

Intra-seasonal variation in foraging behavior among Adélie penguins (*Pygoscelis adeliae*) breeding at Cape Hallett, Ross Sea, Antarctica

P. O'B. Lyver · C. J. MacLeod · G. Ballard ·
B. J. Karl · K. J. Barton · J. Adams ·
D. G. Ainley · P. R. Wilson

Received: 6 July 2009 / Revised: 2 April 2010 / Accepted: 11 May 2010 / Published online: 15 July 2010
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Abstract We investigated intra-seasonal variation in abundances of this species throughout its range, but we lack information about how intra-specific competition for *Pygoscelis adeliae*, during two consecutive summers at Cape Hallett, northwestern Ross Sea. Although foraging behavior of this species has been extensively studied throughout the broad continental shelf region of the Ross Sea, this is the first study to report foraging behaviors and habitat affiliations among birds occupying continental slope waters. Continental slope habitat supports the greatest

P. O'B. Lyver (✉) · B. J. Karl
Landcare Research, P.O. Box 40,
Lincoln 7640, New Zealand
e-mail: lyverp@landcareresearch.co.nz

C. J. MacLeod
Landcare Research, Private Bag 1930,
Dunedin 9054, New Zealand

G. Ballard
PRBO Conservation Science, Petaluma, CA 94954, USA

G. Ballard
Ecology, Evolution, and Behaviour, School of Biological
Sciences, University of Auckland, Auckland, New Zealand

K. J. Barton
Landcare Research, Nelson Mail Centre,
Private Bag 6, Nelson 7042, New Zealand

J. Adams
Western Ecological Research Center, US Geological Survey,
Pacific Science Center, 400 Natural Bridges Drive,
Santa Cruz, CA 95060, USA

D. G. Ainley
H.T Harvey and Associates, 983 University Avenue,
Building D, Los Gatos, CA 95032, USA

P. R. Wilson
17 Modena Crescent, St Heliers, Auckland, New Zealand

slope habitats elsewhere in Antarctic waters, Antarctic krill (*Euphausia superba*) dominated chick meal composition, but fish increased four-fold from guard to creche stages. Foraging-, focal-, and core areas all doubled during the creche stage as individuals shifted distribution in a southeasterly direction away from the coast while simultaneously becoming more widely dispersed (i.e., less spatial overlap among individuals). Intra-specific competition for prey among Adélie penguins appears to influence foraging behavior of this species, even in food webs dominated by Antarctic krill.

Keywords Adélie penguin · Foraging · Intra-seasonal competition · Pack ice · Antarctic krill · Antarctic silver fish

Introduction

The diet composition of seabirds varies temporally and spatially (e.g., Murphy 1925; Ashmole and Ashmole 1967; Ainley and Boekelheide 1990). To cope with such variability, brought by abiotic (e.g., climate cycles, proximity to productive fronts) and biotic (e.g., prey life cycles, inter- and intra-specific competition) factors, seabirds demonstrate the ability to adjust to constraints imposed by morphological, physiological, and behavioral characteristics

(references above; also Ballance et al. 2001; Tremblay and Chelton 2003; Ballard et al. 2010a, b). 2008) requires breeding Adélie penguins to have adaptable foraging behaviors. Even so, in some regions of Antarctica

During the last 3–4 decades, increased variability, and a (i.e., Antarctic Peninsula), where diversity among prey apparent decline in abundance and availability of mid-trophic level organisms that comprise the prey of top predators (Emslie and Patterson 2007) and inter-specific competition has increased (Ainley et al. 2009), it appears that Adélie penguins can no longer indirectly to climate change and directly to intensive commercial fishing and other direct anthropogenic factors (Pauly et al. 1998; Hilborn et al. 2003; Osterblom et al. 2006, 2007; Hinke et al. 2007; Ainley et al. 2010). Watermeyer et al. 2008a, b, Baum and Worm 2009; Perry et al. 2009). These changes increasingly conflict with the ability of some seabirds to successfully adapt aspects related to their foraging strategies in order to acquire sufficient food resources of varying size and proximity to oceanic features to maintain reproduction and survival (Iverson et al. 2007; Grémillet et al. 2008). Our ability to detect the impacts of changing foraging conditions on seabirds is connected largely to long- and well-studied species including Northern gannet (*Morus bassanus*) (Grémillet et al. 2008), Black-legged kittiwake, *Rissa tridactyla* (Lewis et al. 2001; Daunt et al. 2002; Frederiksen et al. 2004), and Common guillemot (*Uria aalge*) (Osterblom et al. 2006; Wanless et al. 2005). These studies allow comparisons with conditions that occurred during an earlier state (i.e., regime) of a system. Yet, few remaining ocean ecosystems have remained unaffected long-term and large-scale changes and other anthropogenic impacts (Hilborn et al. 2003; Halpern et al. 2008). The Ross Sea (a relatively anthropogenically unaffected and intact ecosystem) provides an exemplary natural laboratory to measure ecosystem variability and ecological processes (Weimerskirch 2001). The ability to cope with such variability and trophic relationships among species (Ainley 2002a, 2004; cf. Leopold 1949).

The Adélie penguin, *Pygoscelis adeliae*, is one of two truly Antarctic penguins (the other being the Emperor, *Aptenodytes forsteri*) and is one of the most extensively studied seabirds in the world (recent research summarized in Ainley 2002b). The Adélie penguin is an obligate pack-ice species that typically forages where sea ice concentration is 20–80% (Fraser and Trivelpiece 1996; Smith et al. 1999; Ballard et al. 2010a) but can also forage in open sea (recently vacated by sea ice) and under pack ice and coastal fast ice (Ainley et al. 1998; Clarke et al. 1998; Rodary et al. 2000; Watanuki et al. 1999; Kato et al. 2003). Off the western Antarctic Peninsula, Adélie penguins concentrate foraging in waters overlying bathymetric complexity at the heads of submarine canyons (Fraser and Trivelpiece 1996; Chapman et al. 2004; Ribic et al. 2008). As central-place foragers, breeding Adélie penguins have limitations to how far they can forage and still effectively provision young (Ballance et al. 2009; Ballard et al. 2010a). To cope with dynamic sea ice conditions, varying prey distribution and availability, and the seasonal flux in potential intra- and inter-specific competitors (Ainley et al. 2004, 2006; Lescroë and Bost 2005; Friedlaender et al. Here, we investigate the degree to which Adélie penguins breeding at Cape Hallett, northwestern Ross Sea (northern Victoria Land coast) altered their foraging behavior during the 2004/2005 and 2005/2006 chick-rearing periods. Whereas the foraging behavior of this species has been well studied in continental shelf ecosystems of the Ross Sea (Clarke et al. 1998; Ainley et al. 2003, 2004; Lescroë et al. 2010), this is the first Ross Sea study to examine penguins foraging in a continental slope-dominated ecosystem, a condition that is similar to most other (non-Ross Sea) investigations. Northern Victoria Land also supports the greatest abundance of Adélie penguins throughout its range. Previous work demonstrated that Adélie penguins at a large colony (Cape Crozier) extended foraging trip duration and diving depth, whereas these patterns were not evident at smaller colonies (Capes Royds and Bird; Ballard 2010). We consider evidence to evaluate the following three hypotheses. First, in the absence of intra-specific prey competition we expected that foraging parameters (foraging trip distance, duration, dive depth, and dive frequency) would not increase as the chick-rearing phase progresses because of Cape Hallett's relatively smaller colony size (19,744 breeding

pairs; Lyver and Barton unpublished data) as compared with large colonies such as Cape Crozier (cf. Ballard 2010). Second, consistent with other studies in the southern Ross Sea and East Antarctica, we expected that the proportion of fish in chick meals at Cape Hallett would increase as the season progresses (Puddicombe and Johns 1988; Clarke et al. 2002; Ainley et al. 2003, 2006). Third, we determined the degree to which Adie penguin foraging areas correlate with characteristics of the physical environment (bathymetry and sea ice). We expected that as sea ice conditions allow space sharing would decrease as foraging areas expanded and shifted northwards toward zones of heterogeneous bathymetry and relatively greater productivity, such as the Ross Sea Continental Slope and Shelf-break Front (Ainley et al. 1984; Fraser and Trivelpiece 1996; Chapman et al. 2004; Ribic et al. 2008).

Materials and methods

We conducted all field work at Cape Hallett, Ross Sea (72°19'S, 170°12'E; Fig. 1) between 20 December and 15 January 2004–2005 and 2005–2006. We attached Smart Position or Temperature Transmitting Tags (SPOT4; $n = 26$; Wildlife Computers, Redmond, WA, USA, 52 g, dimensions: 88 × 25 × 12 mm) or Time Depth Recorders (TDR-Mk9; $n = 26$; Wildlife Computers, 30 g, dimensions: 67 × 17 × 17 mm) to breeding Adie penguins using Tesafilm tape (see Wilson and Wilson 1989 and Ballard et al. 2001 for details on attachment). We randomly selected adult Adie penguins and captured them by hand or with the aid of a landing net during pair change-over during the removal period (i.e., when one or both parent birds are present at the nest; 20–31 Dec) and the chick-rearing period (i.e., when chicks are present at the nest; 1–15 Jan) of the chick-rearing season (Table 1). To aid in the relocation of birds we also attached a small VHF transmitter (TX-Sirtrack, NZ, 15 g, dimensions: 43 × 20 × 10 mm) to the penguin's back feathers just above the SPOT or TDR. We attempted to recover devices from each bird after they completed one foraging trip, but several individuals (19%) completed multiple trips at sea (Table 1).

Satellite telemetry

SPOT tags were set to transmit every 45 s for the first 8 transmissions and then once every 90 s thereafter and programmed to turn off after being dry for 23 h in order to conserve batteries. All transmissions were received and processed using the ARGOS system (CLS Corporation) at Ramonville Saint-Agne, FR). Before analysis, we excluded data collected from one SPOT tag that was attached to an individual's location, we did not interpolate track-line

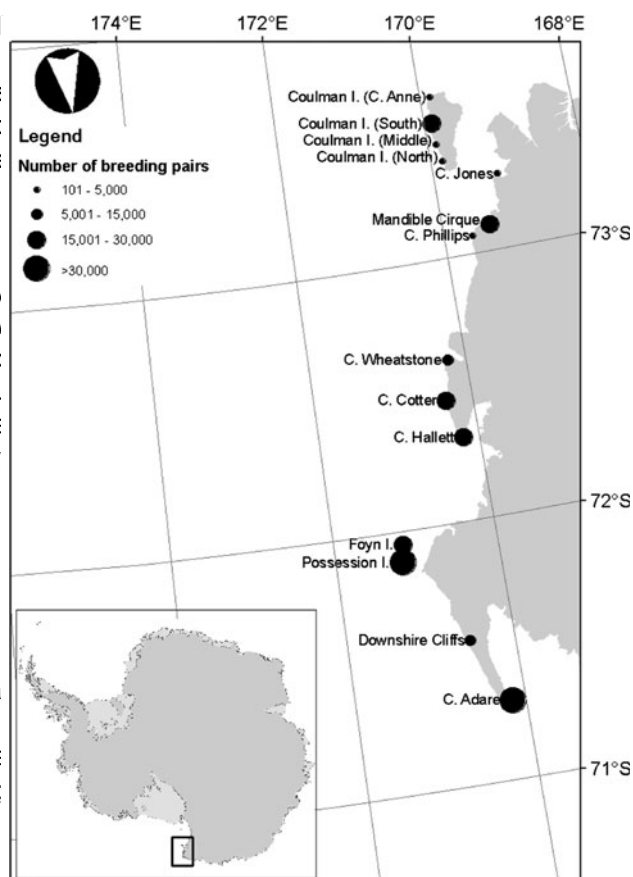


Fig. 1 Location and relative size of Adie penguin colonies in the northern Ross Sea, Antarctica

removed all locations overlapping land/ice shelves or ice tongues outside the colony area. We removed duplicate ARGOS location records (i.e., multiple location records for the same individual recorded within the same minute); in each case we retained the higher-quality location record. To remove potentially erroneous locations for individuals with >4 locations, we used a speed-distance-angle ARGOS filter (Freitas et al. 2008) in the statistical program R (version 2.6.1; R Development Core Team 2007). We specified a maximum speed threshold of 2.2 m s⁻¹ (Ainley 2002b) and used default settings for distance and angle (Freitas et al. 2008). Because the first two and last two locations (i.e., end locations) along each track were retained automatically by the SDAfilter, we then used a purpose-built function to remove

potentially erroneous end locations from the track when the maximum speed threshold 2.2 m s⁻¹ was exceeded.

