Deep-Sea Research II 58 (2011) 1710–1718

Contents lists available at ScienceDirect

Deep-Sea Research II

journal homepage: www.elsevier.com/locate/dsr2

Characterization of winter foraging locations of Adélie penguins along the Western Antarctic Peninsula, 2001–2002

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ARTICLE INFO

Article history:
Received 20 May 2009
Received in revised form
16 August 2010
Accepted 5 October 2010
Available online 16 December 2010

Keywords:
Antarctica
Western Antarctic Peninsula
Adélie penguins
Bathymetry
Environmental factors
Feeding behavior

ABSTRACT

In accord with the hypotheses driving the Southern Ocean Global Ocean Ecosystems Dynamics (SO GLOBEC) program, we tested the hypothesis that the winter foraging ecology of a major top predator in waters off the Western Antarctic Peninsula (WAP), the Adélie penguin (*Pygoscelis adeliae*), is constrained by oceanographic features related to the physiography of the region. This hypothesis grew from the supposition that breeding colonies in the WAP during summer are located adjacent to areas of complex bathymetry where circulation and upwelling processes appear to ensure predictable food resources. Therefore, we tested the additional hypothesis that these areas continue to contribute to the foraging strategy of this species throughout the non-breeding winter season. We used satellite telemetry data collected as part of the SO GLOBEC program during the austral winters of 2001 and 2002 to characterize individual penguin foraging locations in relation to bathymetry, sea ice variability within the pack ice, and wind velocity and divergence (as a proxy for potential areas with cracks and leads). We also explored differences between males and females in core foraging area overlap. Ocean depth was the most influential variable in the determination of foraging location, with most birds focusing their effort on shallow (<200 m) waters near land and on mixed-layer (200–500 m) waters near the edge of deep troughs. Within-ice variability and wind (as a proxy for potential areas with cracks and leads) were not found to be influential variables, which is likely because of the low resolution satellite imagery and model outputs that were available. Throughout the study period, all individuals maintained a core foraging area separated from other individuals with very little overlap. However, from a year with light sea ice to one with heavy ice cover (2001–2002), we observed an increase in the overlap of individual female foraging areas with those of other birds, likely due to restricted access to the water column, reduced prey abundance, or higher prey concentration. Male birds maintained separate core foraging areas with the same small amount of overlap, showing no difference in overlap between the years. While complex bathymetry was an important physical variable influencing the Adélie penguin's foraging, the analysis of sea ice data of a higher resolution than was available for this study may help elucidate the role of sea ice in affecting Adélie penguin winter foraging behavior within the pack ice.

1. Introduction

It is well established, with regard to oceanic systems worldwide, that physical features affect the circulation, distribution and intensity of productivity (e.g. eddies, plumes, and fronts that result in retention of zooplankton) that can affect top predator distributions (Ribic et al. (2011) and review therein). Along the Western Antarctic Peninsula (WAP), top predator distribution and abundance can be linked to two dominant physical environmental variables; complex bathymetry and sea ice (Chapman et al., 2004; Fraser and Trivelpiece, 1996; Ribic et al., 1991; Ribic et al., 2008). That these two physical variables interact with biological characteristics to create predictable areas of high productivity in polar regions is a long-standing hypothesis (Brown, 1980; Fraser and Trivelpiece, 1996). An example of this is observed when nutrient upwelling occurs along deep canyons, combined with vertical stabilization of the water column caused by low density, fresh melt-water creates an environment conducive to the formation of ice edge phytoplankton blooms (Smith and Nelson, 1986).

A recent review of mammalian marine predators in the WAP defined the foraging habitat in terms of physical oceanographic features that enhance the availability of prey (Costa et al., 2010).

Sea ice is a dominant physical feature of the WAP, which affects food webs at all levels, from primary producers to top predators at multiple

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doi:10.1016/j.dsr2.2010.10.054

spatial scales (Fraser and Trivelpiece, 1996; Trivelpiece and Fraser, 1996; Ducklow et al., 2007; Ribic et al., 2011). Phytoplankton blooms can form at the sea ice edge (Smith and Nelson, 1986), Antarctic krill (*Euphausia superba*) are known to feed underneath the sea ice edge (Ainley, 2002), and top predators feed on krill under the ice and use it for rest and refuge (Fraser and Trivelpiece, 1996; Loeb et al., 1997; Ainley, 2002). Seabirds make up a large component of the top predator community in the WAP, and one of the most dominant seabird species in this community is the Adélie penguin (*Pygoscelis adeliae*) (Fraser and Trivelpiece, 1996; Trivelpiece and Fraser, 1996). In this region, Adélie penguins feed primarily on Antarctic krill concentrated under sea ice during winter (Trivelpiece and Fraser, 1996; Loeb et al., 1997; Ainley, 2002).

In support of their hypothesis that Adélie penguin colonies are found in regions with complex bottom bathymetry, Fraser and Trivelpiece (1996) noted that 80% of Adélie breeding pairs are found in 5 colony clusters associated with deep troughs. This association with troughs may continue well beyond the breeding season. Seasonal variability of the Antarctic Circumpolar Current (ACC) and off-shore forcing change the water mass properties and circulation patterns in the WAP 4–6 times throughout the year, causing intrusions of dense, Circumpolar Deep Water (CDW) onto the continental shelf (Klinck et al., 2004). Deep troughs allow this influx onto the shelf region. With temperatures warmer than those at the ocean's surface, the incursion of this nutrient-rich water results in not only higher concentrations of plankton, but also contributes, in winter, to the formation of sensible heat polynyas (i.e. areas of open water where warmer subsurface waters maintain surface temperatures above freezing) (Plötz et al., 1991; Klinck et al., 2004; Karnovsky et al., 2007; Ribic et al., 2008). During the SO GLOBEC winter cruises of 2001 and 2002, Adélie penguins were found concentrated along the deep trough located in Marguerite Bay, even when krill concentrations may have been higher in other parts of the bay (Ribic et al., 2008).

