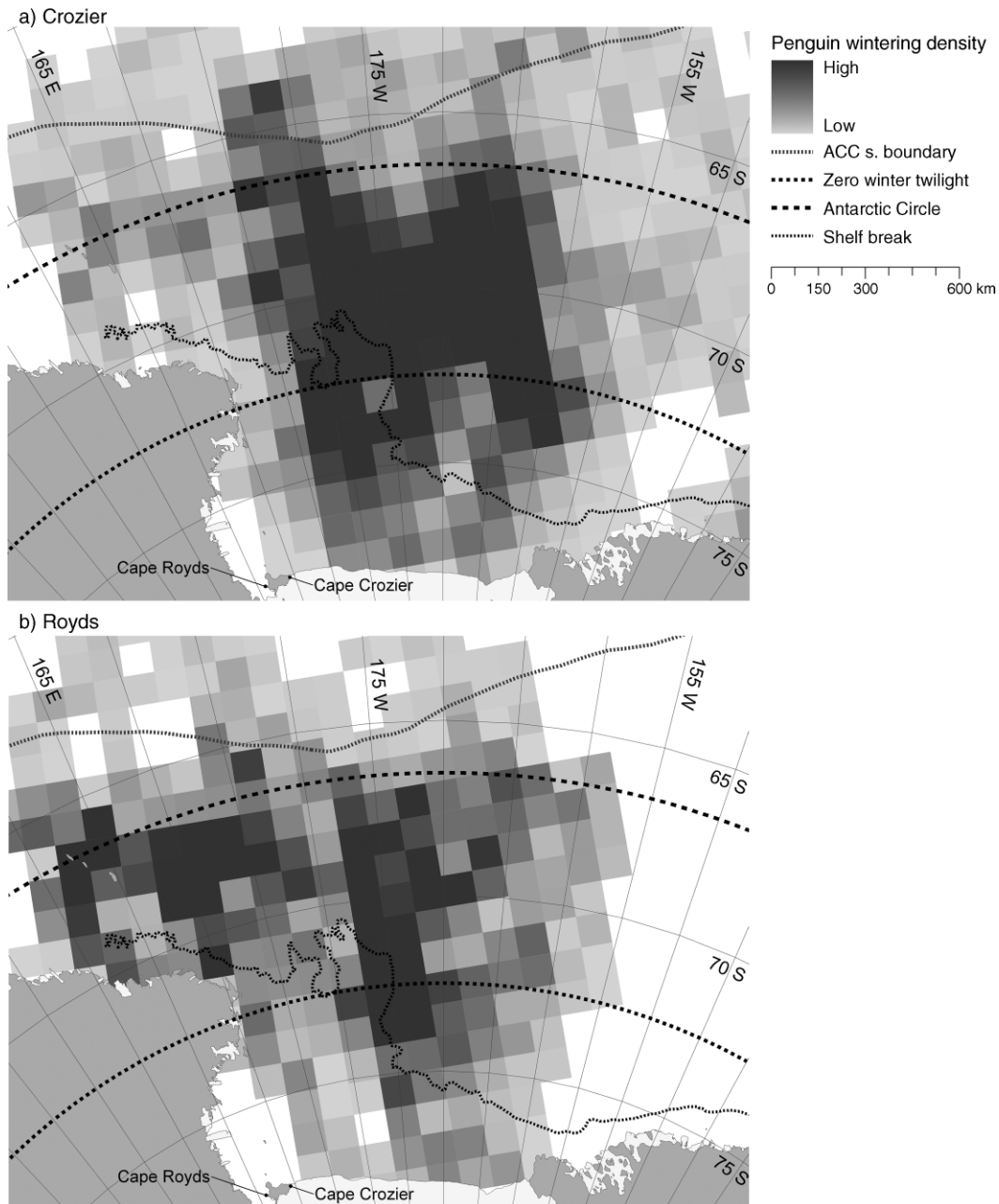
FIG. 3.   Relative wintering density of penguins by colony June–July 2003–2005: (a) Cape Crozier, (b) Cape Royds. Kernel density was calculated from geolocation sensor data for a 100-km grid using the Spatial Analyst extension for ArcGIS version 9.2 (ESRI 2006). Base map layers are from British Antarctic Survey (1998; land and ice shelves), Davey (2004; bathymetry), Orsi et al. (1995; Antarctic Circumpolar Current [ACC] southern boundary), and U.S. Naval Observatory (⟨http://aa.usno.navy.mil/data/docs/RS_OneDay.php⟩; latitude of zero winter twilight).