We used the filtered data and a custom function in MATLAB (MathWorks 2007) to create linearly interpolated locations (Tremblay et al. 2006) every half an hour along each individual track line. To avoid misrepresentation of an individual's location, we did not interpolate track-line

Table 1 Summary satellite tracking data collected from 27 Adelie penguin adults tagged at Cape Hallett breeding colony Ross Sea, including the dates that tags were deployed and retrieved

Bird ID	Breeding season	Stage	Deployment (Julian day)*	Retrieval (Julian day)*	No. of locations for complete track			No. of foraging trips	1st foraging trip	
					Pre-Iter	Post-Itered	Interpolated		No of locations	Final location within 3 km of colony
1	2004/2005	Guard	356	359	17	12	22	1	21	n
2	2004/2005	Guard	357	360	45	30	56	1	26	y
3	2004/2005	Guard	360	363	66	51	97	2	45	y
4	2004/2005	Guard	361	362	38	26	60	2	29	y
5	2004/2005	Guard	362	363	12	7	25	1	23	y
6	2004/2005	Guard	363	365	52	38	94	1	69	y
7	2004/2005	Guard	363	365	34	27	70	1	48	y
8	2004/2005	Guard	366	2	45	33	74	1	38	y
9	2004/2005	Guard	366	2	34	23	68	1	41	y
10	2004/2005	Cheer	6	9	39	29	61	1	35	n
11	2004/2005	Cheer	6	10	107	81	188	1	151	y
12	2004/2005	Cheer	11	16	36	27	53	1	43	y
13	2004/2005	Cheer	11	16	76	51	184	1	177	y
14	2005/2006	Guard	354	357	65	44	86	2	19	y
15	2005/2006	Guard	354	358	95	74	168	2	16	y
16	2005/2006	Guard	357	360	56	46	74	2	38	y
17	2005/2006	Guard	358	360	62	40	86	1	83	n
18	2005/2006	Guard	360	363	81	51	118	1	112	y
19	2005/2006	Guard	360	362	79	54	94	1	82	y
20	2005/2006	Guard	362	364	59	41	93	1	83	y
21	2005/2006	Guard	363	365	47	31	87	1	77	y
22	2005/2006	Guard	364	2	33	27	41	1	20	y
23	2005/2006	Cheer	1	4	106	52	80	1	78	y
24	2005/2006	Cheer	2	5	142	85	154	1	144	y
25	2005/2006	Cheer	4	7	112	92	157	1	150	y
26	2005/2006	Cheer	9	14	152	113	195	1	167	n
27	2005/2006	Cheer	15	18	4	NA	NA	NA	NA	NA

(* Julian days calculated based on Greenwich Mean Time) and the number of locations retained pre- and post- ltering and interpolation for the complete track and 1st foraging trip (see methods)

sections when the interval between ltered locations was ≥ 5 km for high (LC 3, 2, 1) and low (LC 0, A, B) ≥ 6 h. Interpolated locations provided us with a temporally uniform distribution of locations for analysis that, unlike the raw ARGOS locations are not biased by satellite orbital parameters and the penguin's latitudinal position (Georges et al. 1997; BirdLife International 2004).

To simplify analyses and avoid pseudo-replication associated with repeated measures from the same individual, we selected only location data for the first foraging trip for each individual. Therefore, we distinguished independent foraging trips as those tracks which ranged from the colony and were ≥ 6 h in duration (Ballard et al. 2001; Ainley et al. 2004; Ballard 2010). Only tracks with >4 locations post- ltering were retained ($n = 26$ individuals). Nicholls et al. (2007) reported a mean accuracy of 100% for the first foraging trip of each individual: duration, total distance travelled, and maximum straight-line distance from the colony. When calculating total distance travelled for each trip for individuals where >6 -h interval occurred between locations, we assumed a straight-line distance between these locations. When the last known location was away from the colony and the return time to the colony was unknown, we calculated the straight distance to the colony from the last known location and

assumed a maximum travel speed of 2.2 m s⁻¹ to estimate the travel duration for this segment. All distance estimates were calculated using the great circle distance function in the ARGOS-Iter package (Freitas et al. 2008).

Dive parameters

We used Mk9 TDRs to measure the depth (range: 0–1,000 0.5 m) and temperature (range: 40–60 ± 0.05°C) every 10 s. Because a 10-s sampling interval was too coarse to accurately measure maximum dive depth, we only use these data for comparisons within this study, and care should be taken when comparing with other studies where sampling frequency on similar TDRs was typically higher.

We used program *Divesum* (v.7.5.5; G. Ballard unpublished computer script) to process raw diving data. This program corrected the recorded surface pressure and computed dive parameters for each dive: (1) dive duration (s); (2) maximum depth (m); (3) depth change rate (m s⁻¹; calculated as a running average for each 5-s block of the dive duration; slow [$\leq 1 \text{ m s}^{-1}$] and fast [$> 1.5 \text{ m s}^{-1}$] dives with depth change rates $\leq 4 \text{ m s}^{-1}$ were indicative of instrument error and excluded from subsequent analyses; (4) rate of ascent and descent (m s⁻¹); (5) sustained rate of depth change in same direction from surface to bottom and from bottom to surface; we defined bottom as any depth within 60% of the maximum depth (as recorded); and, (5) bottom time (s; the duration within 60% of the maximum depth and with no change in depth exceeding 0.5 m s⁻¹). For analyses, only dives ≥ 5 -m deep and ≥ 30 s in duration were considered.

Because of the 10-s sampling interval of TDRs, we used a 30-s filter in analysis which prevented reliable classification of “foraging” versus “exploratory” dives, so we combined these into a single class (F/E). F/E dives were ≥ 10 m and had either ≤ 15 s bottom time, 30% of the dive duration spent in slow depth change rate and 30% with fast depth change rate, or ≤ 15 s bottom time and rapid ($\geq 1 \text{ m s}^{-1}$) ascent/descent phases. All other dives were categorized as “other” (O) and are thought to be primarily commuting dives. Although we could not quantify these scale dive parameters (cf. Lesch et al. 2010), we used our data to determine the following dive parameters: (1) mean dive duration (2) mean maximum depth during F/E dives (3) mean bottom time during F/E dives (4) number of dives per hour for all types combined and for F/E dives separately, and (5) hourly vertical distance (m) for all dives combined and F/E dives separately.

Diet analysis

We combined four techniques to assess Adelie penguin diet during the breeding seasons (2004/2005: guard = 17

samples; creche = 13; 2005/2006: guard = 18; creche = 52): (1) stomach flushing (Wilson 1984; 58% of samples); (2) spilled prey remains collected from the ground after chick-feeding regurgitations (33% of samples); (3) stomach contents of chicks found dead (7% of samples); and (4) stomach contents of chicks killed by South polar skuas (*Stercorarius maccormicki*; 2% of samples). Stomach flushing did not yield the complete contents of the stomach but rather allowed individuals to regurgitate about a quarter (~250 g) of their stomach contents. As described in Ainley et al. (2003), most of the food beneath the upper portion is a soupy mush which cannot be separated according to prey species. Furthermore, taking only the upper portion allowed the parent to provide at least some food to its chick (Lishman 1985; Ainley et al. 1998). Ainley et al. (2003) also showed that results from stomach flushing were consistent with stable isotope analysis that indicated the relative proportions of krill and fish in the diet. No data exist that indicate Adelie penguin parents feed their chicks a diet different from what they eat themselves (Ainley et al. 2003).

We obtained flushed stomach samples at 7-day intervals beginning 22 December (the beginning of the chick-rearing period) and ending 22 January, with dates closely corresponding between years. In each session, we collected samples from 8 to 10 adults just after they came ashore. To ensure we sampled breeding individuals, we caught birds at their nests just before they fed their chicks. We preserved samples with 70% ethanol for later analysis.

Within each diet sample, we separated euphausiids from fish remains and estimated the relative proportions of each. Whereas we identified euphausiids to species, we did not identify fish otoliths; therefore, the percentage of stomach content samples made up by fish likely under-estimated true dietary contribution because fish are digested more rapidly than krill. Based on previous studies of fish distribution and Adelie penguin diet, we assumed the majority of fish present in samples were Antarctic silver fish *Neuragramma antarcticum* (DeWitt 1970; Eastman and Hubold 1999; Donnelly et al. 2004; O’Driscoll et al. 2009). We compared the relative percentages of fish delivered to chicks during the guard and creche stages of the breeding season. We classified guard and creche season diet samples as those collected during 22 December–2 January and 3–22 January, respectively. Here, we used samples collected approximately 2 days later than the matching foraging trip and dive parameters (described above) to account for the length of foraging trips, which averaged 2.3 days during the creche stage.

Individual utilization distributions

To quantify the location and area among individuals’ distribution at sea, we calculated fixed-kernel utilization

distributions (UD, Van Winkle 1975) for interpolated track maximum likelihood method. We identified the best-fit lines using a 3 × 3 km raster. We selected this cell size as model or subset of models using Akaike's information criteria corrected for small sample sizes (AICc). To normalize the combined ARGOS locations (see above; Nicholls et al. 2007). To calculate kernel values, we specified a bivariate-normal model (R: kernelUD function in the adehabitat package; Calenge 2006) and a smoothing parameter of 9 km to best represent the area used by penguins based on their estimated tracks. We arbitrarily chose three colony-level utilization distributions and hotspots to describe the at-sea distribution of individual Adélie penguins: we defined *foraging area* to be the area within the 90% probability density contour (90UD; Burger et al. 2006); *focal area* to be within the 50% probability density contour (50UD area), and *core area* to be within the 25% probability density contour (25UD area). We used the *kernel.area* function to estimate the total areas of foraging, focal, and core areas. To quantify shifts in the location of UD areas between guard and crèche stages, we calculated the latitude and longitude range limits for individuals' foraging, focal, and core areas.

Spatial overlap among individuals

To quantify space sharing among individuals within guard and crèche stages, we calculated two measures of overlap. First, we used the home range (HR) method (see Equation 1 in Fieberg and Kochann 2005) to estimate the proportion of at-sea distribution area of animal *i* that overlapped with animal *j*. Second, to quantify space sharing of animals *i* and *j* we estimated the volume of intersection statistic (VI index; see Equation 5 in Fieberg and Kochann 2005). The VI method uses the UD estimates of both animals to calculate the degree to which individual *i* and individual *j* sharing space where the UD areas intersect. Both overlap indices were calculated using the *kerneloverlap* function in the adehabitat package in R (Calenge 2006). For each individual's 90, 50 and 25UD, we estimated its mean overlap (both HR and VI) with all other individuals within that stage of the season within the relevant year. Because the maximum VI estimate was determined using 90, 50, and 25UD, we scaled VI estimates to range between 0 and 1.