There are relatively few studies on how individual Adélie penguins use the marine environment during winter (see Ainley et al., 1992, 1993, 1994; Davis et al., 1996; Fraser and Trivelpiece, 1996; Davis et al., 2001; Clarke et al., 2003; Chapman et al., 2004; Ribic et al., 2008), and information on foraging activity is particularly scarce. One focus of the US SO GLOBEC program (Hofmann et al., 2002, 2004) was on the winter dynamics of top predators in the region; a primary hypothesis being investigated was that pertaining to how winter foraging ecology related to physical environmental variables (Hofmann et al., 2002). Our objective in this paper is to characterize winter foraging locations of satellite-tracked Adélie penguins in the WAP in relation to physical characteristics and to see whether the hypothesis of Fraser and Trivelpiece (1996) is supported during winter. Specifically we were interested in (1) whether Adélie penguins forage in different areas with different physical characteristics in a year with lighter than normal ice conditions versus a year with heavier ice conditions, and (2) whether foraging areas differ with sex.

2. Methods

2.1. Study area

Animals were tagged as part of four cruises conducted during austral winters in Marguerite Bay, Antarctica, in 2001 and 2002 (Fig. 1); there were two cruises completed each year (April–May and July–August). In 2001, the air temperature was typically below $-10\,^{\circ}\mathrm{C}$ and southwesterly winds periodically reached gale force (≥ 55 km/h). In 2002, air temperatures were typically below $0\,^{\circ}\mathrm{C}$, falling below $-20\,^{\circ}\mathrm{C}$ during the period between 21 and 24 August. Winds were generally from the south and southwest, and periods of strong winds ≥ 55 km/h were rare. Winter sea ice conditions differed considerably between the two years. In winter 2001, the ice edge extended north to only about 64°S while in winter 2002, the ice edge extended beyond 61°S, to the northern tip of the WAP (Stroeve and Meier, 2002; Perovich et al., 2004). Ice thickness averaged 62 cm in 2001 and 102 cm in 2002 (Perovich et al., 2004).

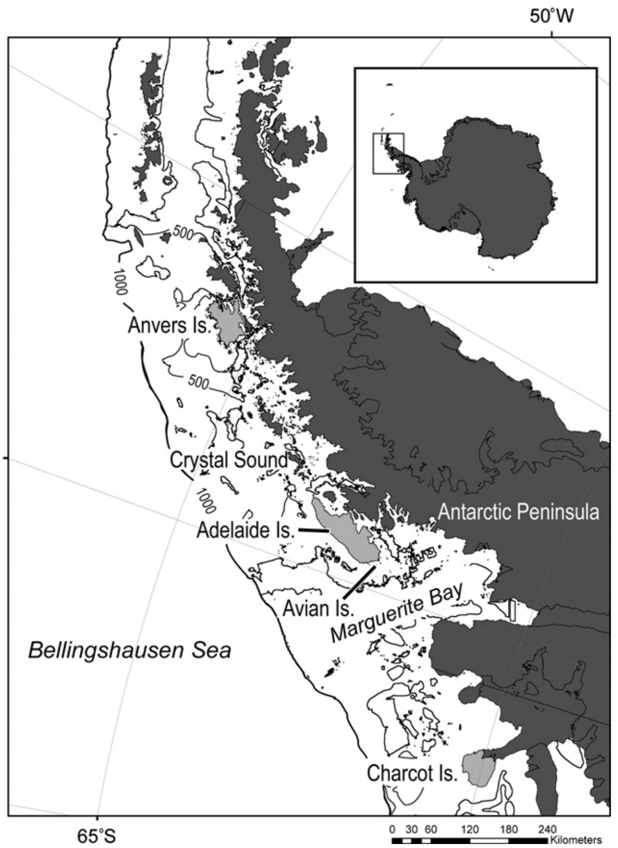

Fig. 1. Region of the Western Antarctic Peninsula Adélie penguins foraged in during this study. The winter SO GLOBEC program was centered on Marguerite Bay (68°29.5′S 70°02.3′W) south of Adelaide Island. The four tagging areas are Avian Island (2001/2002), the vicinity of Adelaide Island (2001) and Charcot Island (2001), and Crystal Sound (2002). Contour lines represent the 500 m isobath on the continental shelf and the 1000 m isobath of the continental shelf break. Coastline shapefiles courtesy of the Antarctic Digital Database V.3, Mapping and Geographic Information Center, British Antarctic Survey.

2.2. Satellite tracking

We attached Platform Terminal Transmitters (PTT) (80–82 g and 108 mm long) to the feathers of the lower backs of penguins using plastic cable ties and waterproof tape. Initially, we placed 52 PTTs on 52 individuals captured in 4 tagging areas within our study area: off Avian Island on the northern edge of Marguerite Bay (13 in 2001 and 17 in 2002), the Crystal Sound area, north of Adelaide Island (8 in 2002), off the western edge of Adelaide Island (2 in 2001 and 7 in 2002), and off Charcot Island south of Marguerite Bay (5 in 2001, Fig. 1).

We received location fixes from the ARGOS satellite-based location and data collection system (Service ARGOS, Toulouse, France, and Landover, Maryland, USA). At least four successive uplinks with the satellite during a pass are required for ARGOS to assign accuracy classes to locations (Vincent et al., 2002). These accuracy classes range from 3 (<150 m) to 0 (>1000 m). Locations with no estimate of accuracy are also collected and occur when only two (class B) or three (class A) successive uplinks are recorded: a common occurrence in the tracking of marine animals

(Vincent et al., 2002). The PTTs were programmed to send signals during daylight hours since Adélie penguins are visual foragers (Ainley, 2002). However, in an attempt to maximize battery life of the transmitters, the transmission time (duty cycle) of each PTT was varied between individuals. For example, some PTTs were programmed to transmit signals to the satellites for 16 h each day while other tags were programmed to transmit on every second or third day.

We used a variant of the Austin et al. (2003) algorithm to filter the locations. The algorithm evaluates an individual point in relation to the two points immediately preceding and the two points following it. It then employs a maximum-speed based method to filter the satellite locations. Each ARGOS location has a time/date stamp that, after the calculation of distances between consecutive points in ArcMap (ESRI, 2009), allowed us to calculate the speed of travel. We made three assumptions when developing our filtering method. First, all quality 3 points were initially considered valid, second, quality 2, 1, and 0 points are more likely (in that order) to be valid than are the A and B quality points; and third, all points (no matter the quality) have to satisfy the maximum-speed threshold of <7 km/h, in order to be valid. The maximum of 7 km/h is assumed to be the maximum rate of speed an individual penguin travels when not being pursued by a predator (Ainley, 2002; Clarke et al., 2006).