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DISCUSSION

Ocean, ice, and biological boundaries

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Several factors appear to affect penguin migratory and winter movements: (1) annual sea ice motion and extent; (2) the seasonal shortening and lengthening of daylight; (3) the location of polynyas; (4) the location of the rich waters of the Antarctic Slope Front (Ainley and Jacobs 1981, Jacobs 1991); and (5) differences in timing of departure from the breeding colony. Sea ice dictates the maximum and mean latitudes where Ross Island penguins will spend midwinter. As noted by Clarke et al. (2003) and confirmed by our study, oceanic gyres, especially during molt when the birds are moving

passively on an ice floe, determine much of the migration route.

Ross Island penguins face the greatest distance of any Adélies between their breeding colony and the vicinity of the Antarctic Circle, the location where sufficient light and divergent sea ice are reliably available during midwinter, a distance of 16° latitude (1778 km). In contrast, Adélie Penguins studied at Prydz Bay, Princess Elizabeth Land (69° S; Clarke et al. 2003), Anvers, and the South Shetland Islands (62–64° S; Fraser and Trivlepiece 1996), breeding close to if not north of the Antarctic Circle, would need to travel only as far as the nearest divergent sea ice. That means for Prydz Bay birds about 5° latitude north; for Anvers Island birds about 3° latitude south; and for South Shetland birds, about 10–15° longitude southeast (equivalent distance to about 4° latitude). Therefore, as currently there are no Adélie Penguin colonies south of 64° S in the Weddell Sea (Woehler 1993), the Ross Island penguins make the longest migration of this species, traveling as far as 17 600 km round trip between autumn and spring.

Our results are consistent with a previous study (Emlen and Penney 1964, Penney and Emlen 1967) showing that displaced penguins from Ross Island immediately headed NNE, as well as with the study by Davis et al. (1996, 2001), who tracked post-molt penguins from Cape Bird, Ross Island (77° S), and Cape Hallett, Victoria Land (72° S), and showed that in each instance ($n = 3$) the birds wintered near the Balleny Islands. In the latter study, all the birds were among a very small minority of birds that had molted at the colonies and thus had a relatively late start on migration, as was true of the Royds birds in our study. The difference in timing and direction of departure between birds in our study (presumably pre-molt) and in Davis et al. (1996, 2001) (post-molt) is probably due to difference in ice conditions encountered by the two groups. The initial NE direction of the pre-molt birds in our study might also be a way for the birds to compensate for the northwest circulation of the Ross Sea Gyre while moving north (Penney and Emlen 1967, Ainley 2002).

For Ross Island penguins, polynyas may provide important "stepping stones" on the way to the outer edge of the pack ice, especially the Pennell and Ross Passage polynyas (see Jacobs and Comiso 1989), which are located along the autumn migratory route, and the Balleny Islands Polynya, one of only a few polynyas in the Antarctic that is not along the continental coast and lies closer to the large-scale ice edge. In the autumn and winter, these stretches of open water are likely to be full of life (including penguins, seals, whales, and their prey), although little is known about the mid- to upper-trophic-level ecology of these open areas in the Antarctic ice pack (see Smith and Barber 2007).

Timing of departure at Cape Royds is delayed by a week or more compared to birds at Cape Crozier. Unique to Cape Royds, at such high latitude, about one-
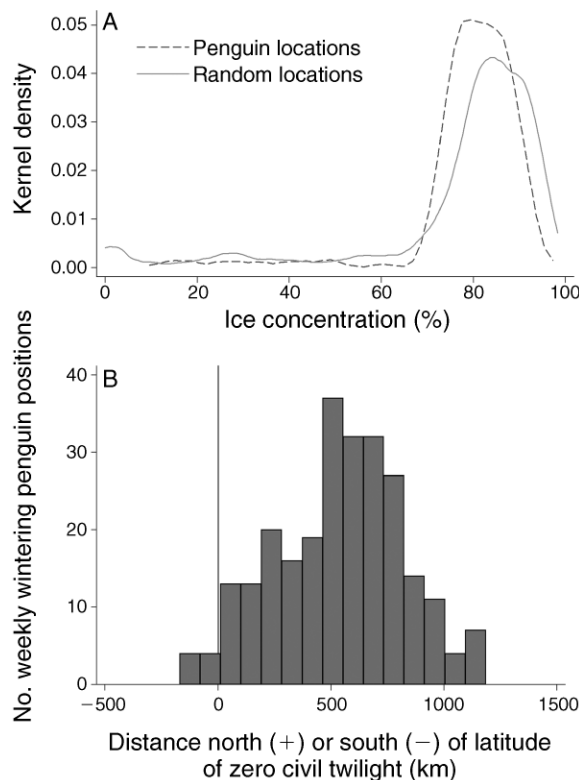

