

Chinstrap penguin foraging area associated with a seamount in Bransfield Strait, Antarctica



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ABSTRACT

Identifying marine features that support high foraging performance of predators is useful to determine areas of ecological importance. This study aimed to identify marine features that are important for foraging of chinstrap penguins (*Pygoscelis antarcticus*), an abundant upper-trophic level predator in the Antarctic Peninsula region. We investigated the foraging locations of penguins breeding on King George Island using GPS-depth loggers. Tracking data from 18 birds (4232 dives), 11 birds (2095 dives), and 19 birds (3947 dives) were obtained in 2007, 2010, and 2015, respectively. In all three years, penguins frequently visited an area near a seamount (Orca Seamount) in Bransfield Strait. The percentage of dives (27.8% in 2007, 36.1% in 2010, and 19.1% in 2015) and depth wiggles (27.1% in 2007, 37.2% in 2010, and 22.3% in 2015) performed in this area was higher than that expected from the size of the area and distance from the colony (8.4% for 2007, 14.7% for 2010, and 6.3% for 2015). Stomach content analysis showed that the penguins fed mainly on Antarctic krill. These results suggest that the seamount provided a favorable foraging area for breeding chinstrap penguins, with high availability of Antarctic krill, possibly related to local upwelling.

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1. Introduction

When studying the marine environment, it is important to identify and quantify environmental factors that affect the foraging behavior of top predators. This research is useful to determine areas of high ecological significance and to address conservation concerns (Block et al., 2002; Hindell et al., 2011). Foraging hotspots are defined as areas associated with particular marine features that result in high foraging performance (Hastie et al., 2006; Seminoff et al., 2014). Understanding the underlying physical and biological processes that create foraging hotspots is key to ecological monitoring, conservation, and marine spatial planning (Hazen et al., 2013). Several types of marine features are associated with foraging hotspots. These include persistent hydrographic features such as oceanic fronts (Biuw et al., 2007; Bost et al., 2009); ephemeral hydrographic features such as mesoscale eddies (Cotté

et al., 2007); and static bathymetric features such as continental shelves (Clarke et al., 2006; Costa et al., 2008), submarine canyons (Santora and Reiss, 2011), and seamounts and banks (Barlow and Croxall, 2002; Lea et al., 2008; Hindell et al., 2011). Static foraging hotspots driven by bathymetric features are especially important for marine predators, because of their high predictability (Hazen et al., 2013).

Chinstrap penguins (*Pygoscelis antarcticus*) are one of the most abundant top predators in the Antarctic Peninsula region (Brooke, 2004). During the breeding season, they are land-based, central place foragers, and their foraging efforts are concentrated in near-shore areas within 100 km from the colony (Lynnes et al., 2002). Their ecological niche is less ice-dependent compared to that of congeneric Adélie penguins (*P. adeliae*; Lynnes et al., 2002; Forcada et al., 2006) and more pelagic compared to that of gentoo penguins (*P. papua*; Kokubun et al., 2010; Miller et al., 2010). Populations of chinstrap penguins have declined in the Antarctic Peninsula region in recent decades, and this has been attributed to both climate-driven and fisheries-related changes in the availability of Antarctic krill (Trivelpiece et al., 2011). However, relatively little is known about the local marine features that affect the foraging behavior of

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this species (but see Takahashi et al., 2003; Ichii et al., 2007). With GPS-depth loggers it is possible to record the foraging locations of marine predators at high resolution and to relate their foraging performance to the marine environment at spatial scales of <1 km (Ryan et al., 2004). Previous studies using GPS-depth loggers have shown that penguin foraging behaviors are closely related to fine-scale (about 1 km) bathymetric features. For example, yellow-eyed penguins (*Megadyptes antipodes*) follow the same movement paths across multiple trips, possibly using bottom topography as a landmark (Mattern et al., 2007). Gentoo penguins frequently visit particular coastal areas with shallow depths and perform benthic dives (Kokubun et al., 2010). Investigations into foraging locations of top predators using GPS-depth loggers are key to marine spatial planning in terms of conservation and ecosystem-based management.