Following initial filtering, we used a second filtering process to estimate foraging locations. This process also used a maximum-speed threshold to discriminate locations into those of foraging and traveling behaviors. Previous studies on marine predators have found transit rates to be a good indicator of foraging effort (Kuhn et al., 2009; Robinson et al., 2010). In this procedure, 4 km/h was considered the maximum speed that would be found between locations in cases where individuals were active in foraging (Clarke et al., 2006). Locations ≤ 4 km/h were separated into categories defined by the critical rates of ≤ 1, 1–2, 2–3, and 3–4 km/h. All points ≤ 4 km/h were grouped into clusters, where a cluster was defined as at least 3 valid points of speeds ≤ 4 km/h within a satellite listening period (duty cycle). Within each cluster, we identified the number of points in each of the 4 categories of critical rates. Those clusters with $\geq 50\%$ of their locations in the ≤ 1 and 1–2 km/h ranges were assumed to be foraging clusters. Those clusters that had $\geq 50\%$ of their locations in the 2–3 and 3–4 km/h ranges were flagged for additional scrutiny (questionable clusters). At least one point in a cluster must have an associated speed of ≤ 2 km/h for the cluster to be considered a foraging cluster. All foraging clusters were then replaced by a single foraging point positioned at the geographic center of the cluster. This allowed us to avoid pseudo-replication when associating physical variables with foraging locations.

2.3. Bathymetry

We generated a multi-resolution map layer of bathymetry of the WAP from the Antarctic Multibeam Bathymetry Synthesis (AMBS) project, an Internet resource providing integrated bathymetry and geophysical data from the Southern Ocean for researchers (Carbotte et al., 2007). Using the data exploration and visualization map portal, GeoMapApp, we downloaded sections of this multi-resolution gridded dataset, and merged them into one grid of 50 m resolution in ArcMap (Environmental Systems Research Institute (ESRI, 2009). High-resolution bathymetry data (50 m) on the WAP is limited to specific canyons and troughs and areas that lay along the cruise tracks of Antarctic research vessels (Carbotte et al., 2007). The remaining areas covered by this data layer were of varying resolutions, the coarsest being 5 km derived from the BEDMAP (Bed Elevation DEM-map) seabed topography compilation developed by the British Antarctic Survey (Lythe and Vaughan, 2000). This multi-resolution bathymetry layer represented the best data available for analysis at the time.

2.4. Sea ice

Daily sea ice concentration and extent were determined through the use of satellite imagery provided by NASA's Defense Meteorological Satellite Program's (DMSP) Special Sensor Microwave/Imager (SSM/I) near-polar orbiting satellite (Stammerjohn and Smith, 1996). The 25 km resolution images processed using the Bootstrap algorithm were downloaded from the National Snow and Ice Data Center (NSIDC) website (Stroeve and Meier, 2002) and were imported into ArcMap (ESRI, 2009).

Because the resolution of the sea ice images could obscure the presence of cracks and leads as well as potentially polynyas, we used wind velocity and divergence as proxy variables that could indicate the presence of openings (i.e. cracks and leads) in the sea ice. Along with ocean circulation and currents, wind can affect sea ice development and movement and is responsible primarily for formation of latent heat polynyas adjacent to coastlines (Maqueda et al., 2004). Surface winds have been associated with fluctuations in sea ice thickness and concentration through sea ice movement and ridging (Rigor et al., 2002; Köberle and Gerdes, 2003). Large values of wind velocity and divergence, especially near land, could indicate a local sea ice structure favorable for accessing the water column not evident at the 25 km satellite resolution of the sea ice imagery available to us. We determined the horizontal wind field parameters of velocity and divergence (the horizontal outflow of wind from an area) from the output of the Antarctic Mesoscale Prediction System (AMPS) model (provided by M. Dinniman and J. Klinck, Old Dominion University). The AMPS model serves as a real-time, multi-resolution forecast system for all of Antarctica, and aids in science efforts and emergency operations of the continent (Powers et al., 2003). The daily AMPS model, whose resolution was 30 km, was limited in its geographic coverage to mostly inshore regions. Bathymetry, sea ice, and wind divergence and velocity data were imported into ArcMap (ESRI, 2009) as ESRI GRID files, and foraging locations were assigned the parameter value of the grid cell they were located in.

3. Data analysis

3.1. Foraging in relation to physical variables

We used data collected from 9 May through 30 September 2001 and from 19 April through 30 September 2002. This allowed for the greatest temporal overlap among tagged individuals within a year. We only used those individuals with >25 foraging data points in the analysis. Although below the minimum of 30 observations recommended by Seaman et al. (1999), a minimum of 25 observations per individual allowed us to keep as many individuals as possible without potentially influencing the analysis with small sample sizes. This resulted in the analysis of 36 out of the original 52 individuals tagged. In 2001 the birds studied were from Avian Island (4 males and 5 females), from the vicinity of Adelaide Island (1 male and 1 female), and from Charcot Island (5 males). In 2002, the birds studied were from Avian Island (5 males and 9 females), and from Crystal Sound (4 males and 2 females) (Fig. 1).

We used as explanatory variables, the bathymetry, sea ice concentration, and wind velocity and divergence. Using the Spatial Analyst extension in ArcMap (ESRI, 2009), we extracted values of these variables at each foraging location from the datasets described above.