Fig. 4. Characteristics of penguin wintering locations (June–July 2003–2005). (A) Kernel density in relation to ice concentration for 253 penguin locations compared with 630 random locations. Kernel densities of real and randomly generated positions were estimated for the full range of sea ice concentration possible (for each 2% increment, 0–100%) using the Epanechnikov kernel function to extrapolate distributions from the samples. (B) Penguin locations in relation to distance from the latitude of zero twilight.

third or more of the population also molt at the colony (Taylor 1962). This means that departure may be delayed by as much as a month compared to Cape Crozier. Birds that depart later are likely to encounter more consolidated pack ice, but also a stream of relatively rapidly northward-moving ice in the western Ross Sea (Appendix C; also see Jeffries and Kozlenko [2002], who report monthly average buoy drift up to 16 km/d in this area). In any case, the fact that they usually spend the winter 8° west of Crozier penguins means that their return to Cape Royds may more commonly be against a stronger flow of ice than what Crozier penguins encounter (Appendix C). It also might mean that they spend their winters in the vicinity of many more penguins from other colonies, with potential consequences to food availability (Ainley et al. 2004) and energy expenditure (Ballance et al. 2009). However, return trip travel speeds for Royds penguins did not differ from Crozier penguins, so if they were handi-capped by fighting stronger currents, they were able to compensate, potentially by expending more energy. This could help to explain why Cape Royds phenology is

delayed compared to Cape Crozier, and may also have negative consequences to over-winter survival (K. Dugger, D. Ainley, and G. Ballard, *unpublished data*). It does not seem to affect breeding success or fledging mass of chicks (Ainley et al. 2004). We did not discover any other differences in wintering area characteristics between the two colonies at the scale permitted by our methods.

Wintering areas of Ross Island penguins were at the edge of the consolidated pack ice (and the edge of darkness), well back from the large-scale ice edge itself. This was contrary to our expectations, which were based on a previous winter observation that Adélie Penguins were most concentrated in a belt ~100 km inside the large-scale edge, but not necessarily at the edge of the consolidated pack in the Weddell Sea; they appeared to be avoiding only the outermost area where ice extent expands and contracts weekly, depending on wind strength and direction (Ainley et al. 1993). Judging from the eastward gradient in longitudinal dispersion of penguins, these birds originated from colonies at the tip of the Antarctic Peninsula (Ainley et al. 1993). Assuming that Ross Sea penguins could also occupy a habitat of relatively lower ice concentration, there potentially exists a wide swath with few Ross Island penguins between the 75–85% ice cover where we found them wintering and the 15% ice edge farther north. One factor that could help to explain this pattern, and the differences from that of the Weddell Sea, is the probable unusually high density of penguins in this more northern extent of the Ross Sea pack. Of the world's population of Adélie Penguins, 30% (i.e., 1.5 million breeders, plus nonbreeders) are associated with the northern Victoria Land colonies (e.g., Cape Hallett north to Cape Adare) compared to fewer penguins found over a much larger area in the western Weddell Sea (1.1 million breeders) from the South Shetlands, South Orkneys, and northern Antarctic Peninsula coast (see Woelher 1993). In other words, we hypothesize that the Ross Island/southern Victoria Land penguins (0.75 million breeders) would winter farther north were it not for the probable presence of huge numbers of penguins from northern Victoria Land already wintering there, because we have shown that penguins adjust their foraging areas in response to both inter- and intraspecific competition (Ainley et al. 2004, 2006). However, it is also possible that the Ross Island penguins simply try to stay as close to their home colonies as possible, given light and ice conditions, reducing the amount of time and energy required to return for breeding. In addition, they appear to remain, as long as ice conditions allow, in the vicinity of the Ross Sea continental slope and the Antarctic Slope Front, an exceedingly rich area (Ainley et al. 1984). No studies on the migration of Adélie Penguins in northern Victoria Land have been conducted to address these hypotheses.