The aim of this study was to investigate whether the foraging behavior of chinstrap penguins is associated with particular marine habitats characterized by bathymetric features, such as small-scale seamounts. In addition, we discuss the possible factors driving the patterns of habitat use in chinstrap penguins.

2. Materials and methods

2.1. Study site

The field study was conducted in a colony on Barton Peninsula (62°14.3'S, 58°46.5'W), King George Island, Antarctica, where 2961 pairs of chinstrap penguins and 1719 pairs of gentoo penguins bred in the 2006/2007 season. The study colony is located in the Antarctic Specially Protected Area (ASPA) #171 Narębski Point (ATCM, 2009). The study was conducted for three austral summers, from 25 December 2006 to 28 January 2007 (hereafter described as 2007), 30 December 2009 to 23 January 2010 (hereafter described as 2010), and 29 December 2014 to 19 January 2015 (hereafter described as 2015). The study periods corresponded to the chick-guarding period of chinstrap penguins.

2.2. Environmental setting

The sea around the study colony is characterized by two important bathymetric features (Fig. 1): Maxwell Bay, a 6–14 km wide bay surrounded by King George Island and Nelson Island, which features a U-shaped submarine valley with a maximum depth of 550 m (Khim and Yoon, 2003); and Bransfield Strait, a 110 km wide strait between the Antarctic Peninsula and the South Shetland Islands, with a maximum depth of 2000 m (Schreider et al., 2014). Maxwell Bay and the northern part of Bransfield Strait can be subdivided into shelf (≤ 200 m in depth) and offshore (> 200 m in depth) areas. In the offshore area of Bransfield Strait, there is a seamount of volcanic origin, called Orca Seamount (62°26'S, 58°24'W). The summit of this seamount is 700 m below the sea surface, and its relative elevation from the ocean floor of Bransfield Strait is 550 m. The approximate diameter is 20 km (Schreider et al., 2014). This is the only seamount within the penguin foraging range from the study colony.

We classified the penguin foraging areas into five zones based on bathymetry (Fig. 1): 1) the King George Island shelf zone, defined by bottom depth ≤ 200 m along the King George Island coast; 2) the Nelson Island shelf zone, defined by bottom depth ≤ 200 m along the Nelson Island coast; 3) the Maxwell Bay zone, defined by bottom depth > 200 m and within 10 km from Narębski Point; 4) the Bransfield Strait slope zone, defined by bottom depth > 200 m and > 10 km from Narębski Point, excluding the Seamount zone; and 5) the Seamount zone, defined as the area within a circle of 10 km radius from the center of the Orca Seamount.

We analyzed the chlorophyll *a* concentration around the study area during the study period using satellite imagery, because it is an environmental factor potentially reflect local marine productivity. We used monthly-averaged chlorophyll *a* concentration data for January of 2007, 2010, and 2015, acquired from the Chlorophyll *a*, Aqua MODIS, NPP, L3SMI, Global, Science Quality, (Monthly Composite) dataset available at the National Oceanic and Atmospheric Administration Earth Research Division's Data Access Program (ERDDAP) webpage, <http://coastwatch.pfeg.noaa.gov/erddap/griddap/erdMH1chlmday.graph?chlorophyll>. The chlorophyll *a* data with a 2.5' \times 2.5' resolution were extracted for the colored area shown in Fig. 1, which covers the maximum foraging range of the penguins. Next, the chlorophyll *a* concentration was compared among the five zones or the 3 study years using generalized linear models (GLMs). We used the likelihood ratio test (LRT) to investigate the effect of zones or years and a gamma error distribution in the GLMs, because the errors are not normally distributed. We used R[®] 3.1.1 software (R Development Core Team, 2014) to conduct the GLMs.