For analysis of satellite telemetry data, we based our study design on the sampling design II of Manly et al. (2002), where the individual is the primary sampling unit. We compared the sample of used resource units (i.e. the foraging locations) with a sample of available units (i.e. randomly chosen points) (sampling protocol A; Manly et al., 2002). To determine the available resource units, we generated random points using the Hawth's Tools extension (Beyer, 2004) in ArcMap (ESRI, 2009). An equivalent number of random locations as active foraging locations were generated for each individual. We restricted random point generation to within a geographical area bounded by the mainland peninsula, the sea ice edge (defined as having $\leq 15\%$ ice concentration), and the maximum north–south range in which all individual locations were observed in that season. This limited spatially the areas available to those where an individual could reasonably be expected to be found during the study period. Physical variable values were then determined for each random point in the same manner as the foraging points described above. Additional explanatory variables used were sex, individual, year, and tagging area.

We restricted our analysis, which included wind field variables, to birds that were tagged off Avian Island and foraged in Marguerite Bay (2001: 3 males, 5 females; 2002: 5 males, 7 females). This required us to remove 1 male (2001) and 2 females (2002) from this analysis because they left Marguerite Bay soon after they were tagged. We could not use the wind variable in analysis of the full dataset because the geographic extent of the output we received from the AMPS model was not large enough to include foraging locations of all individuals. A separate set of random points was generated in this analysis, using the procedures described above; in this case, the maximum north–south range was based on the individuals that foraged in Marguerite Bay.

We used logistic regression to model the variable effects on foraging locations. Since previous studies have identified nonlinear relationships between top predators and the physical variables in this system (Chapman et al., 2004; Ribic et al., 2008), we used generalized additive models (GAMs) (Wood, 2006). To prevent overfitting in the estimation of smoothing parameters, we used Wood's (2006) recommended gamma value of 1.4. GAMs also have the ability to identify linear terms (Wood, 2006), hence linear models were used where appropriate.

We developed a set of *a priori* models for analysis; the models were the individual physical variables singly and in combination with the other explanatory variables. We also included the interaction of the physical variables with the year to determine if the overall ice condition affected how the penguins foraged in relation to the physical variables. We used Akaike's Information Criterion (AIC) to rank models (Burnham and Anderson, 2002). The best model was indicated by the lowest AIC value (minAIC). Differences between minAIC and the remaining models were calculated (deltaAIC), as were the Akaike weights. Akaike weights are considered evidence in favor of a model being the best Kullback–Leibler (K–L) model, given a suite of alternative models and a common dataset and were also used to calculate variable importance weights (Burnham and Anderson, 2002). Competitive models were those within 2 AIC units of the best model (Burnham and Anderson, 2002), and the variable with the greatest importance weight was determined. Analyses were performed in the statistics package R (R 2007).

To aid in the interpretation of relationships, we grouped ocean depth and ice concentration values into categories. Ocean depth classes were classified into surface (depth to ocean floor <200 m), mixed-layer (200–500 m), and deep trough (>500 m). Ocean depth classes were assigned so as to represent ocean depth at foraging locations and they represented hydrographic boundaries in the water column, specifically the depth of the permanent pycnocline (200 m), that of the CDW (200–500 m), and that of the Lower CDW (LCDW) (>500 m) that is characteristic of deep, off-shelf waters (Klinck et al., 2004). The ice concentration classes considered were the open water/ice edge (0–20% ice concentration), light ice (21–50% ice concentration), medium ice (51–79% ice concentration), and heavy ice (80–100% ice concentration).

3.2. Overlap in foraging areas

To determine whether differences exist between the locations of foraging areas of individuals and those between sexes, we calculated kernel density estimates of the core foraging areas (50% probability level) (Worton, 1989; Wood et al., 2000). We used only birds that were tagged on Avian Island for this analysis, because most birds were tagged at that site during both years. Furthermore, only those birds that stayed in Marguerite Bay were included in the overlap analysis (2001: 3 males, 5 females; 2002: 5 males, 7 females) since we were interested in evaluating the degree of overlap of those individuals that did not exhibit the winter migrating behavior observed in previous studies (Davis et al., 1996, 2001; Clarke et al., 2003). We used the most common technique, a two-dimensional (2-D) Gaussian kernel density estimator to determine the core foraging areas. This kernel method has been recommended for the estimation of an animal's utilization distribution (UD) (Worton, 1989, 1995), a measure of an individual's probability of use across a landscape (Kernohan et al., 2001). The estimator weights locations according to a bivariate Gaussian distribution, centered on a point on a grid placed across the landscape of point locations (Wood et al., 2000; Amstrup et al., 2004). Percent volume contour levels of UDs are calculated and represent the boundary of the area that contains *x*% of the volume of the probability density distribution. We calculated core foraging areas (50% volume contour) with the "adehabitat" package in R (Calenge, 2006), using a 50 m grid cell size, and plotted them in ArcMap (ESRI, 2009). For consistency, a smoothing parameter was chosen using the *ad hoc* method, because, as verified from our initial attempts, the Least Squares Cross Validation (LSCV) method does not work in some cases (Seaman and Powell, 1998). To quantify the amount of overlap of core foraging areas, we used the utilization distribution overlap index (UDOI) (Fieberg and Kochanny, 2005). Values of this index range from 0 (no overlap) to 1 (both UDs have a uniform distribution and 100% overlap) (Fieberg and Kochanny, 2005). For each individual, we averaged the UDOI values of the same-sex overlap, opposite-sex overlap, and overall (all birds) overlap. We compared the UDOI values to determine whether core foraging area overlap was different between males and females or between years using the Wilcoxon Rank-Sum test (Conover, 1999). We chose an alpha value of 0.01 as our threshold for statistical significance as a Bonferroni-type adjustment for the numerous pairwise comparisons that we made.

4. Results

4.1. Foraging in relation to bathymetry and sea ice

While all the foraging locations occurred within the pack ice, the ocean depth alone was associated with Adélie penguin foraging

Table 1
Top 10 models for Adélie penguins foraging along the Western Antarctic Peninsula during austral winter 2001 and 2002.