In years of more extensive ice, the zone of consolidated ice shifts north (sea ice extent and sea ice concentration covary at the large scale; Jacobs and Comiso 1989, Stammerjohn et al. 2008) and, as we observed, shifts the wintering area of Ross Island penguins farther north as well. This would move the penguins away from the Slope Front and closer to the ACC Southern Boundary, across which there is less food available (Tynan 1998, Nicol et al. 2000), and perhaps would also add to the density of the northern Victoria Land wintering penguins.

Astronomical boundaries

Our finding that the penguins are limited by the availability of twilight, and not necessarily daylight, is consistent with the findings of Emlen and Penney (1964) and Penney and Emlen (1967), who found that Adélie Penguins' navigational ability is challenged by the lack of sunlight. As they and others have noted (summarized in Ainley 2002), penguins remain in place where they have no geographic navigational cues and when the sun is not shining. The slow northward migration of Ross Island penguins in our study is probably the result of being advected with the ice upon which they spend most of a day, rather than swimming and actually navigating. The fact that the penguins travel much more quickly when going south during the spring migration, much faster than ice motion, is consistent with movement guided by sun navigation.

However, Adélies (and all penguins) require some light in order to forage, although apparently less than is required for navigation. Wilson et al. (1993) found that Adélies made most of their foraging dives to depths where there was at least 1 lux of light available, and that foraging depth and success were much lower during darkness than during daylight. The range of light available at the surface during civil twilight ranges from 3.4 to 400 lux (Bond and Henderson 1963), so some shallow diving would be possible even at the darkest end of this range; during darker hours, prey are likely to migrate closer to the surface, where they would be silhouetted against the surface/sky (Wilson et al. 1993, Fuiman et al. 2002).

Migration and long-term sea ice variability

The ability to migrate over the long distances exhibited by Ross Island Adélie Penguins may be an ongoing adaptation in the evolution of the species, and (if such adaptation has a genetic basis, as has been shown in at least one other organism; Zhu et al. 2009) seemingly within the genetic plasticity documented at the millennial (1000-yr) timescale for this species (Shepherd et al. 2005). At the Last Glacial Maximum (LGM, ~19 000 yr BP), the West Antarctic Ice Sheet (WAIS) covered most of the Ross Sea (Anderson 1999). Given that the Ross Sea Adélie Penguin has a genome that differs from members of this species in all other regions (Roeder et al. 2001), and that any offshore islands in the Pacific sector (of which there are very few) were almost certainly ice covered (e.g., Balleny Islands,

Scott Island; Anderson 1999), a Ross Sea colony probably existed during the LGM. Ainley (2002) proposed that Cape Adare was the likely location, because the northwest corner of the Ross Sea has been ice-sheet-free during recent glaciations, unlike the continental shelf everywhere else (which had grounded ice sheets to the shelf break; Anderson 1999), and sediment cores from the vicinity indicate a polynya there (Thatje et al. 2008). Moreover, Cape Adare has been free of land ice for ~16 000 yr (Johnson et al. 2008), i.e., going back to nearly the ice maximum and before retreat of the WAIS across the Ross Sea began. Although evidence of colonies near Cape Adare from this time period has not been discovered, such locations may now be underwater as a result of the 120-m sea level rise since the LGM (an option in data interpretation left open by Emslie et al. [2007]). Beginning about 12 000 yr BP, the WAIS began to withdraw south, exposing new, suitable nesting habitat along the Victoria Land coast. Adélie Penguins colonized the Victoria Land coastline sporadically southward, depending on sea ice concentration (Emslie et al. 2003, 2007), breeding farther and farther from the large-scale winter sea ice edge, the Antarctic Circle, and winter daylight. However, at the southernmost extent of the current range (Cape Royds), the penguin breeding period is already significantly shorter than at colonies farther north, and probably could not be shortened further (Ainley 2002). Therefore it seems unlikely that this species would colonize terrain south of the current WAIS boundary, were it available, even if the species is forced to retreat from lower latitudes as sea ice disappears (Ainley et al. 2010).

In summary, the life history patterns of the Adélie Penguin have been in a state of flux, owing largely to adjustments in migratory behavior and routes. Although the species apparently has contended with this successfully throughout its 3 million year history, as ice ages have come and gone with coincident changes in breeding and sea ice habitat, the current rate of habitat change may be unprecedented for this species. We predict that the response of Adélie Penguins to the large-scale decrease in sea ice projected by climate models (Ainley et al. 2010) will be affected by migratory adjustments to the spatial availability of light before the pack ice disappears entirely.