Comparative analysis of foraging range and trip parameters

We tested for temporal variation in foraging behavior by fitting a set of candidate linear regression models, where the foraging parameter was the response variable and year (2004/2005 and 2005/2006), the stage of the season (guard or crèche) or stage of season (nested within year) were the potential explanatory variables (Appendix 3). We evaluated all models in R using the *stepAIC* function and the

For guard and crèche stages, we identified hotspots of distribution at sea (i.e. areas where the individual UD values were relatively high and also where multiple individuals overlapped in space; MacLeod et al. 2008). First, we estimated the number of individuals' 90UD areas that occupied each 3 × 3 km grid cell. We then summed the relevant individuals' 90UD surfaces (90UD) to calculate a colony-level estimate of the total proportional amount of time spent within each 3 × 3 km grid cell. Finally, we weighted the summed UD values for each 3 × 3 km grid cell according to the number of individuals that co-occupied it: $\sum_n 90UD/n^{-1}$, where *n* was the number of individual 90UD kernel surfaces which overlapped that grid cell. Thus, $\sum_n 90UD/n^{-1}$ estimates for grid cells that were only occupied by a few individuals were down-weighted relative to those visited by a greater number of penguins.

Bathymetry and sea ice coverage

We obtained sea ice imagery (250-m pixel resolution) coinciding with our study for the northwest portion of the Ross Sea from the Moderate Resolution Imaging Spectroradiometer (MODIS) platform (<http://rapid.re.sci.gsfc.nasa.gov/subsets/?RossSea>). Frequent cloud cover in our study area limited our evaluations to only one image per breeding stage in each of the breeding seasons. MODIS sea ice data were presented for the following Julian days during the guard and crèche stages: 357 and 024 in 2004/2005, respectively; and 354 and 016 in 2005/2006, respectively. Bathymetric maps show the 200-, 500-, 900-, and 1,500-m contours (Data reproduced from the GEBCO Digital Atlas published by the British Oceanographic Data Centre on behalf of IOC and IHO 2003).

track-line interpolation, we retained 7± 8% (SD; range= 49–82%) of locations after speed-distance-angle filtering. Among the 26 penguins tracked, 18 and 8 foraging trips occurred during the guard and core stages, respectively.

Foraging trip parameters

During guard stage, foraging trips averaged 22 h, 79 km, and were a maximum straight-line distance of 35 km from the colony (Table 2). The duration of foraging trips, the total distance travelled, and the maximum straight-line distance from the colony were approximately three times longer and farther during the core stage, respectively (Table 2). In all cases, the subset of best-fit models included season and season (nested within year), highlighting the importance of stage of season as a predictor of temporal variance in foraging trip parameters (Appendix 1)

Dive parameters

Mean maximum depth, dives per hour, and hourly vertical distance travelled for F/E dives were less during the core stage than during the guard stage (Table 2; Appendix 2). There was no evidence of intra-seasonal change in mean dive duration or mean bottom time for F/E dives (Table 2; Appendix 2). The hourly vertical distance travelled for all dives also was less during the core stage (Table 2; Appendix 2).

Foraging, focal, and core areas

Individual foraging, focal, and core areas (as determined by the 90, 50 and 25UD, respectively) doubled between the guard and core stages (Table 3; Appendix 3). Within each stage, individual focal and core areas were about third and tenth the area of the corresponding foraging areas, respectively; the latter increased from an average 2,125–4,352 km² between guard and core stages.

Latitudinal-longitudinal extent of utilization distributions

Changes in the latitudinal and longitudinal extent of the UD areas occurred and were primarily associated with the southern and eastern boundaries (Table 4; Appendix 4). The northern limits of individual foraging, focal, and core areas retreated during the core stage in 2004/2005 (see best-fit model in Appendix 4; Table 3). The western extent of the UD areas increased between the guard and core stage in 2004/2005 but decreased in 2005/2006 (see best-fit model in Appendix 4; Figs. 2, 3, 4, 5; Table 3).

Table 2 Summary of foraging trip and dive depth parameters for breeding Adelie penguins tracked using satellite tags and depth recorders in the guard and core stages of two breeding seasons (2004/2005 and 2005/2006) at Cape Hallett, Antarctica

Aspect	Parameter	2004/2005						2005/2006					
		Guard stage			Core stage			Guard stage			Core stage		
		Estimate	LCL	UCL	Estimate	LCL	UCL	Estimate	LCL	UCL	Estimate	LCL	UCL
Foraging trip*	Maximum distance from colony (km)	38.6	21.0	71.0	94.6	49.1	182.6	31.8	18.6	54.4	110.6	49.5	247.4
	Total distance travelled (km)	70.6	37.3	133.7	209.4	105.1	417.3	86.6	49.3	152.1	310.6	133.5	722.8
	Total duration (h)	18.2	11.1	29.9	47.5	27.9	81.0	26.1	16.9	40.4	71.0	37.0	135.6
Foraging and exploratory dives	Mean dive duration (s)	111.2	101.1	121.3	113.5	92.1	134.9	108.4	97.7	119.1	102.9	91.4	114.3
	Mean maximum depth (m)	67.5	57.9	77.1	55.0	34.6	75.5	57.8	47.6	68.0	50.2	39.3	61.1
	Mean bottom time (s)	56.7	51.6	61.7	64.5	53.7	75.3	58.0	52.6	63.4	60.4	54.7	66.2
	Number of dives per hour	11.3	9.8	12.9	7.1	3.9	10.4	11.6	9.9	13.2	9.8	8.0	11.6
All dives	Hourly vertical distance (m)	1,524.3	1,245.6	1,803.0	853.6	262.3	1,444.9	1,324.7	1,029.1	1,620.4	982.7	666.6	1,298.7
	Number of dives per hour	16.1	14.2	17.9	14.6	10.7	18.6	16.9	14.9	18.9	16.6	14.5	18.7
	Hourly vertical distance (m)	1,617.5	1,343.7	1,891.3	996.5	415.8	1,577.2	1,428.1	1,137.7	1,718.4	1,120.1	809.7	1,430.6

The parameter estimates (with 2.5 and 97.5% confidence levels) presented were extracted from model 3 (Year/season) in Appendix 1. Estimates have been back transformed (as data were log-transformed for analysis)

Table 3 Intra-seasonal variation in the area (km²) and latitudinal and longitudinal extent of the foraging, focal, and core ranges (90, 50, and 25UD, respectively) of Adélie penguin adults tracked during two breeding seasons (2004/2005 and 2005/2006) at Cape Hallett, Antarctica

Variable	Range	2005/2006																				
		2004/2005				Core stage				Guard stage				Core stage				Guard stage				
		Estimate	LCL	UCL	UCL	Estimate	LCL	LCL	UCL	Estimate	LCL	LCL	UCL	Estimate	LCL	LCL	UCL	Estimate	LCL	LCL	UCL	
UD area (km ²)*	Core	209	136	320	366	231	582	232	159	338	558	317	983	983								
	Focal	648	417	1,008	1,217	756	1,959	736	499	1,086	1,703	950	3,051	3,051								
	Foraging	2,004	1,345	2,986	3,932	2,556	6,049	2,245	1,579	3,191	4,771	2,815	8,085	8,085								
North latitude (S)	Core	72.20	72.14	72.26	72.31	72.25	72.37	72.24	72.19	72.19	72.29	72.23	72.16	72.31								
	Focal	72.16	72.11	72.22	72.28	72.22	72.34	72.21	72.16	72.16	72.26	72.20	72.13	72.28								
	Foraging	72.09	72.03	72.15	72.21	72.15	72.28	72.13	72.07	72.07	72.18	72.13	72.05	72.21								
South latitude (S)	Core	72.33	72.24	72.43	72.49	72.39	72.59	72.35	72.26	72.26	72.43	72.49	72.36	72.61								
	Focal	72.36	72.28	72.45	72.53	72.44	72.63	72.38	72.30	72.30	72.46	72.51	72.39	72.63								
	Foraging	72.43	72.34	72.52	72.59	72.49	72.68	72.44	72.36	72.36	72.52	72.45	72.68	72.68								
East longitude (E)	Core	171.06	169.96	172.16	173.37	172.18	174.56	171.61	170.64	172.58	173.66	172.21	175.11	175.11								
	Focal	171.23	170.14	172.33	173.53	172.35	174.71	171.72	170.75	172.69	173.82	172.38	175.27	175.27								
	Foraging	171.57	170.51	172.64	173.83	172.69	174.98	171.99	171.06	172.93	174.16	172.75	175.57	175.57								
West longitude (E)	Core	170.35	169.69	171.01	170.88	170.17	171.60	170.42	169.84	171.01	170.72	169.85	171.59	171.59								
	Focal	170.19	169.58	170.80	170.70	170.04	171.36	170.20	169.66	170.73	170.36	169.55	171.17	171.17								
	Foraging	169.80	169.67	169.93	169.71	169.56	169.85	169.76	169.64	169.88	169.94	169.77	170.12	170.12								

The parameter estimates (with 2.5 and 97.5% confidence levels) presented were extracted from model 3 (Year/season) in [Appendix 1](#). Estimates have been back transformed (as data were log-transformed for analysis)

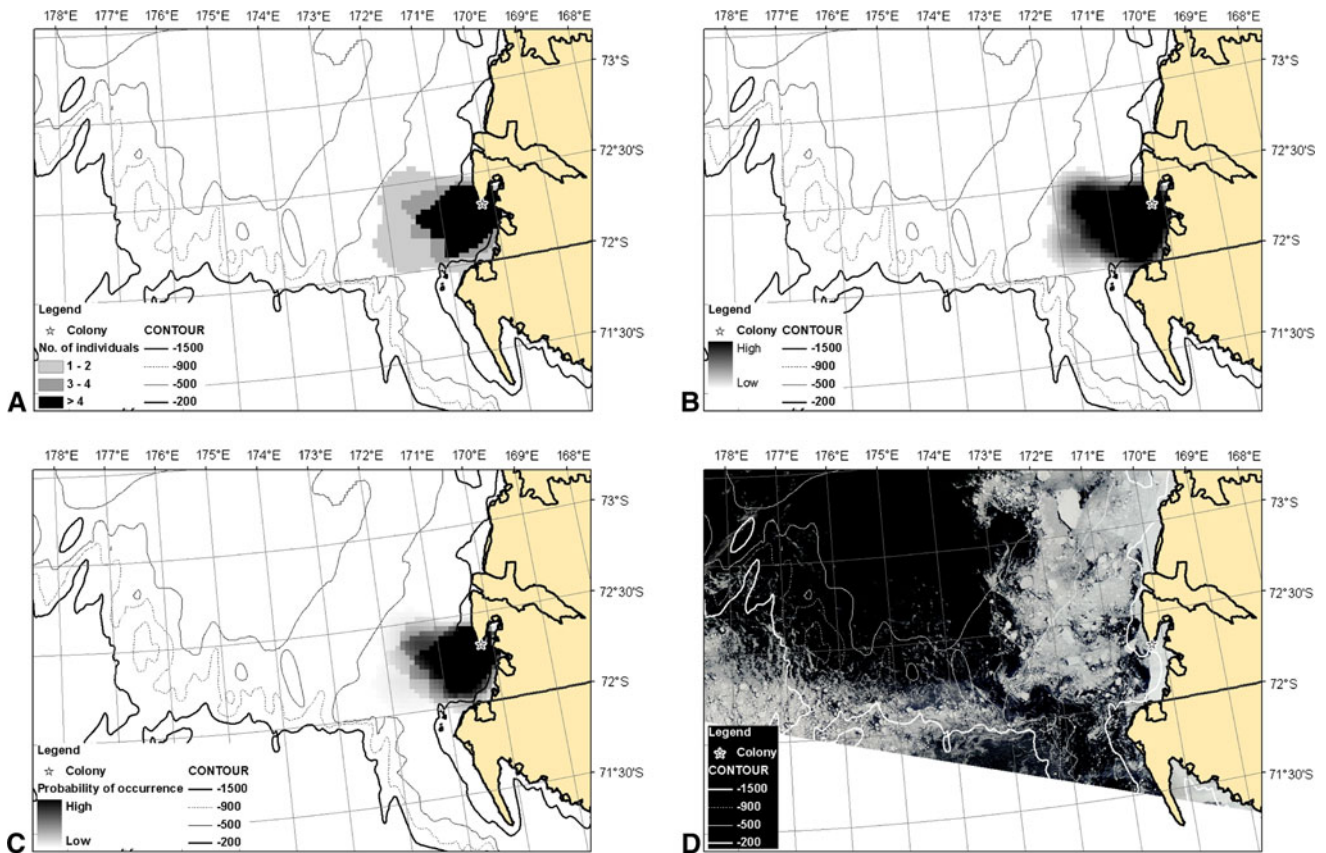


Fig. 2 At-sea distribution of satellite tracked *Adelie* penguins ($n = 9$) from the Cape Hallett breeding colony (as indicated by the black star) during the guard stage of the 2004/2005 breeding season spent in each 3×3 km grid cell; d the pack-ice distribution around a the number of foraging areas (90UD) which overlapped each the colony (Julian day 357). All maps show the 200, 500, 900, and 3×3 km grid cell; b the summed, 90UD estimates; c the weighted, 90UD estimates, which provide a measure of the cumulative