Rank	Model	AIC	deltaAIC	Akaike weights
1	s(ocean depth)	5119.2	0	0.385
2	s(ocean depth)+sex	5120.2	0.93	0.242
3	s(ocean depth)+individual	5120.9	1.66	0.168
4	s(ocean depth)+year	5121.2	1.97	0.144
5	s(ocean depth)+tagging area	5122.9	3.67	0.062
6	s(ice concentration)+year	5283.3	164.09	9.00E−36
7	s(ice concentration)	5297.8	178.6	6.36E−40
8	s(ice concentration)+tagging area	5298.3	179.02	5.15E−40
9	s(ice concentration)+individual	5299	179.77	3.54E−40
10	s(ice concentration)+sex	5300.7	181.49	1.49E−40

Included are AIC values, deltaAIC, and Akaike weights. Models with rankings greater than 10 had Akaike weights smaller than 10E−40 and were not included in the table. s(variable)=spline smoothing parameter used to fit nonlinear relationship.

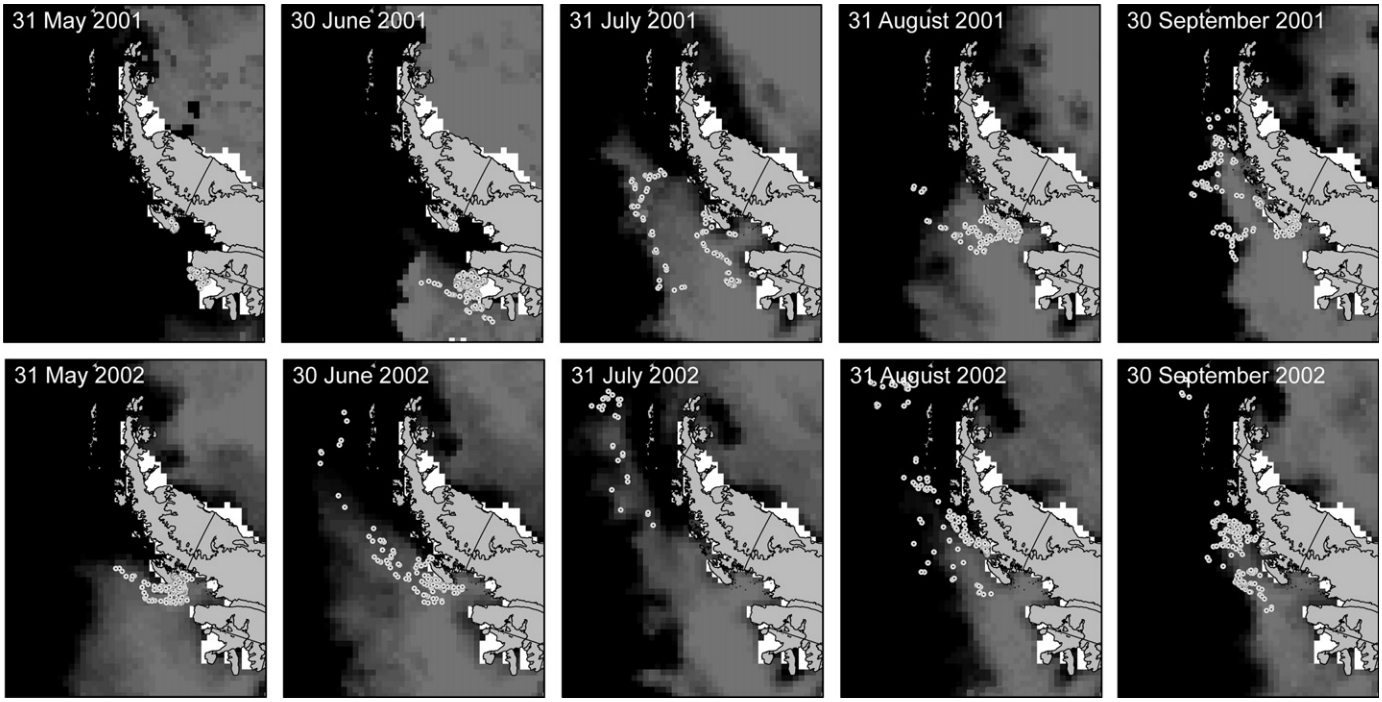

Fig. 2. Sea ice extent and concentration over the study period in 2001 and 2002 as derived from the DMSP/SSMI satellite data. Foraging locations for all individuals tracked each month are plotted on sea ice imagery from the last day of the month.

Table 2
Top 4 ranked models for the subset of Adélie penguins foraging within Marguerite Bay, Antarctica, during austral winter 2001 and 2002.

Year	Rank	Model	AIC	deltaAIC	Akaike weights
2001	1	s(ocean depth)+sex	1023.4	0	0.43
	2	s(ocean depth)	1023.8	0.33	0.37
	3	s(ocean depth)+individual	1024.9	1.49	0.20
	4	s(ice concentration)	1118.2	94.78	1.13E−21
2002	1	s(ocean depth)	987.6	0	0.55
	2	s(ocean depth)+individual	989.2	1.64	0.24
	3	s(ocean depth)+sex	989.5	1.86	0.21
	4	s(ice concentration)	1156.5	168.89	1.16E−37

Included are AIC values, deltaAIC, and Akaike weights. This subset was analyzed separately in order to include wind divergence and velocity generated from the AMPS wind model. s(variable) = spline smoothing parameter used to fit nonlinear relationship.

locations in the pack ice when analyzing our full dataset (Table 1). The minAIC model contained ocean depth as the only physical variable, with variable importance equal to 1. Adélie penguin foraging locations within the pack ice (Fig. 2) were not associated with variability in ice concentration when we considered our full dataset. Ice concentration was not present in any of the competing models and possessed a variable importance weight of $<10E-30$ (Table 1). As for the subset of Avian Island birds, which included wind divergence and velocity (as a proxy for potential areas with cracks and leads), only ocean depth was important in the determination of foraging locations in both years since either the minAIC model (2002) or the most parsimonious of the competing models (2001) contained ocean depth alone as a variable (Table 2).

Foraging location had a nonlinear relationship with ocean depth (Table 1). The probability of occurrence of a foraging bird reached a maximum where ocean depths were between 150 and 175 m and declined in areas with increasing ocean depths (Fig. 3). Specifically, birds fed in waters where the ocean depth was less than 200 m (surface depth class), which is more than that expected by chance (29% for foraging points; 12% for random points), as well as in waters where the ocean depth was 200–500 m (mixed-layer depth class) (45% for foraging points; 35% for random points). The birds fed less than expected in areas where ocean depths were greater than 500 m (deep trough depth class), or in waters that were off the continental shelf (26% for foraging points; 53% for random points).