2.3. Deployment of data loggers

To collect location and dive data, three types of GPS-depth loggers were deployed on 20, 17, and 20 chick-guarding chinstrap penguins in 2007, 2010, and 2015, respectively. The GPS-depth loggers used in 2007, 2010 and 2015, were GPL380-DT and GPS-TD log, GPL380-DT, and GPL400-D3GT, respectively. The details of the GPS-depth loggers used are as follows: the GPL380-DT (Little Leonardo, Tokyo, Japan), a rectangular container (58 mm in length \times 28 mm in width \times 20 mm in height) with a cylindrical battery section (20 mm in diameter and 47 mm in length) and a mass in air of 92 g; the GPS-TD logger (Earth and Ocean Technologies, Kiel, Germany), a stream-lined fiber-composite container unit, 96 mm in length \times 36 mm in width \times 27 mm in height, with a mass in air of 86 g; and the GPL400-D3GT (Little Leonardo), a cylindrical unit 20 mm in diameter and 113 mm in length, with a mass in air of 55 g. We instrumented only one bird per breeding pair. The weight of these loggers represented 1.1–2.7% of the body mass of the study birds. The loggers were attached on the lower medial portion of the back using tesa[®] tape, plastic cable ties, and instant glue (Loctite 401[®]; Loctite Corporation). The loggers were set to record dive depth, water temperature, and location every second. The loggers were attached to the penguins before their departure for a foraging trip, and were removed upon return to the colony.

2.4. Foraging parameters

Foraging trip duration was defined as the time between the start of the first dive (deeper than 1 m) after departure from the colony and the end of the last dive before arriving back at the colony. Only dives deeper than 1 m were included because of possible measurement error in the instruments (Takahashi et al., 2003). Maximum distance from the colony during the foraging trips was defined as the distance between the colony and the most distant point of each trip. Dives deeper than 5 m were considered to be potentially related to foraging. The majority of dives were shallower than 5 m ($43.9 \pm 18.1\%$, $46.3 \pm 13.0\%$, and $49.0 \pm 14.6\%$ for 2007, 2010, and 2015, respectively), but these dives accounted for only a small portion of the total dive duration ($7.0 \pm 4.4\%$, $10.9 \pm 8.2\%$, and $9.6 \pm 6.2\%$ for 2007, 2010, and 2015, respectively). Therefore, these shallow dives (< 5 m) are likely to constitute traveling dives, as noted in previous studies (Takahashi et al., 2003; Kokubun et al., 2010). Hereafter “dives” refers to the potential foraging dives deeper than 5 m unless stated otherwise.