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APPENDIX A

A table showing GLS (geolocation sensor) deployment and retrieval dates, locations, and sample sizes (*Ecological Archives* E091-142-A1).

APPENDIX B

A figure showing GLS-derived penguin locations and sea ice concentration and extent, 2003–2005 (*Ecological Archives* E091-142-A2).

APPENDIX C

A figure showing monthly average ice flow vectors for March, June, and September 2003 (*Ecological Archives* E091-142-A3).

Ecological Archives E091-142-A1

Grant Ballard, Viola Toniolo, David G. Ainley, Claire L. Parkinson, Kevin R. Arrigo, Phil N. Trathan. YEAR. Responding to climate change: Adélie Penguins confront astronomical and ocean boundaries. *Ecology* 91: 2056-2069.

Appendix A (table A1). GLS (geolocation sensor) deployment and recovery locations, timing, and sex for Adélie penguins on Ross Island. Number retrieved functioning is listed in parentheses, 3 more tags were retrieved after 2 -3 winters but were not included in these analyses.

| Date	Location	# Deployed			# Retrieved after 1 winter		
		Male	Female	Unk.	Male	Female	Unk.
Jan. 2003	C. Crozier	13	5	0	12 (7)	4 (1)	0
Feb. 2003	C. Royds	6	4	0	5 (1)	2 (2)	0
Jan. 2004	C. Crozier	7	9	4	3 (2)	6 (3)	4 (3)
Jan. 2004	C. Royds	7	14	0	5 (2)	7 (3)	0
Jan. 2004	C. Crozier	Reference tags (3)					
Jan. 2004	C. Hallett	Reference tags (3)					
Jan. 2005	C. Crozier	11	6	3	7 (5)	4 (3)	2 (2)
Jan. 2005	C. Royds	7	3	5	4 (4)	2 (2)	1 (1)
Totals		51	41	12	37 (16)	25 (13)	7 (4)
		104 total deployed			68 total retrieved (41 functioning)		

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Appendix B. Penguin locations and sea ice concentration and extent for February - October, 2003-2005. Penguin locations are excluded for March and September due to inaccuracy in GLS positions near equinoxes (see text). Sea ice concentration was derived from the Special Sensor Microwave Imager on board the F13 satellite of the Defense Meteorological Satellite Program. Black is ocean, light colors represent sea ice (lighter = higher ice concentration). Orange starbursts are Cape Crozier penguins, blue crosses are Cape Royds penguins as determined by GLS tags. The average southern boundary of the Antarctic Circumpolar Current is shown near the top of each image, along with the Antarctic Circle (more northerly latitude line) and the latitude of zero winter twilight (72.7° S). Ross Sea shelf break is indicated with solid white line (2000 m isobath; Davey 2004), and the average location of the Balleny Island polynya is indicated with gray oval with cross-hatching (based on combined winter sea-ice data 2003-2004). The Ross Ice Shelf is at the center of the bottom of each image. Base map layers are from British Antarctic Survey (1998).