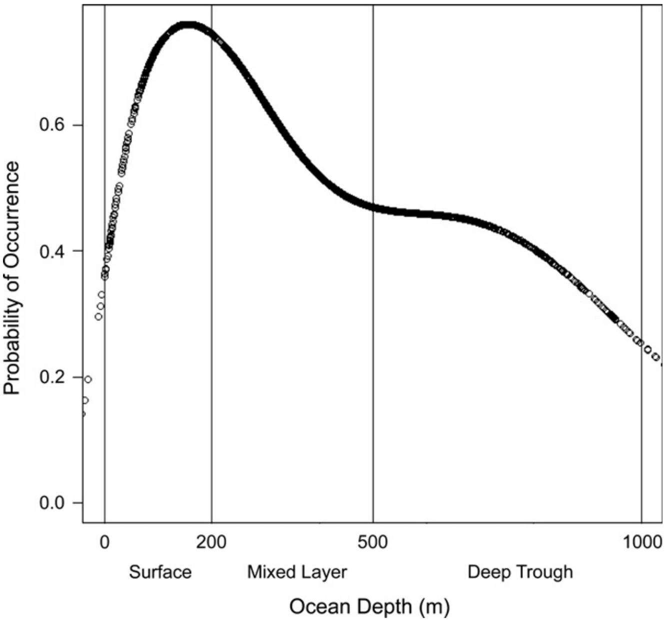

Fig. 3. Probability of occurrence of foraging birds by ocean depth for Adélie penguins foraging along the Western Antarctic Peninsula during austral winter 2001 and 2002. Solid lines represent cutoffs for three depth classes.

Foraging locations in waters with deeper bottom depths were largely due to 3 birds, one male (2001) and two females (2002), that traveled far from the Avian Island tagging area, up the peninsula and well off the continental shelf region (Fig. 4A). These birds were

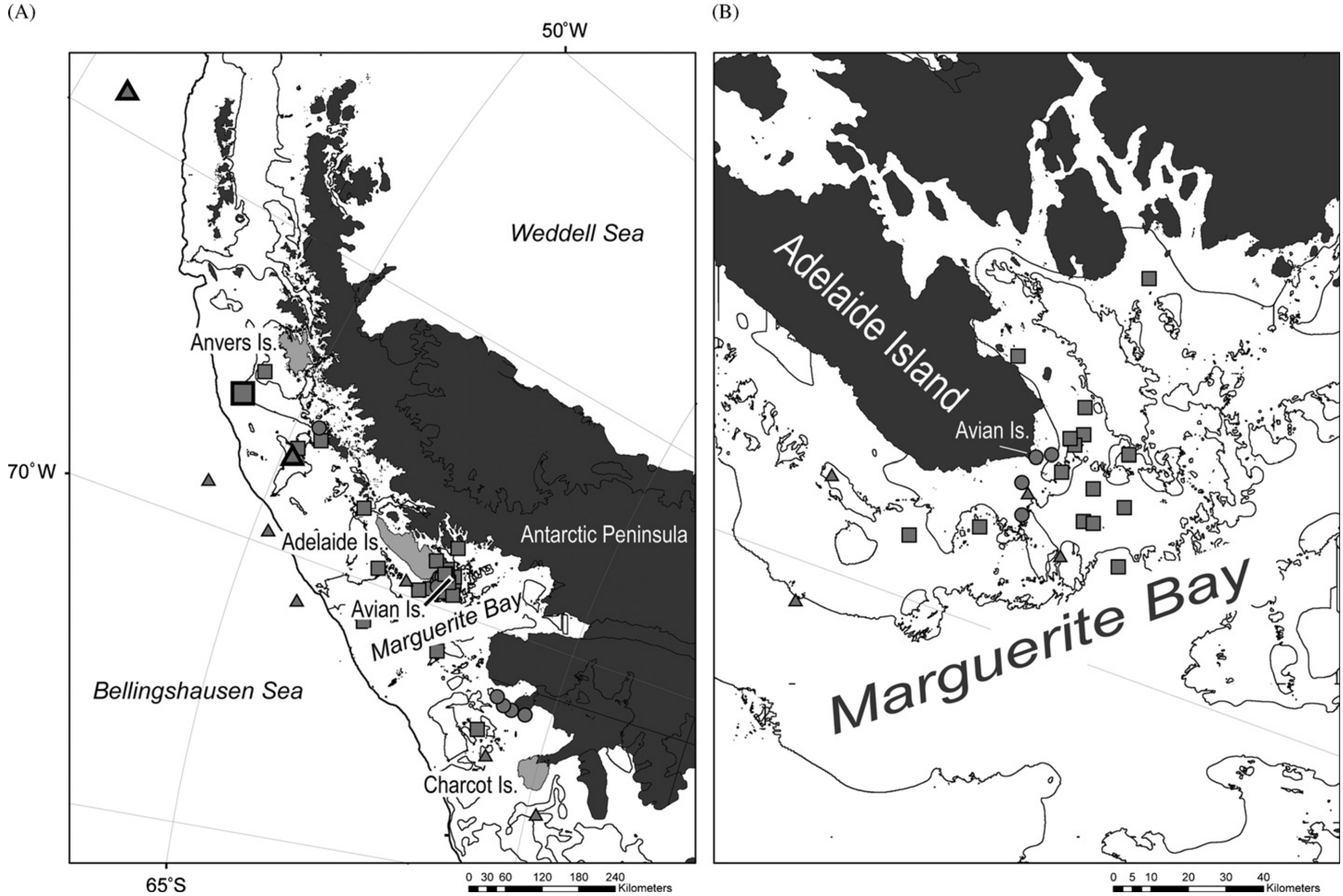

Fig. 4. Geographic center points of the 50% core foraging areas for (A) all Adélie penguins foraging along the Western Antarctic Peninsula and (B) Adélie penguins foraging in Marguerite Bay during austral winter 2001 and 2002. Symbols represent depth classes; circle: <200 m, square: 200–500 m, triangle: >500 m. Contour lines represent the 500 m isobaths and the 1000 m continental shelf break. Individuals may have >1 core foraging point. Individuals that moved far from their tagging location on Avian Island are indicated by larger symbols with bold outlines.