The last location just prior to a dive was used as the location of

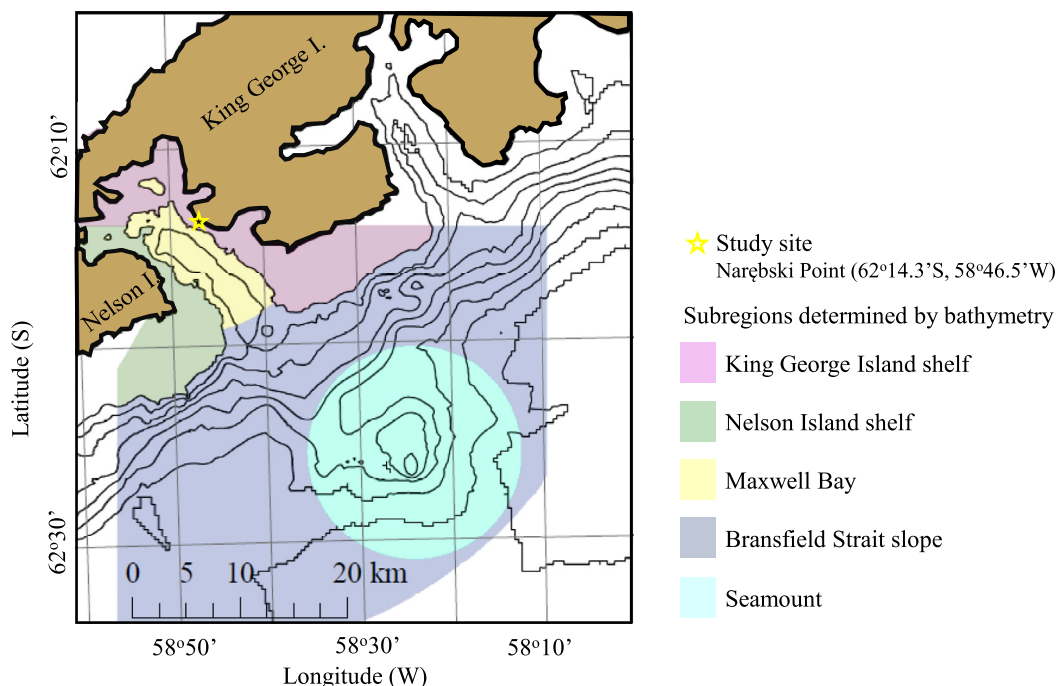


Fig. 1. Sea around the study colony was classified into five habitat zones based on bathymetry. The colors represent the five different zones (See Section 2.2. Environmental setting in Materials and methods for definitions). Isobaths are shown at 200 m intervals, derived from digitized bathymetric data around King George Island (See Section 2.4. Foraging parameters).

the dive. The loggers sometimes failed to record the location of a dive. In these cases, the locations of dives were interpolated linearly using the locations of the dives prior to and after the one without a location, associated with the times when the dives occurred (Kokubun et al., 2010). If the GPS location of the dives was recorded for less than half of all dives in a foraging trip, the data for that trip were not used. If data for multiple trips were obtained from one bird, all the data were used to calculate trip and dive parameters, because the random effect induced by individuals can be dealt with in mixed-effect models (see next two paragraphs for details). However, for analyses of foraging habitat, if multiple trips were available only the trip with the best GPS data was used (see Section 2.5. Analyses of foraging habitat for details), to ensure equal statistical weight for each individual. The bathymetry where dives occurred was investigated using ArcView[®] with digitized bathymetric data around King George Island (Admiralty Chart No. 1776).

We calculated maximum dive depth, dive duration, dive bottom duration (the time between the start and end of the time when birds showed depth change of 0 m), and number of depth wiggles (defined as events when birds changed swimming direction from descending to ascending during the dive bottom phase; Fig. 2) for each dive. The number of depth wiggles was used as a proxy of foraging effort, because previous studies have shown that the number of depth wiggles is correlated with other direct foraging indices such as the number of beak opening events (Takahashi et al., 2004), drops in esophageal temperature (Bost et al., 2007), and head movement (Kokubun et al., 2011). We also calculated the frequency of dives per hour for each trip.

Trip parameters (foraging trip duration, maximum distance from the colony) and dive parameters (frequency of dives per hour, dive depth, dive duration, and the number of depth wiggles) were compared among the three study years using a generalized linear mixed model (GLMM) and LRT with bird identity as a random effect, to account for repeat sampling from the same individuals. Dive depth was included as a fixed effect in the analyses of dive duration and the number of depth wiggles (Kokubun et al., 2010). We used a

gamma error distribution in the GLMMs, because the errors are not normally distributed. We used the “lme4” package in R[®] 3.1.1 software (R Development Core Team, 2014) to conduct the GLMMs. Data are presented as mean values \pm standard deviation (SD) with significance set at the 0.05 level.