Overlap in utilization distributions

Using the HR method, the degree of spatial overlap among individual foraging areas (90UD) decreased from 61% in guard and crèche stages, respectively. However, the proportion of overlap among focal and core areas was approximately halved (Table 4; Appendix 5). Using the VI method, individual overlap also decreased from the guard to crèche stages (Table 4; Appendix 5). This pattern was consistent across all three area classes (i.e. foraging, focal and core areas).

Diet composition

We identified two euphausiid species in stomach contents ($n = 100$) collected from breeding *Adelie* penguins during 2004/2005 and 2005/2006: Antarctic krill (*Euphausia superba*) and Crystal krill (*E. crystallophias*). *E. superba* was more frequent and occurred in 80% of all samples. *E. crystallophias* occurred in only 3% of samples.

Unidentified shes and amphipods were present in 52 and 49% of samples, respectively. *E. superba* comprised 85 and 44% of the estimated stomach content material during the guard and crèche stages, respectively. However, the proportion of sh in chick diet (likely underestimated) increased fourfold between the guard and crèche stages (Parameter estimate [2.5 and 97.5% CL] from the best-fit model (Year/season) in Appendix 6; guard stage: 2004/2005, 4% [0–14%], 2005/2006, 2% [0–9%]; crèche stage: 2004/2005, 24% [10–42%], 2005/2006, 8% [4–14%]).

Colony-level UD estimates and hotspots of at-sea distribution in relation to bathymetry and pack ice

In both years, the colony-level UD area was greater during the crèche stage, when individuals also were more widely dispersed (Fig. 2: 2004/2005: guard stage = 4,158 km²; crèche stage = 15,327 km²; 2005/2006: guard stage = 6,408 km²; crèche stage = 12,510 km²). At all stages, overlap among individuals generally was greatest close to

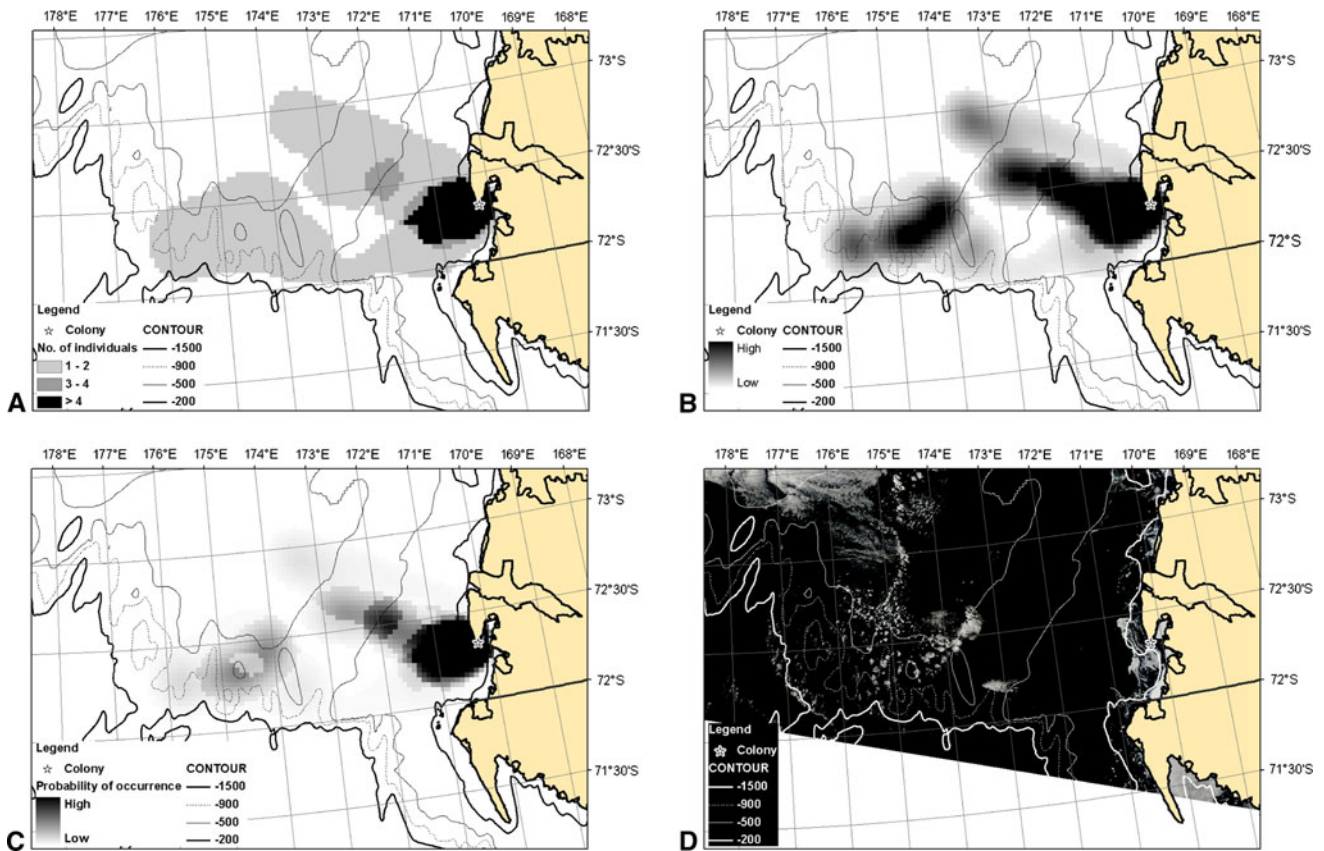


Fig. 3 At-sea distribution of satellite tracked Adie penguins cell; b the summed Σ_n 90UD estimates; c the weighted Σ_n 90UD estimates (see caption of Fig. 2 for explanation); d the pack-ice distribution around the colony (Julian day 24). All maps show the a the number of foraging areas which overlapped each 3 km grid 200, 500, 900, and 1,500-m bathymetric contours

the colony (Figs 2a, 5a) and was greater overall in 2005/2006 than in 2004/2005. Overlapping distributions, especially near the colony, reflect the commuting activity of individuals. However, the more area-restricted distribution of individuals and greater occurrence (as determined by the summed UD estimates, Figs 3b, 5b) within the vicinity of the colony during the guard stage, compared with the creche stage, indicates that most foraging activity occurred relatively close to the colony during the guard stage. After down-weighting summed UD estimates to identify those areas visited by several individuals and where those individuals spent more time, the hotspot of at-sea distribution during the guard stage occurred close to the colony (Figs 3c, 5c). Thus, most individuals foraged over the relatively shallower waters (≤ 500 m deep) over or adjacent to the continental shelf break. During the creche stage, two additional hotspots emerged: one over the Victoria Land Trough (especially in 2005/2006) and another 60 km to the colony, however, the overlap (i.e. density) among penguin foraging areas were less as birds expanded their foraging areas into regions of ocean with less concentrated pack ice.

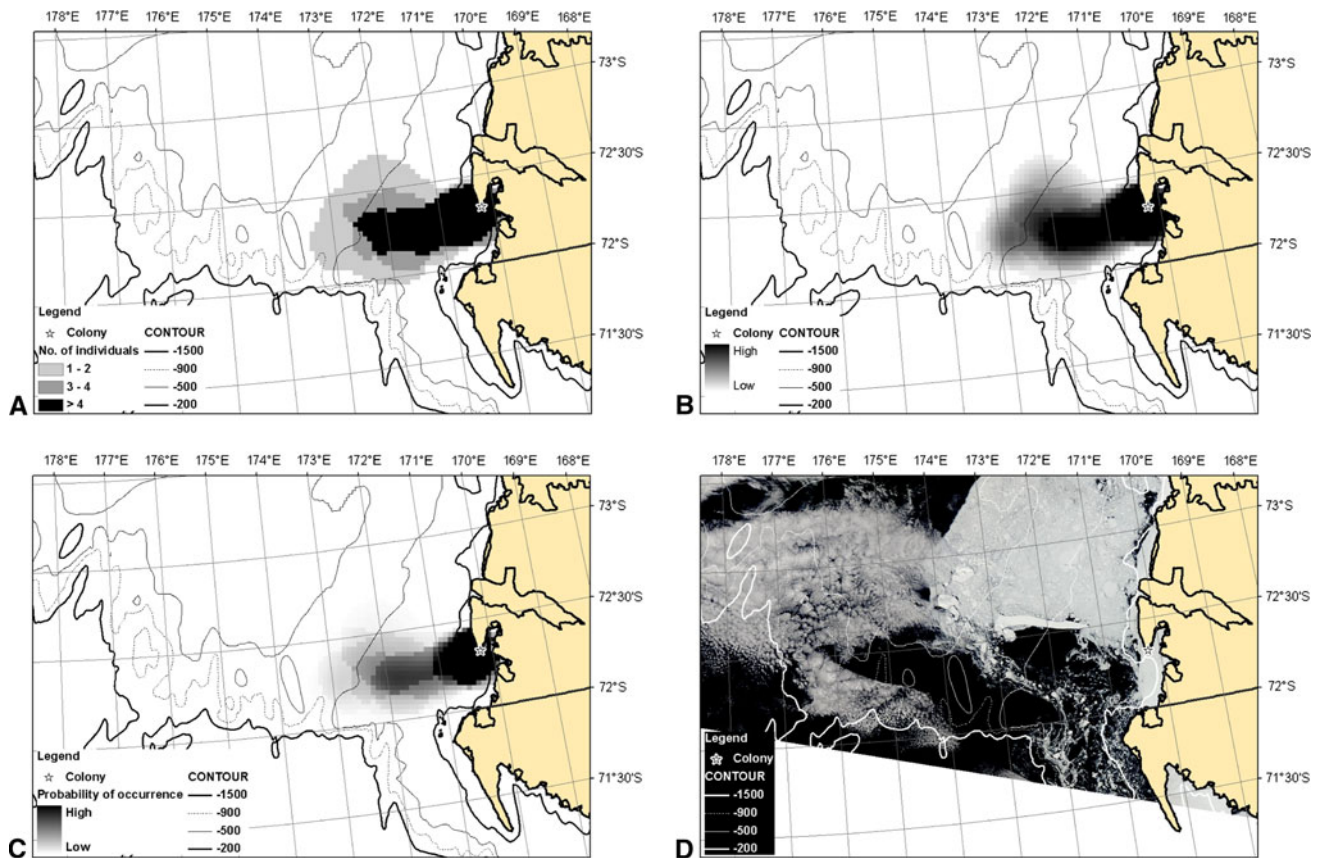


Fig. 4 At-sea distribution of satellite tracked Adélie penguins ($n = 9$) from the Cape Hallett breeding colony (as indicated by the black star) during the guard stage of the 2005/2006 breeding seasons: a the number of foraging ranges which overlapped each 3 km grid cell; b the summed $\Sigma_{i=1}^n$ 90UD estimates; c the weighted $\Sigma_{i=1}^n$ 90UD estimates (see caption of Fig. 1 for explanation); d the pack-ice distribution around the colony (Julian day: 354). All maps show the 200, 500, 900, and 1,500-m bathymetric contours

Discussion

Limitations of methods and effects of devices

We acknowledge that externally attached devices can have an effect on swimming ability, reducing speed (Wilson et al. 1986, 1997), and generally increasing energy expenditure (Bannasch et al. 1994; Kato et al. 2003). In this study, a VHF tag also was deployed on each bird to maximize instrument recoveries. It is possible that the addition of the VHF tag could further compromise the streamlining of the birds, although we do not think this is likely given the lack of effect found for such configurations from our previous work (Ballard et al. 2001).