Table 3
Average UDOI overlap values for core foraging areas of Adélie penguins foraging within Marguerite Bay, Antarctica during austral winter 2001 and 2002.

Year	Sex	n	UDOI overlap		
			Same sex	Opposite sex	Overall
2001	Females	5	0.027 (0.011)	0.026 (0.008)	0.027 (0.009)
	Males	3	0.025 (0.009)	0.026 (0.013)	0.026 (0.012)
2002	Females	7	0.094 (0.012)	0.067 (0.009)	0.081 (0.010)
	Males	5	0.035 (0.006)	0.067 (0.024)	0.055 (0.017)

Same sex = UDOI overlap of females (males) with just other females (males). Opposite sex = UDOI overlap of females (males) with males (females). Overall = UDOI overlap of females (males) with all other individuals (both female and male). n = number of individuals. Standard error is in parentheses.

atypical compared to all other birds that remained in the general area where they were tagged.

4.2. Overlap in core foraging areas

Core foraging areas of most birds occurred in waters with shallow depths (<200 m) or in those where ocean depths were 200–500 m (mixed-layer depth class) near deep troughs (Fig. 4B). Few individuals foraged in deep troughs or off-shelf waters (>500 m) (Fig. 4A).

Overall, there was very little overlap of individual core foraging areas in 2001 and 2002 (Table 3, Fig. 5). Male overlap did not differ between years, regardless of category ($p>0.05$, all tests). In contrast, female overlap of core areas increased in 2002 compared to that in 2001 in the same-sex ($W=2$, $p=0.015$), opposite-sex ($W=2$, $p=0.01$), and overall overlap categories ($W=1$, $p=0.005$) (Table 3). The increase in overlap in 2002 occurred at the southern tip of Adelaide Island (Fig. 5B).

5. Discussion

5.1. Foraging in relation to physical characteristics

Both sea ice and bathymetry represent two dominant physical features of the WAP ecosystem, but only ocean depth was considered important in the determination of Adélie penguin foraging locations within the pack ice in this study. Specifically, when foraging in the ice, all birds used areas of shallow ocean depths. Crabeater seals (*Lobodon carcinophagus*) in the WAP during winter are also known to spend more time than is expected foraging in shallow regions characterized by complex bathymetry and heavy sea ice (Burns et al., 2004, 2008; Ribic et al., 2008). The use of surface and mixed-layer waters by birds in this study, especially along the margins of deep, across shelf canyons like Marguerite Trough, is consistent with the survey work done in that area (Ribic et al., 2008) and supports Fraser and Trivelpiece's (1996) hypothesis that birds forage in or near areas of complex bathymetry.

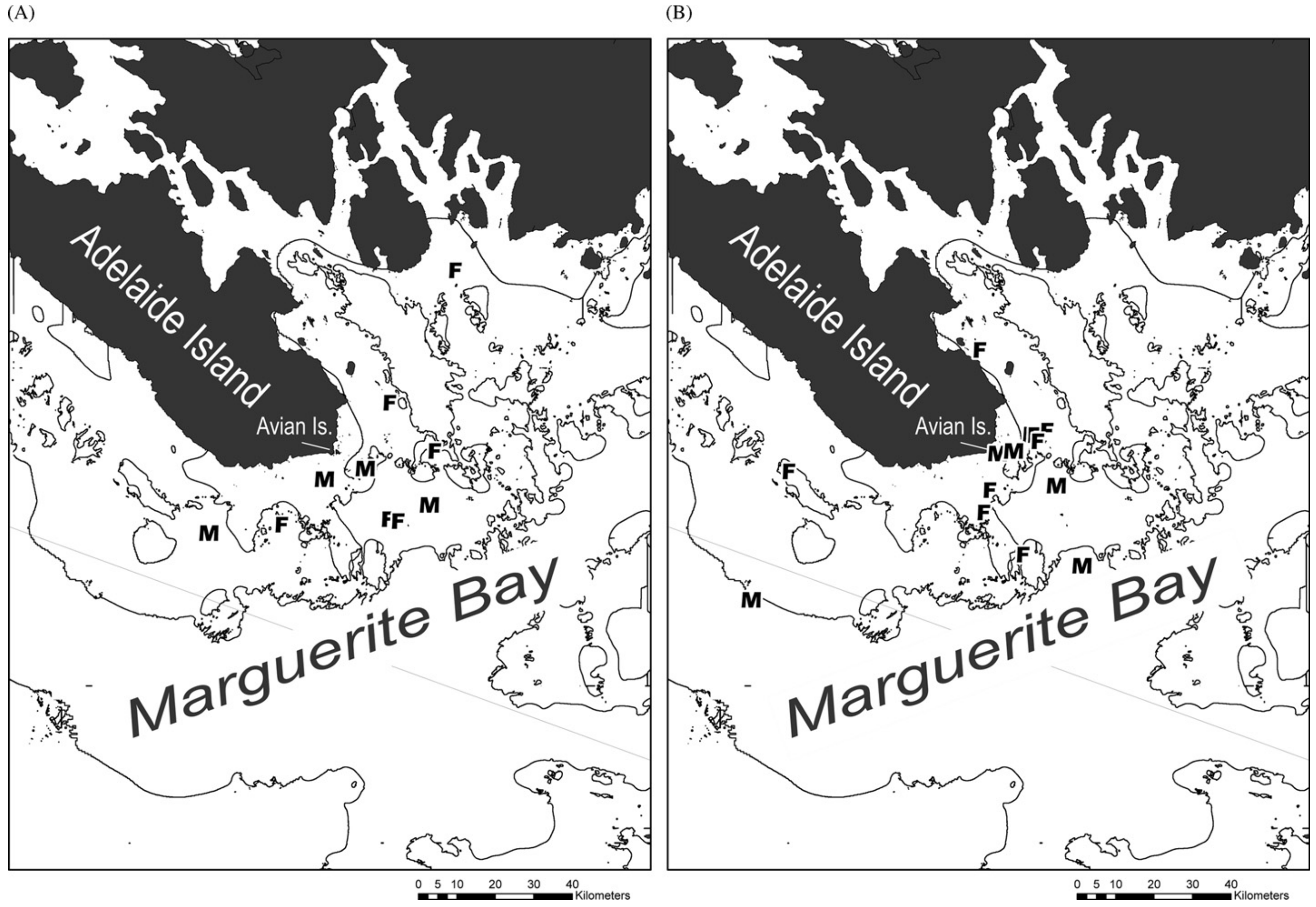

Fig. 5. Geographic center points of the 50% core foraging areas for male (M) and female (F) Adélie penguins foraging in Marguerite Bay during austral winter (A) 2001 and (B) 2002.