2.5. Analyses of foraging habitat

To analyze the foraging habitat use of penguins, first we calculated the kernel density distribution of dive locations. We defined the foraging area as the 95% kernel contour of dive location distribution (Kokubun et al., 2010). Second, we calculated the proportion of the 95% kernel boundary area within each of the five zones defined based on bathymetry (King George Island shelf, Nelson Island shelf, Maxwell Bay, Bransfield Strait slope, and Seamount). Third, we investigated regional variations in the number of dives and the number of depth wiggles as follows. We hypothesized that, if penguins do not have particular preference to forage in any of the five zones, they should distribute their foraging effort (number of dives or number of depth wiggles) into five zones proportional to the relative size of the 95% kernel boundary area in each zone. We also considered distance from the colony as a factor affecting habitat use, because it is well known that bird density is inversely related to distance from the colony because of geometric spreading as birds travel to and from the colony (Decker and Hunt, 1996). Therefore, our null hypothesis was that the number of dives or the number of depth wiggles would be proportional to the relative size of the 95% kernel boundary area and inversely proportional to the distance from the colony in each of the five zones. We calculated the expected number of dives (or number of depth wiggles) for each of the five zones as follows (cf. Decker and Hunt, 1996): 1) 100 m \times 100 m grids covering the foraging area (95% kernel boundary area) were prepared; 2) the expected number of dives for each grid is $\frac{N}{p}$, if no distance effect is assumed, where p is the total number of grids, and N is the total number of dives; 3) the distance from the colony (d_i) to each grid i was calculated; 4) the

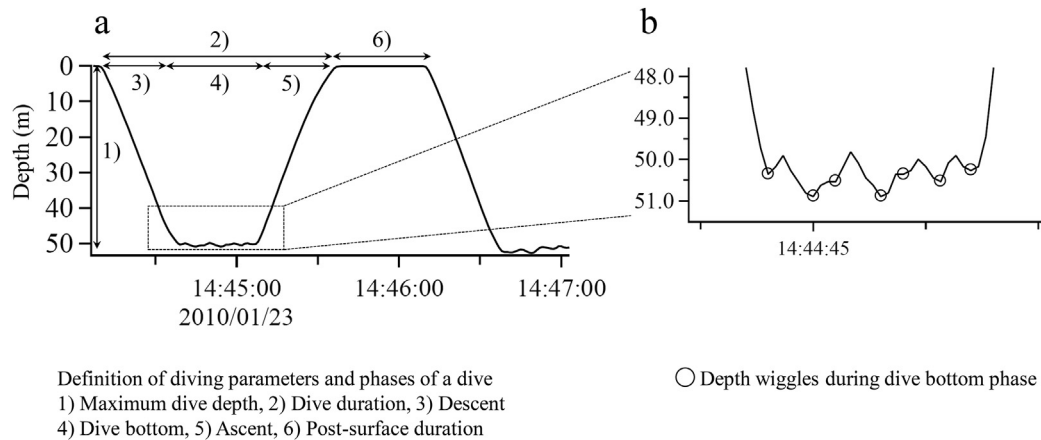


Fig. 2. Dive profile of a chinstrap penguin (a) and enlarged part of the dive bottom phase (b). The definitions of dive parameters and the phases of a dive are shown.

expected number of dives for each grid was divided by distance with a coefficient a , as $\frac{a}{d_i} \times \frac{N}{p}$ (weighted number of dives) for each grid i , where a is a coefficient that meets the condition $\sum_{i=1}^p \frac{a}{d_i} \times \frac{N}{p} = N$; and 5) the weighted number of dives for each grid was summed. The resulting total number of dives within each of the five zones was the expected number of dives (or depth wiggles) for the zone accounting for the inverse relationship to the distance from the colony. We compared the number of dives and the number of depth wiggles in each zone expected based on the null hypothesis with those empirically observed, using χ^2 tests conducted with Minitab[®] v. 12.