Human disturbance also can affect penguin behavior and breeding success (Giese 1996). Although we did not collect foraging or breeding behavior data on non-instrumented birds, other studies have shown that similar devices and level of researcher disturbance did not affect foraging duration (Ballard et al. 2001; Kato et al. 2003), chick growth, chick survival, meal mass (Watanuki et al. 1992, 1997) nor breeding success of Adélie penguins (Wilson

et al. 1989, 1991). Therefore, we believe the foraging behaviors observed in this study are representative of the species.

Adélie penguin foraging patterns likely are affected by a range of prey-related factors including the type and size of prey available, daily vertical migration, prey density, and the dispersion of prey patches (Watanuki et al. 1993; Endo et al. 2002) and also by abiotic factors including sea ice dynamics and oceanic productivity. Since we were not able to measure prey-related parameters directly, we based our interpretations on observed foraging patterns.

Do foraging trips indicate competition for prey?

Competition for food arises from two sources: (1) an increase in predator abundance or (2) a decrease in food resource availability driven by factors other than predation (e.g., persistent summer sea ice coverage). Our first prediction that intra-specific competition would not affect penguins from the Cape Hallett colony was challenged by the tendency for breeding adults to travel farther, for longer, and over a greater area later in the breeding season.

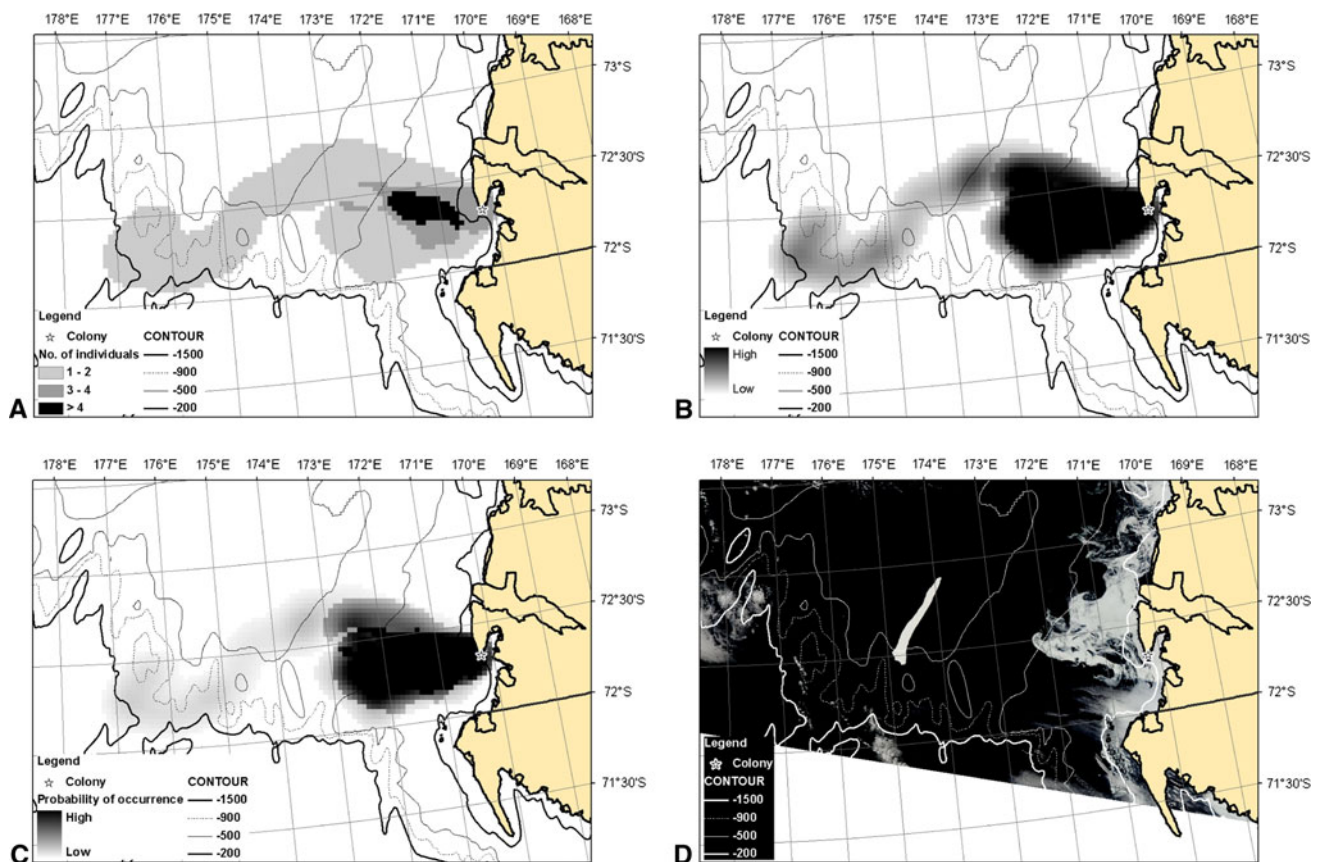


Fig. 5 At-sea distribution of satellite tracked Adie penguins (n = 4) from the Cape Hallett breeding colony (as indicated by the black star) during the creche stage of the 2005/2006 breeding season (Julian day: 16). All maps show the distribution around the colony (a the number of foraging ranges which overlapped each 3 km grid cell; b the summed 90UD estimates; c the weighted 90UD estimates (see caption of Fig. 4 for explanation); d the pack-ice distribution around the colony (Julian day: 16). All maps show the 200, 500, 900, and 1,500-m bathymetric contours

Table 4 Intra-seasonal variation in the degree of spatial overlap among individuals foraging, focal, and core areas (90, 50, and 25UD, respectively; UD= utilization distribution)

Overlap measure	Range	2004/2005						2005/2006					
		Guard stage			Creche stage			Guard stage			Creche stage		
		Estimate	LCL	UCL	Estimate	LCL	UCL	Estimate	LCL	UCL	Estimate	LCL	UCL
HR	Foraging	0.62	0.48	0.74	0.45	0.31	0.60	0.60	0.49	0.72	0.43	0.26	0.61
	Focal	0.31	0.19	0.46	0.17	0.07	0.30	0.32	0.20	0.44	0.16	0.05	0.33
	Core	0.17	0.06	0.32	0.08	0.01	0.21	0.18	0.08	0.31	0.04	0.00	0.17
VI	Foraging	0.75	0.70	0.80	0.53	0.47	0.59	0.68	0.64	0.73	0.58	0.51	0.65
	Focal	0.53	0.43	0.64	0.32	0.21	0.44	0.49	0.40	0.59	0.36	0.22	0.50
	Core	0.38	0.24	0.51	0.22	0.07	0.36	0.37	0.25	0.49	0.18	0.00	0.36

Home range (HR) is a measure of the proportion of the area of each UD class that overlaps with all other individuals. Volume of intersection (VI) provides a relative measure of the proportional time of two individuals overlapping within the area of overlap within each UD area class. The back-transformed parameter estimates (with 2.5 and 97.5% confidence levels) presented were extracted from model 3 (Year/season) in Appendices 5 (where data were arcsin-transformed for analysis)

This indicates that there is a change in prey availability throughout the season as a function of distance to Cape Ross and Beaufort islands, where at the larger colony Hallett. Our results are consistent with Ainley et al. (2004) (Cape Crozier, ~135,000 breeding pairs; Ballance et al. and Ballance et al. (2009) who suggested that intra-specific breeding penguins foraged farther and for longer

later in the season than during the early season (see also intra-specific competition mitigated by prey type? Ainley et al. 2004, 2006). However, in contrast to our findings from Cape Hallett, parents from Cape Crozier in the Antarctic marine ecosystem, *E. superba* dominated also exhibited deeper dives, dived more frequently, and prey biomass that support most of the upper-trophic-level for greater durations later in the breeding season (Lescroart et al. 2002). Although prey resources were not directly measured by Lescroart et al. (2010), they attributed this pattern to intra-specific foraging competition as prey with higher latitude colonies on Ross Island where the stocks were gradually depleted as the breeding season progressed (see also Ballance et al. 2009). Among other species taken (Ainley et al. 2003), *E. crystallophias* was frequently delivered during both seasons at Cape Hallett. These findings are consistent with krill distribution patterns observed by Sala et al. (2002), Azzali et al. (2006), and Taki et al. (2008) who determined using acoustics and net sampling that *E. superba* were the most abundant euphausiid along the Ross Sea shelf break and in the northern Ross Sea region. Presumably, penguins foraging farther offshore from Cape Hallett would be less likely to encounter *E. crystallophias* as evidenced in the stomach samples. It is possible also that the greater mean relative biomass of *E. superba* (9.3 g/1,000 l of filtered water) in surface waters overlying the continental shelf break compared with lesser *E. crystallophias* (3.0 g/1,000 l of filtered water) over the continental shelf south of 74°S (Sala et al. 2002), buffered the Cape Hallett penguins from the effects of more intense intra-specific competition with large neighboring colonies—a situation perhaps more likely to occur within the Ross Island metapopulation (Ainley et al. 2004, Ballance et al. 2009).

So, why did penguins from Cape Hallett, a colony of similar size to Cape Bird and larger than Cape Royds display patterns consistent with the prey depletion hypothesis observed at Cape Crozier? We suggest that the close proximity of three additional large Adie penguin breeding colonies (Cape Adare, Foyn Is. and Possession Is.; combined 449,858 breeding pairs; Woehler et al. 1993) to the north of Cape Hallett and two immediately to the south (Cape Cotter and Cape Wheatstone; together 46,235 breeding pairs; Fig. 1) exposed the birds from Cape Hallett to a lower relative level of intra-specific competition than previously observed at Crozier, yet significant enough to alter foraging patterns. We suggest that Adie penguins from Cape Hallett increased their foraging areas to source adequate prey, but not so much as to increase aspects of their diving behavior. By foraging farther, for longer, and over a greater area, breeding Adie penguins from Cape Hallett could have adjusted in response to intra-specific competition with the large Adie penguin colonies to the north. The seasonal shift more to the southeast also could be a response to avoid competition with the large number of penguins associated with colonies to the north, which likely also would be seasonally expanding their foraging ranges, much as the Cape Crozier colony causes a seasonal shift in the foraging area of the adjacent Beaufort Island colony (Ainley et al. 2004).