It is clear that Adélie penguins are associated with pack ice regions on the large scale (Ainley et al., 1992, 1994; Whitehouse and Veit, 1994; Fraser and Trivelpiece, 1996; Trivelpiece and Fraser, 1996). However, how the within-ice variability affects foraging locations is more difficult to determine. In this study, variation in ice concentration did not appear to influence Adélie penguins as to where they foraged in the pack ice. Foraging Adélie penguins can utilize cracks in the ice to gain access to the water column, and many of the cracks are at the scale of tens or hundreds of meters (Watanuki et al., 1994, 1997, 1999; Kato et al., 2003). Features at this scale are not detectable at the low satellite image resolution that we had to use in our study; not enough cloud-free, high-resolution sea ice imagery (e.g. Advanced Very High Resolution Radiometer imagery) was available in our entire study area or study period. For example, high-resolution satellite imagery did identify a large polynya that formed on the lee side of Adelaide Island in mid-October 2001 at the edge of Marguerite Trough (Massom et al., 2006) where some of the penguins in our study concentrated their feeding activity; however, that polynya was not seen in the low resolution imagery. It is likely that smaller openings in the ice existed in the area as well. In addition, the model we used to generate proxy variables to identify potential areas with cracks and leads also had low spatial resolution and limited geographic coverage of the WAP region. We speculate that a more rigorous quantification of ice-type or structure and that of ice concentration from high-resolution imagery could result in variation in sea ice along with bathymetry becoming an important physical variable that affects the foraging pattern of Adélie penguins within the pack ice.

5.2. Overlap in foraging areas

We found that individual foraging areas generally did not overlap within Marguerite Bay. However, there was an increase in foraging area overlap in females in the year with the heaviest ice cover. This increased overlap may be explained by the heavy sea ice in that year, which restricted access to the water column. Marrari et al. (2011) found that, during fall 2002, lower chlorophyll concentrations during the previous spring and summer, combined with the lower surface temperatures and extensive sea ice that year, resulted in lower plankton abundances in the Marguerite Bay area. This reduced prey abundance, which could result in increased prey concentration, combined with reduced access to the water column would require individuals to concentrate their foraging in a smaller geographic area. These conditions could result in the increase in overlap of foraging areas seen by females in this study. Other studies on Adélie penguins during the breeding season have found sex differences in foraging areas the locations of which are dependent on breeding stage and nutritional requirements of chicks (Clarke et al., 1998). The partitioning of foraging locations between the sexes may be a means of reducing intraspecific competition (Clarke et al., 1998) that is maintained into winter but is affected by environmental variability.

Previous studies of Adélie penguin winter movements from the Ross Sea region have observed individuals traveling to common overwinter feeding grounds (Davis et al., 1996, 2001). These migrations can involve distances of ≥ 1500 km and seem to follow the ocean-current-driven westward drift of the pack ice, before eventually moving north towards the edge of the pack ice region (Davis et al., 1996, 2001; Clarke et al., 2003). In our study, few birds followed a strategy of moving northward up the peninsula with the expanding ice edge. The majority of birds remained near their tagging areas throughout the study. The complex bathymetry of much of the WAP shelf region appears to maintain local areas of high productivity along the peninsula, greatly reducing the need for long-distance winter migrations seen in other regions of Antarctica. Predictable and regularly accessible food sources during winter, in close proximity to breeding colonies, would provide an attractive alternative to long-distance migration given its associated higher energetic cost.

6. Conclusions

Very little is known about the Adélie penguin's foraging during winter, especially in the WAP region (Fraser and Trivelpiece, 1996; Ribic et al., 2008). Consistent with previous research in our study area (Ribic et al., 2008), bathymetry appears to be an important physical variable in the determination of Adélie penguin within-ice foraging locations during the austral winter. In addition, the partitioning of foraging resources between the sexes during the breeding season appears to be maintained in the non-breeding season but is affected by environmental conditions. The majority of the birds remained in the general area where they were tagged throughout the winter. These areas are characterized by the presence of deep troughs and canyons. The upwelling that occurs in these areas of complex bathymetry is known to contribute to the formation of open-water polynyas (Plötz et al., 1991; Klinck et al., 2004; Karnovsky et al., 2007; Ribic et al., 2008), thus allowing the Adélie penguins access to the water column and food resources. It appears that complex bathymetry influences not only summer breeding colony locations (Fraser and Trivelpiece, 1996) but also winter foraging at numerous locations along the peninsula.

Acknowledgments

This material is based upon work supported by the National Science Foundation under OPP-0217282 and OPP-0224727 (W. Fraser). Analysis was supported by the National Science Foundation under OPP-0520961 (C. Ribic). We are grateful for the assistance provided by field technicians and colleagues throughout the duration of the cruises. Logistics and support were provided by Raytheon Polar Services Company and the crews of the ARSV *Laurence M. Gould* and the RVIB *Nathaniel B. Palmer*. We thank M. Dinniman and J. Klinck at Old Dominion University for the running of the AMPS wind model. We thank J. Burt, T. Van Deelen, L. Ballance, and one anonymous reviewer for their comments on previous versions of the manuscript. We thank the Department of Forest and Wildlife Ecology, University of Wisconsin, Madison, for assistance with publication expenses. The mention of trade names or commercial products does not constitute endorsement for use by the US government. This is contribution 695 of the SO GLOBEC program.

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