2003
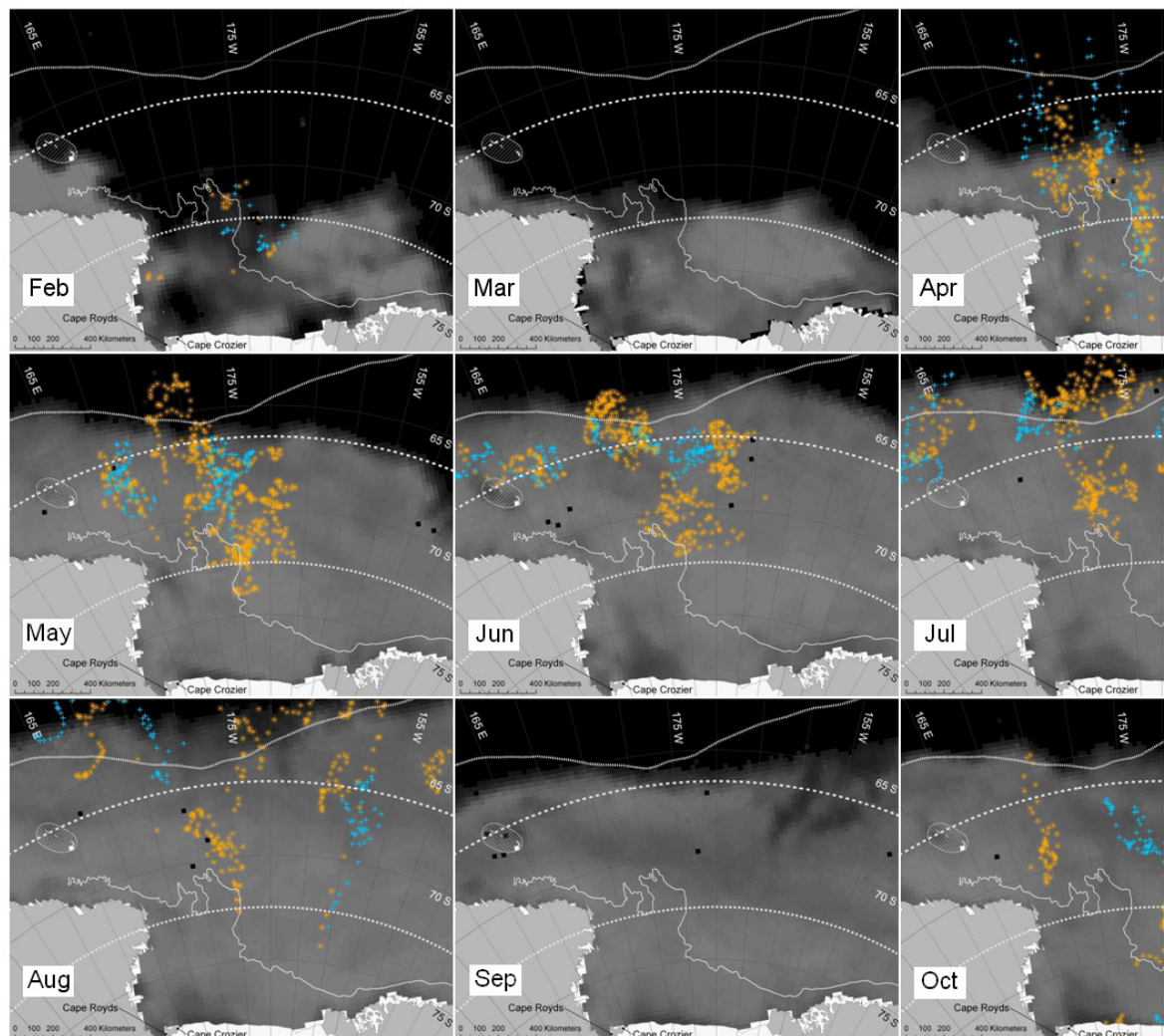
2004
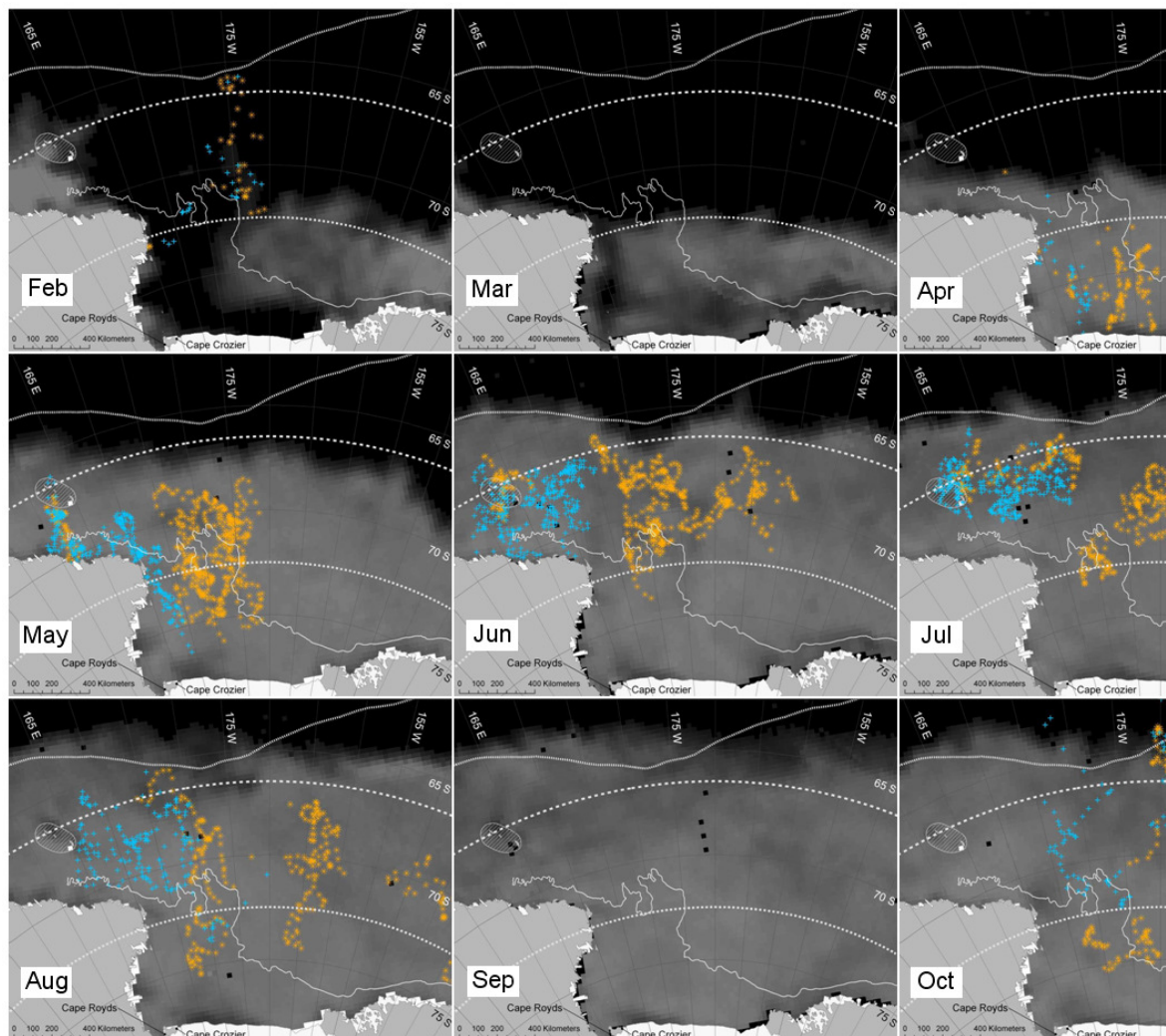