Ainley et al. (2006) also suggest that other large krill eating species such as Minke whales (*Balaenoptera bonaerensis*) could contribute to prey depletion and contribute in part to the observed increase in foraging effort among breeding Adie penguins around Ross Island. Minke whales are most abundant in the Ross Sea along the shelf break (Ainley 1985), but unfortunately we lack observations of cetacean abundances within the foraging area of the penguins breeding at Cape Hallett. Besides krill, shrimps are the second most important dietary component for top predators in Antarctic waters (Fischer and Hureau 1985) and particularly, energy-rich pelagic myctophid species in open waters of the Southern Ocean and *Pleuragramma* over the shelf (Barrera-Oro 2002). Based on the sh distribution patterns reported by (DeWitt 1970, Eastman and Huber 1999, Donnelly et al. 2004, see also O'Driscoll et al. 2009) and our measured penguin distributions, Adie penguins from Cape Hallett were most likely to encounter and have consumed *Pleuragramma* while foraging over the continental shelf. No myctophids (*Electrona* sp.) were detected in net hauls over the Ross Sea continental shelf (references above); therefore, the probability that myctophids would have been encountered and taken by Hallett penguins was low.

As predicted, the amount of sh in adult Adie penguin diet samples increased significantly as the season progressed, consistent in pattern but not amount with observations at Ross Island Adie penguin colonies. In the southern Ross Sea, sh can comprise almost 100% of the diet at times (Ainley et al. 2006). Although, large aggregations of

Pleuragramma have been detected over the deeper waters of the Victoria Land Trough (O'Driscoll et al. 2009) given the relatively low percentages detected in our samples. Adie from Hallett did not appear to specifically target *Pleuragramma* but may take *E. superba* when sufficiently abundant and available.

Unfortunately, we cannot yet disentangle whether adult penguins from Cape Hallett were targeting *Pleuragramma* or were opportunistically catching these fish as they encountered them more frequently farther off-shore. Although fish are more energy dense, Adie penguin chicks can be sustained on pure krill diets (Salihoglu et al. 2001; Ainley et al. 2003). In some years in parts of East Antarctica, Adie penguins switch to fish species' other than *Pleuragramma* (such as *Trematomus* sp. and *Pagothenia borchgrevinkii*; Watanuki et al. 1993; Clarke et al. 2002).

Effects of prey availability and physical habitat

The at-sea UD areas of Adie penguins from Cape Hallett indicated that provisioning adults were closely associated with coastal fast and pack ice during the guard stage; however, this association lessened somewhat during the crèche stage as penguins increased their foraging areas and the sea ice dispersed. During the crèche stage, a greater proportion of Adie penguin foraging areas were characterized by lesser pack ice concentrations.

Ainley et al. (1984) determined that the most important feature affecting Adie penguin distribution in the Ross Sea after the presence of pack ice and proximity to breeding areas was the Antarctic Slope Front (the region herein referred to as the Ross Sea Slope Front (RSSF); Ainley and Jacobs 1981; Ainley 1985; Jacobs 1991). They also suggested that penguins preferred pack ice to open ocean habitats and that the biological activity in the water column beneath the ice probably was more important in determining where in the ice Adie penguins occurred (i.e. the degree to which the ice co-occurred with the RSSF). Greater densities of Adie penguins were observed by Ainley et al. (1984) across an area extending southeast from Cape Adare in the pack ice over the Ross Sea Slope, and their concurrent absence from the pack ice to the north and in the open polynya waters to the south also was obvious (Ainley et al. 1984, 2006). In our study, when chick-rearing demands increased with the crèche stage, we found that Cape Hallett penguins began to aggregate spatially in the vicinity of the RSSF. This habitat feature also is important for penguins from other

colonies in East Antarctica (Clarke et al. 1998). We found little evidence that penguins specifically targeted canyons, as is the case off the western Antarctic Peninsula. Rather, they gradually expanded foraging areas in one direction to eventually overlie the Victoria Land Trough and the continental slope.

Flores et al. (2009) found densities of post-larval *E. superba* were greater under sea ice than the open ocean because of enhanced conditions for ice algal and phytoplankton production. From a predator's perspective, this would support our observations that focal and core foraging areas among penguins were associated with pack ice and that small hot-spots of activity later in each season appeared to overlap with small pack ice patches over highly productive waters offshore. Alternatively, it is possible that concentrations of pack ice around Cape Hallett earlier in the breeding season created a temporary barrier and prevented penguins from accessing more prey-rich waters offshore. Once the pack ice began to break up during the crèche stage and become increasingly dispersed, penguins were able to swim to feeding areas (which is energetically less demanding than transiting across sea or pack ice); this would allow penguins to expand their foraging areas into areas presumably with less depleted prey stocks. And in doing so, the birds seemingly were able to maintain a relatively low level of diving effort during the crèche stage.

Crucial to understanding the foraging behavior of Adie penguins (and other predator species') is knowledge about the abundance and distribution of their different prey species'. Concurrent prey abundance and distributions surveys would be advantageous for better interpreting how these predators use the seascape and employ different foraging strategies.

Acknowledgments We thank the following persons for planning and field assistance: Peter Dilks, Shulamit Gordon, Rachel Brown and Gus McAlister. Antarctica New Zealand provided extensive logistic support for the NZ Adie Penguin Program (K122b) through their Latitudinal Gradient Program, while the US Antarctic Program supported members from the US Adie Penguin Program (B031). This project was funded by the New Zealand Foundation for Research, Science and Technology (C09X0510) and Office of Polar Programs, National Science Foundation (OPP 0125608, 0440643). Draft manuscripts received valuable review from the editor and three anonymous referees. Reference to trade names does not imply endorsement of these products.

Appendix 1
See Table 5.

Table 5 Candidate models fitted to the foraging trip parameter data and best set of models identified by the model selection (highlighted in bold, based on $\Delta AICc$ threshold value <4)

Parameter	Model	Covariate	<i>df</i>	AICc	$\Delta AICc$	Weight
Maximum distance (km)	m0	Null	2	65.6	11.31	0.002
	m1	Year	3	65.2	10.89	0.002
	m2	Season	3	54.7	0.40	0.448
	m3	Year/season	5	54.3	0.00	0.548
Total distance travelled (km)	m0	Null	2	68.6	11.81	0.002
	m1	Year	3	68.5	11.75	0.002
	m2	Season	3	57.7	0.94	0.383
	m3	Year/season	5	56.8	0.00	0.614
Total duration (h)	m0	Null	2	57.1	13.70	0.001
	m1	Year	3	56.6	13.11	0.001
	m2	Season	3	46.0	2.54	0.219
	m3	Year/season	5	43.5	0.00	0.779

Appendix 2

See Table 6.

Table 6 Candidate models fitted to the dive parameter data and best set of models identified by the model selection (highlighted in bold, based on $\Delta AICc$ threshold value <4)

Parameter	Model	Covariate	<i>df</i>	AICc	$\Delta AICc$	Weight
Mean dive duration (s)	m0	Null	2	208.6	1.82	0.150
	m1	Year	3	207.4	0.67	0.267
	m2	Season	3	207.9	1.15	0.210
	m3	Year/season	5	206.8	0.00	0.373
Mean maximum depth (m)	m0	Null	2	211.0	6.61	0.023
	m1	Year	3	207.1	2.73	0.162
	m2	Season	3	206.9	2.51	0.181
	m3	Year/season	5	204.4	0.00	0.634
Mean bottom time (s)	m0	Null	2	173.8	2.69	0.116
	m1	Year	3	173.6	2.56	0.125
	m2	Season	3	171.8	0.72	0.312
	m3	Year/season	5	171.1	0.00	0.447
Dives per hour	m0	Null	2	117.4	8.07	0.013
	m1	Year	3	117.4	8.03	0.014
	m2	Season	3	111.9	2.51	0.216
	m3	Year/season	5	109.4	0.00	0.757
Hourly vertical distance (m)	m0	Null	2	388.7	9.26	0.006
	m1	Year	3	386.8	7.37	0.016
	m2	Season	3	380.8	1.38	0.327
	m3	Year/season	5	379.4	0.00	0.651
Dives per hour	m0	Null	2	120.3	1.49	0.175
	m1	Year	3	119.4	0.61	0.272
	m2	Season	3	120.2	1.40	0.184
	m3	Year/season	5	118.8	0.00	0.369
Hourly vertical distance (m)	m0	Null	2	386.8	8.27	0.010
	m1	Year	3	385.0	6.53	0.024
	m2	Season	3	379.8	1.29	0.332
	m3	Year/season	5	378.5	0.00	0.634

Appendix 3

See Table 7.

Table 7 Candidate models fitted to the UD area data for the foraging, focal and core ranges and best set of models identified by the model selection (highlighted in bold, based on $\Delta AICc$ threshold value <4)

Range	Model	Covariate	df	AICc	$\Delta AICc$	Weight
Foraging	m0	Null	2	43.45	11.15	0.002
	m1	Year	3	43.43	11.13	0.002
	m2	Season	3	32.93	0.63	0.42
	m3	Year/season	5	32.30	0.00	0.576
Focal	m0	Null	2	47.58	10.05	0.004
	m1	Year	3	47.43	9.90	0.005
	m2	Season	3	38.75	1.22	0.349
	m3	Year/season	5	37.52	0.00	0.642
Core	m0	Null	2	46.40	10.48	0.004
	m1	Year	3	46.16	10.24	0.004
	m2	Season	3	37.72	1.80	0.287
	m3	Year/season	5	35.92	0.00	0.705

Appendix 4

See Table 8.

Table 8 Candidate models fitted to the latitudinal and longitudinal extent of the foraging, focal, and core ranges data and best set of models identified by the model selection (highlighted in bold, based on $\Delta AICc$ threshold value <4)

Extent	Range	Model	Covariate	df	AICc	$\Delta AICc$	Weight
North	Foraging	m0	Null	2	-57.8	9.12	0.009
		m1	Year	3	-58.2	8.78	0.011
		m2	Season	3	-62.5	4.42	0.097
		m3	Year/season	5	-67.0	0.00	0.883
	Focal	m0	Null	2	-60.3	8.45	0.013
		m1	Year	3	-60.4	8.36	0.013
		m2	Season	3	-64.3	4.45	0.095
		m3	Year/season	5	-68.7	0.00	0.879
	Core	m0	Null	2	-59.7	7.65	0.019
		m1	Year	3	-59.9	7.51	0.020
		m2	Season	3	-63.2	4.15	0.107
		m3	Year/season	5	-67.4	0.00	0.854
South	Foraging	m0	Null	2	-37.2	10.00	0.003
		m1	Year	3	-37.5	9.74	0.004
		m2	Season	3	-47.1	0.14	0.478
		m3	Year/season	5	-47.2	0.00	0.514
	Focal	m0	Null	2	-35.3	10.49	0.003
		m1	Year	3	-35.5	10.30	0.003
		m2	Season	3	-45.6	0.19	0.474
		m3	Year/season	5	-45.8	0.00	0.520
	Core	m0	Null	2	-33.5	9.31	0.005
		m1	Year	3	-33.6	9.20	0.005
		m2	Season	3	-42.8	0.05	0.489
		m3	Year/season	5	-42.8	0.00	0.502

Table 8 continued

Extent	Range	Model	Covariate	df	AICc	$\Delta AICc$	Weight
East	Foraging	m0	Null	2	97.6	14.22	0.000
		m1	Year	3	97.6	14.22	0.000
		m2	Season	3	84.0	0.60	0.425
		m3	Year/season	5	83.4	0.00	0.574
	Focal	m0	Null	2	98.4	13.54	0.001
		m1	Year	3	98.4	13.52	0.001
		m2	Season	3	85.5	0.68	0.415
		m3	Year/season	5	84.8	0.00	0.584
	Core	m0	Null	2	98.4	13.32	0.001
		m1	Year	3	98.3	13.29	0.001
		m2	Season	3	85.9	0.81	0.399
		m3	Year/season	5	85.0	0.00	0.599
West	Foraging	m0	Null	2	-19.2	5.23	0.058
		m1	Year	3	-20.0	4.51	0.083
		m2	Season	3	-19.4	5.08	0.063
		m3	Year/season	5	-24.5	0.00	0.796
	Focal	m0	Null	2	56.6	2.09	0.138
		m1	Year	3	56.2	1.72	0.166
		m2	Season	3	55.0	0.52	0.303
		m3	Year/season	5	54.5	0.00	0.393
	Core	m0	Null	2	60.3	1.96	0.140
		m1	Year	3	60.3	1.89	0.144
		m2	Season	3	58.5	0.15	0.344
		m3	Year/season	5	58.4	0.00	0.372

Appendix 5

See Table 9.

Table 9 Candidate models fitted to the UD overlap data and best set of models identified by the model selection (highlighted in bold, based on $\Delta AICc$ threshold value <4)

Overlap measure	Range	Model	Covariate	df	AICc	$\Delta AICc$	Weight
HR	Foraging	m0	Null	2	-17.40	6.09	0.023
		m1	Year	3	-17.43	6.06	0.023
		m2	Season	3	-23.43	0.06	0.469
		m3	Year/season	5	-23.49	0.00	0.484
	Focal	m0	Null	2	-13.66	5.74	0.027
		m1	Year	3	-13.79	5.61	0.029
		m2	Season	3	-19.39	0.00	0.472
		m3	Year/season	5	-19.40	0.00	0.473
	Core	m0	Null	2	-7.11	4.77	0.047
		m1	Year	3	-7.11	4.77	0.047
		m2	Season	3	-11.36	0.51	0.396
		m3	Year/season	5	-11.87	0.00	0.510

Table 9 continued

Overlap measure	Range	Model	Covariate	df	AICc	Δ AICc	Weight
VI	Foraging	m0	Null	2	-45.69	27.03	0.000
		m1	Year	3	-45.70	27.02	0.000
		m2	Season	3	-67.42	5.29	0.066
		m3	Year/season	5	-72.72	0.00	0.934
	Focal	m0	Null	2	-26.67	10.22	0.003
		m1	Year	3	-26.77	10.12	0.004
		m2	Season	3	-36.28	0.62	0.420
		m3	Year/season	5	-36.89	0.00	0.573
	Core	m0	Null	2	-17.41	6.60	0.019
		m1	Year	3	-17.42	6.59	0.019
		m2	Season	3	-23.85	0.16	0.462
		m3	Year/season	5	-24.01	0.00	0.501

Appendix 6

See Table 10.

Table 10 Candidate models fitted to the observed diet composition data and best set of models identified by the model selection (highlighted in bold, based on Δ AICc threshold value <4)

Model	Covariate	df	AICc	Δ AICc	Weight
m0	Null	2	76.6	9.6	0.007
m1	Year	3	75.2	8.2	0.015
m2	Season	3	71.8	4.8	0.082
m3	Year/season	5	67.0	0.0	0.896

References

- Ainley DG (1985) The biomass of birds and mammals in the Ross Sea. In: Siegfried WR, Candy PR, Laws RM (eds) Antarctic nutrient cycles and food webs. Springer, Berlin, pp 498–575
- Ainley DG (2002a) The Ross Sea, Antarctica: where all ecosystem processes still remain for study. *Mar Ornithol* 30:55–62
- Ainley DG (2002b) The Adie penguin: bellwether of climate change. Columbia University Press, New York
- Ainley DG (2004) Acquiring a base datum of normality for a marine ecosystem: the Ross Sea, Antarctica. CCAMLR document number: WG-EMM-04/20. Hobart
- Ainley DG, Boekelheide RJ (1990) Seabirds of the Farallon Islands: ecology, dynamics, and structure of an upwelling-system community. Stanford University Press, USA
- Ainley DG, Jacobs SS (1981) Affinity of seabirds for ocean and ice boundaries in the Antarctic. *Deep-Sea Res* 28A:1173–1185
- Ainley DG, O'Conner EF, Boekelheide RJ (1984) The marine ecology of birds in the Ross Sea, Antarctica. *Ornithol Mono* 32:97
- Ainley DG, Wilson PR, Barton KJ, Ballard G, Nur N, Karl B (1998) Diet and foraging effort of Adie penguins in relation to pack-ice conditions in the southern Ross Sea. *Polar Biol* 20:311–319
- Ainley DG, Ballard G, Barton KJ, Karl BJ, Rau GH, Ribic CA, Wilson PR (2003) Spatial and temporal variation of diet within a presumed metapopulation of Adie penguins. *Condor* 105:95–106
- Ainley DG, Ribic CA, Ballard G, Heath S, Gaffney I, Karl BJ, Barton KJ, Wilson PR, Webb S (2004) Geographic structure of Adie penguin populations: overlap in colony-specific foraging areas. *Ecol Mono* 74:159–178
- Ainley DG, Toniolo V, Ballard G, Barton K, Eastman J, Karl B, Focardi S, Kooyman G, Lyver P, Olmastroni S, Stewart BS, Testa JW, Wilson P (2006) Managing ecosystem uncertainty: critical habitat and dietary overlap of top-predators in the Ross Sea. CCAMLR document EMM 06–07. Hobart
- Ainley DG, Ballard G, Blight LK, Ackley S, Emslie SD, Lescroart A, Olmastroni S, Townsend SE, Tynan CT, Wilson P, Woehler E (2009) Impacts of cetaceans on the structure of southern ocean food webs. *Mar MammSci*. doi:10.1111/j.1748-7692.2009.00337.x
- Ainley DG, Russell J, Jenouvrier S, Woehler E, Lyver POB, Fraser WR, Kooyman GL (2010) Antarctic penguin response to habitat change as earth's troposphere reaches 2 above pre-industrial levels. *Ecol Mono* 80:49–66
- Ashmole NP, Ashmole MJ (1967) Comparative feeding ecology of sea birds of a tropical oceanic island. Peabody Museum. Yale University, Bulletin 24, 131
- Azzali M, Leonori I, De Felice A, Russo A (2006) Spatial-temporal relationships between two euphausiid species in the Ross Sea. *Chem and Ecol* 22(Suppl 1):219–233
- Ballance LT, Ainley DG, Hunt GL Jr (2001) Seabird foraging ecology. In: Steele J, Thorpe S, Turekian K (eds) Encyclopedia of ocean sciences. Academic Press, London, pp 2636–2644
- Ballance LT, Ainley DG, Ballard G, Barton K (2009) An energetic correlate between colony size and foraging effort in seabirds, an example of the Adie penguin *Pygoscelis adeliae*. *J Avian Biol* 40:279–288
- Ballard G (2010) Biotic and physical forces as determinants of Adie penguin population location and size. Ph. D. thesis. University of Auckland, New Zealand
- Ballard G, Ainley DG, Ribic CA, Barton KJ (2001) Effect of instrument attachment and other factors on foraging trip duration and nesting success of Adie penguins. *Condor* 103:481–490
- Ballard G, Ainley DG, Barton KJ, Lescroart A, Toniolo V, Lyver P, Wilson PR (2006) The influence of competition and physical processes on penguin foraging strategies: a study of Adie penguins at three colonies of radically different size. 6th international penguin conference, 3–7 Sept 2006, Hobart
- Ballard G, Dugger KM, Nur N, Ainley DG (2010a) Foraging strategies of Adie penguins: adjusting body condition to cope with environmental variability. *Mar Ecol Prog Ser* 405: 287–302
- Ballard G, Toniolo V, Ainley DG, Parkinson CL, Arrigo KR, Trathan PN (2010b) Responding to climate change: Adie penguins confront astronomical and ocean boundaries. *Ecol* 91:2044–2069
- Bannasch R, Wilson RP, Culik B (1994) Hydrodynamic aspects of design and attachment of a back-mounted device in penguins. *J Exp Biol* 194:83–96
- Barrera-Oro E (2002) The role of fish in the Antarctic marine food web: differences between inshore and offshore waters in the southern scotia arc and west Antarctic Peninsula. *Antarct Sci* 14:293–309
- Baum JK, Worm B (2009) Cascading top-down effects of changing oceanic predator abundances. *J Animal Ecol*. doi:10.1111/j.1365-2656.2009.01531.x
- BirdLife International (2004) Tracking ocean wanderers: the global distribution of albatrosses and petrels. Results from the global procellariiform tracking workshop, 1–5 Sept 2003, Gordon's Bay, South Africa. BirdLife International, Cambridge