2005
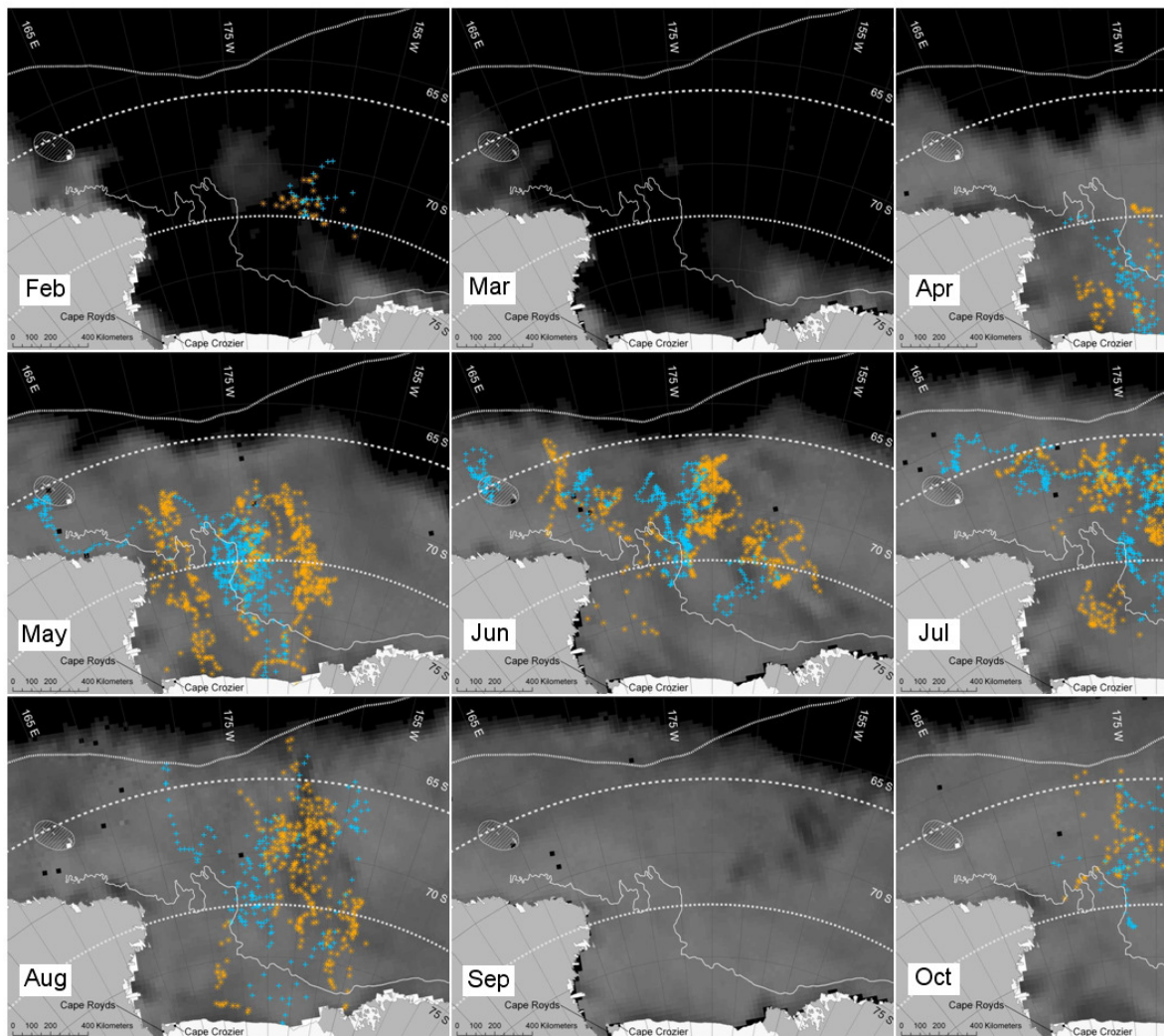
References Cited:

British Antarctic Survey. 1998. Antarctic Digital Database, Version 2.0. Manual and bibliography. Scientific
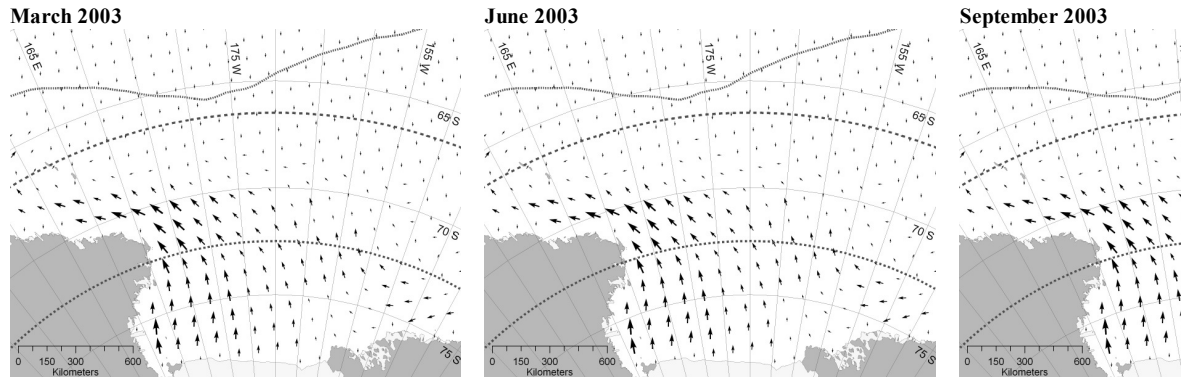Committee on Antarctic Research, Cambridge. 74 pp.

Davey, F. J., 2004, Ross Sea Bathymetry, 1:2,000,000, version 1.0, Institute of Geological & Nuclear Sciences
geophysical map 16, Institute of Geological & Nuclear Sciences Limited, Lower Hutt, New Zealand.

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Ecological Archives **E091-142-A3**

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Appendix C. Monthly average ice flow vectors for March, June, and September 2003 (the last year for which data are available) obtained from the Polar Remote Sensing Group of the Jet Propulsion Laboratory. Arrow size represents speed of ice movement (larger = faster), direction represents bearing. Base map layers are from British Antarctic Survey (1998).

References Cited

British Antarctic Survey. 1998. Antarctic Digital Database, Version 2.0. Manual and bibliography. Scientific Committee on Antarctic Research, Cambridge. 74 pp.

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