- Börger L, Franconi N, De Michele G, Gantz A, Meschi F, Manica A, Freitas C, Lydersen C, Fedak MA, Kovacs KM (2008) A simple new algorithm to iter marine mammal Argos locations. *Mar Mammal Sci* 24:315–325
- Calenge C (2006) The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecol Model* 197:516–519
- Chapman EW, Ribic CA, Fraser WR (2004) The distribution of seabirds and pinnipeds in marguerite bay and their relationship to physical features during austral winter 2001. *Deep Sea Res Part II* 51:2261–2278
- Clarke J, Manly B, Kerry K, Gardner H, Franchi E, Corsolini S, Focardi S (1998) Sex differences in Adélie penguin foraging strategies. *Polar Biol* 20:248–258
- Clarke J, Kerry K, Irvine L, Phillips B (2002) Chick provisioning and breeding success of Adélie penguins at becharvais Island over eight successive seasons. *Polar Biol* 25:21–30
- Daunt F, Benvenuti S, Harris MP, Dall'Antonia L, Elston DA, Wanless S (2002) Foraging strategies of the black-legged kittiwake *Rissa tridactyla* at a north sea colony: evidence for a maximum foraging range. *Mar Ecol Prog Ser* 245:239–247
- DeWitt HH (1970) The character of the midwater sh fauna of the Ross Sea, Antarctica. In: Holdgate MW (ed) *Antarctic Ecology*, vol 1. Academic Press, London, pp 305–314
- Donnelly J, Torres JJ, Sutton TT, Simoniello C (2004) Fishes of the eastern Ross Sea, Antarctica. *Polar Biol* 27:637–650
- Ducklow HW, Baker K, Martinson DG, Quetin LB, Ross RM, Smith RC, Stammerjohn SE, Vernet M, Fraser WR (2007) Marine pelagic ecosystems: the west Antarctic Peninsula. *Phil Trans Royal Soc B* 362:67–94
- Eastman JT, Hubold G (1999) The sh fauna of the Ross Sea, Antarctica. *Antarc Sci* 11:293–304
- Emslie SD, Patterson WP (2007) Abrupt recent shift in $\delta^{18}C$ and $\delta^{15}N$ values in Adélie penguin eggshell in Antarctica. *Proc Nat Acad Sci* 104:1666–11669
- Endo Y, Asari H, Watanuki Y, Kato A, Kuroki M, Nishikawa J (2002) Biological characteristics of euphausiids preyed upon by Adélie penguins in relation to sea-ice conditions in lutzow-holm bay, Antarctica. *Polar Biol* 25:730–738
- Fieberg J, Kochanny CO (2005) Quantifying home-range overlap: the importance of the utilization distribution. *J Wild Manage* 69:1346–1359
- Fischer W, Hureau JC (1985) *FAO species identification sheets for fishery purposes: Southern Ocean, Vols 1, 2*. United Nations, FAO, Rome, Italy
- Flores H, van Franeker JA, Siegel V, Haraldsson M, Strass V, Meesters EHWG, Bathmann U, Wolff WJ (2009) Antarctic krill species (Crustacea: Euphausiidae) under sea ice and in the open surface layer. In: Flores H (ed) *Frozen desert alive. The role of sea ice for pelagic macrofauna and its predators: implications for the Antarctic pack-ice food web*. Ponsen and Looien, Germany, pp 155–179
- Forcada J, Trathan PN, Reid K, Murphy EJ, Croxall JP (2006) Contrasting population changes in sympatric penguin species in association with climate warming. *Global Change Biol* 12:411–423
- Forcada J, Trathan PN, Murphy EJ (2008) Life history buffering in Antarctic mammals and birds against changing patterns of climate and environmental variation. *Global Change Biol* 14:2473–2488
- Fraser WR, Trivelpiece WZ (1996) Factors controlling the distribution of seabirds: winter-summer heterogeneity in the distribution of Adélie penguin populations. *Antarc Res Series* 70:257–272
- Frederiksen M, Wanless S, Harris MP, Rothery P, Wilson LJ (2004) The role of industrial fisheries and oceanographic change in the decline of north sea black-legged kittiwakes. *J App Ecology* 41:1129–1139
- Friedlaender AS, Lawson GL, Halpin PN (2008) Evidence of resource partitioning between humpback and minke whales around the western Antarctic Peninsula. *Mar Mammal Sci* 25:402–415
- Georges JY, Guinet C, Jouventin P, Weimerskirch H (1997) Satellite tracking of seabirds: interpretation of activity pattern from the frequency of satellite locations. *Ibis* 139:403–405
- Giese M (1996) Effects of human activity on Adélie penguin *Pygoscelis adeliae* breeding success. *Biol Cons* 75:157–164
- Grémillet D, Sue Lewis S, Drapeau L, van Der Lingen CD, Huggett JA, Coetsee JC, Verheye HM, Daunt F, Wanless S, Ryan PG (2008) Spatial match-mismatch in the benguela upwelling zone: should we expect chlorophyll and sea-surface temperature to predict marine predator distributions? *J Appl Ecol* 45:610–621
- Halpern BS, Walbridge S, Selkoe KA, Kappel CV, Micheli F, D'Agrosa C, Bruno JF, Casey KS, Ebert C, Fox HE, Fujita R, Heinemann D, Lenihan HS, Madin EMP, Perry MT, Selig ER, Spalding M, Steneck R, Watson R (2008) A Global map of human impact on marine ecosystems. *Science* 319:948–952
- Hilborn R, Branch TA, Ernst B, Magnusson A, Minte-Vera CV, Scheuerell MD, Valero JL (2003) State of the world's fisheries. *Annu Rev Environ Resour* 28:359–399. doi:1146/annurev.energy.28.050302.105509
- Hinke JT, Salwicka K, Trivelpiece SG, Watters GM, Trivelpiece WZ (2007) Divergent responses of *Pygoscelis* penguins reveal a common environmental driver. *Oecologia* 153:845–855
- Iverson SJ, Springer AM, Kitaysky AS (2007) Seabirds as indicators of food web structure and ecosystem variability: qualitative and quantitative diet analyses using fatty acids. *Mar Ecol Prog Ser* 352:235–244
- Jacobs SS (1991) On the nature and significance of the Antarctic slope front. *Mar Chem* 35:9–24
- Kato A, Ropert-Coudert Y, Naito Y (2002) Changes in Adélie penguin breeding populations in lutzow-holm bay, Antarctica, in relation to sea-ice conditions. *Polar Biol* 25:934–938
- Kato A, Watanuki Y, Naito Y (2003) Annual and seasonal changes in foraging site and diving behavior in Adélie penguins. *Polar Biol* 26:389–395
- Leopold A (1949) *A sand county almanac*. Ballantine, New York
- Lescroart A, Bost C-A (2005) Foraging under contrasting oceanographic conditions: the gentoo penguin at kerguelen archipelago. *Mar Ecol Prog Ser* 302:245–261
- Lescroart A, Ballard G, Toniolo V, Barton KJ, Wilson PR, Lyver POB, Ainley DG (2010) Working less to gain more: when breeding quality relates to foraging efficiency. *Ecol* 91:2044–2055
- Lewis S, Wanless S, Wright PJ, Harris MP, Bull J, Elston DA (2001) Diet and breeding performance of black-legged kittiwakes *Rissa tridactyla* at a north sea colony. *Mar Ecol Prog Ser* 221:277–284
- Lishman GS (1985) The food and feeding ecology of Adélie penguins (*Pygoscelis adeliae*) and Chinstrap Penguins (*P. antarctica*) at Signy Island, South Orkney Islands. *J Zool* 205:245–263
- MacLeod CJ, Adams J, Lyver POB (2008) At-sea distribution of satellite-tracked grey-faced petrel *Pterodroma macroptera gouldi*, captured on the ruamaahua (Aldermen) Islands, New Zealand. *Papers Proc Royal Soc Tas* 142:73–88
- MathWorks (2007) *MATLAB Version 2006*. The MathWorks Inc., Natick
- Murphy RC (1925) *Bird islands of Peru: the record of a sojourn on the west coast*. G.P. Putnam's Sons, New York
- Nicholls DG, Robertson CJR, Murray MD (2007) Measuring accuracy and precision for CLS: argos satellite telemetry locations. *Notornis* 54:137–157
- O'Driscoll RL, Macaulay GJ, Gauthier S, Pinkerton M, Hanchet S (2009) Preliminary acoustic results from the New Zealand

- IPY-CAML survey of the Ross Sea region in Feb–Mar 2008. Van Winkle W (1975) Comparison of several probabilistic home-range models. *J Wild Manage* 39:118–123
- Osterblom HO, Casini M, Olsson O, Bignert A (2006) Fish, seabirds and trophic cascades in the Baltic Sea. *Mar Ecol Prog Ser* 323:233–238
- Osterblom HO, Hansson S, Larsson U, Hjerne O, Wulff F, Elmgren R, Folke C (2007) Human-induced trophic cascades and ecological regime shifts in the Baltic Sea. *Ecosystems* 10:877–889
- Pauly D, Christiansen V, Dalsgaard J, Froeser R, Torres F Jr (1998) Fishing down marine food webs. *Science* 279:860–863
- Perry RI, Cury P, Brander K, Jennings S, Moann C, Planque B (2009) Sensitivity of marine systems to climate and fishing: Concepts, issues and management responses. *J Mar Syst*. doi: 10.1016/j.jmarsys.2008.12.017
- Puddicombe RA, Johnstone GW (1988) The breeding season diet of Adélie penguins at the Vestfold Hills, East Antarctica. *Hydrobiologia* 165:239–253
- R Development Core Team (2007) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. ISBN 3-900051-07-0. <http://www.R-project.org>
- Ribic CA, Chapman E, Fraser WR, Lawson GL, Wiebe PH (2008) Top predators in relation to bathymetry, ice and krill during austral winter in Marguerite Bay, Antarctica. *Deep Sea Res Part II* 55(3–4):485–499
- Rodary D, Wienecke BC, Bost CA (2000) Diving behavior of Adélie penguins *Pygoscelis adeliae* at Dumont d'Urville, Antarctica: nocturnal patterns of diving and rapid adaptations to changes in sea-ice condition. *Polar Biol* 23:113–120
- Sala A, Azzali M, Russo A (2002) Krill of the Ross Sea: distribution, abundance and demography of *Euphausia superba* and *Euphausia crystallorophias* during the Italian Antarctic expedition (Jan–Feb 2000). *Sci Mar* 66:123–133
- Salihoglu B, Fraser WR, Hofmann EE (2001) Factors affecting edging weight of Adélie penguin (*Pygoscelis adeliae*) chicks: a modeling study. *Polar Biol* 24:328–337
- Smith RC, Domack E, Emslie S, Fraser WR, Ainley DG, Baker K, Kennett J, Leventer A, Mosley-Thompson E, Stammerjohn S, Vernet M (1999) Marine ecosystem sensitivity to historical climate change: Antarctic Peninsula. *Bioscience* 49:393–404
- Taki K, Yabuki T, Noiri Y, Hayashi T, Naganobu M (2008) Horizontal and vertical distribution and demography of euphausiids in the Ross Sea and its adjacent waters in 2004/2005. *Polar Biol* 31:1343–1356
- Tremblay Y, Cherel Y (2003) Geographic variation in the foraging behavior, diet and chick growth of rockhopper penguins. *Mar Ecol Prog Ser* 251:279–297
- Tremblay Y, Shaffer SA, Fowler SL, Kuhn CE, McDonald BI, Weise MJ, Bost CA, Weimerskirch H, Crocker DE, Goebel ME, Costa DP (2006) Interpolation of animal tracking data in a fluid environment. *J Exp Biol* 209:128–140
- Watanuki Y, Mori Y, Naito Y (1992) Adélie penguin parental activities and reproduction: effects of device size and timing of its attachment during chick rearing period. *Polar Biol* 12:539–544
- Watanuki Y, Kato A, Mori Y, Naito Y (1993) Diving performance of Adélie penguins in relation to food availability in fast sea-ice areas: comparison between years. *J Animal Ecol* 62:634–646
- Watanuki Y, Mori Y, Naito Y (1994) *Euphausia superba* dominates in the diet of Adélie penguins feeding under the sea-ice in the shelf areas of Enderby Land in summer. *Polar Biol* 14:429–432
- Watanuki Y, Kato A, Naito Y, Robertson G, Robinson S (1997) Diving and foraging behavior of Adélie penguins in areas with and without fast sea-ice. *Polar Biol* 17:296–304
- Watanuki Y, Miyamoto Y, Kato A (1999) Dive bouts and feeding sites of Adélie penguins rearing chicks in an area with fast sea-ice. *Waterbirds* 22:120–129
- Watermeyer KE, Shannon LJ, Roux JP, Griffiths CL (2008a) Changes in the trophic structure of the southern Benguela before and after the onset of industrial fishing. *Afr J Mar Sci* 30:351–382
- Watermeyer KE, Shannon LJ, Roux JP, Griffiths CL (2008b) Changes in the trophic structure of the northern Benguela before and after the onset of industrial fishing. *Afr J Mar Sci* 30:383–403
- Weimerskirch H (2001) Seabird demography and its relationship with the marine environment. In: Schreiber EA, Burger J (eds) (2001) *Biology of marine birds*. CRC Marine Biology Series, 1 pp 115–135
- Wilson RP (1984) A new improved stomach pump for penguins and other seabirds. *J Field Ornithol* 55:109–112
- Wilson RP, Wilson M-PTJ (1989) Tape: a package-attachment technique for penguins. *Wild Soc Bull* 17:77–79
- Wilson RP, Grant WS, Duffy DC (1986) Recording devices on free-ranging marine animals: does measurement affect foraging performance? *Ecology* 67:1091–1093
- Wilson RP, Coria NR, Spairani HJ, Adelung D, Culik B (1989) Human-induced behavior in Adélie penguins *Pygoscelis adeliae*. *Polar Biol* 10:77–80
- Wilson RP, Culik B, Danfeld R, Adelung D (1991) People in Antarctica—how much do Adélie penguins *Pygoscelis adeliae* care? *Polar Biol* 11:363–370
- Wilson RP, Putz K, Peters G, Culik B, Sclaro JA, Charrassin J-B, Ropert-Coudert Y (1997) Long-term attachment of transmitting and recording devices to penguins and other seabirds. *Wild Soc Bull* 25:101–106
- Woehler EJ (1993) The distribution and abundance of Antarctic and Subantarctic. Scientific Committee on Antarctic Research, Cambridge