We examined the areas where the birds concentrated their foraging effort using analysis of area-restricted search (ARS; Pinaud and Weimerskirch, 2007) behavior as follows. We calculated first passage time (FPT; Fauchald and Tveraa, 2003), the time required for a bird to cross a circle with a given radius r . We used foraging tracks for every minute to calculate FPT. When GPS positioning failed, locations were interpolated linearly using the locations prior to and after the one without a recorded position. The radius r that gave the largest variance in log FPT was assumed as the spatial scale at which birds increased their foraging effort (Fauchald and Tveraa, 2003). We plotted the FPT (calculated with the radius r) along the trip then selected the locations with higher FPT values exceeding a threshold (determined by the 75% quantile of the FPT; Trathan et al., 2008). These locations were called ARS zones (Pinaud and Weimerskirch, 2007), and dives were extracted within these zones. The ARS analyses were carried out using IGOR Pro (Wave-metrics, v. 6.3) with the 'Spatial analysis' function of the Ethographer (v. 2.0; Sakamoto et al., 2009).

2.6. Diet

Stomach contents were collected from the instrumented birds using the standard stomach-flushing method (CCAMLR, 2004). Stomach contents were weighed, visually sorted, and identified into the lowest taxon as much as possible. Krill and fish species were identified following Makarov and Denys (1981) and Gon and Heemstra (1990).

3. Results

3.1. Data recovery

All tagged birds ($n = 20$, 17, and 20 in 2007, 2010, and 2015, respectively) were recaptured within 1–3 days after release. Tracking and dive data for 22, 13, and 26 trips from 18, 11, and 19

birds were successfully obtained in 2007, 2010, and 2015, respectively. Data from the other birds were not available because of malfunction of the loggers or insufficient position data. In total, 4,904, 2,245, and 4512 dives were used for calculating trip and dive parameters in 2007, 2010, and 2015, respectively, and 4,232, 2,095, and 3947 dives from 18, 11, and 19 trips (one trip per bird) were used for foraging habitat analyses.

Trip and dive parameters in each year are shown in Tables 1 and 2. Trip duration and maximum distance from the colony were not different among the years (Table 1). The frequency of dives during trips was highest in 2007 followed by 2015 and 2010 (Table 2). The averaged dive depth was deepest in 2010 followed by 2015 and 2007, and the averaged dive duration showed the same trend when the effect of dive depth was taken in account (Table 2). The number of depth wiggles per dive was highest in 2015 followed by 2007 and 2010 (Table 2).

The number of ARS zones detected was 56 in 2007 (from 17 birds, one bird did not show any ARS zones, a total of 2098 min was spent in those zones, equivalent to 20.1% of total foraging trip duration), 37 in 2010 (from 11 birds; 1670 min, equivalent to 21.2% of total foraging trip duration), and 93 in 2015 (from 19 birds, 2576 min, equivalent to 20.3% of total foraging trip duration). The number of dives in the ARS zones was 1,030, 613, and 1196 (equivalent to 24.3%, 29.3%, and 30.3% of total dives) in 2007, 2010, and 2015, respectively, and the number of depth wiggles in the ARS zones was 5,936, 2,848, and 7919 (equivalent to 28.7%, 35.4%, and 36.3% of total depth wiggles) in 2007, 2010, and 2015, respectively (Fig. 3). Because the number of dives or depth wiggles that occurred within the ARS zones exceeded those expected from % time spent in the ARS zones, we considered that the ARS zones represented the areas where the penguins spent time foraging. The radius r to calculate FPT was 1.45 ± 1.41 km, 1.78 ± 1.58 km, and 1.41 ± 1.56 km in 2007, 2010, and 2015, respectively.

3.2. Foraging habitat

The Bransfield Strait slope zone occupied the largest area in the 95% kernel boundary zone, followed by the Seamount and Maxwell Bay zones in every year (Table 2). Nine of 18, 7 of 11, and 6 of 19 birds visited the Seamount zone in 2007, 2010, and 2015, respectively (Fig. 3). In 2007 and 2010, the number of dives was highest in the Seamount zone (27.8 and 36.1% of all dives, respectively), followed by the Bransfield Strait slope and Maxwell Bay zones. In 2015, the number of dives was highest in the Bransfield Strait slope zone (Table 3). In 2007 and 2010, the number of depth wiggles was highest in the Seamount zone (27.1 and 37.2% of all depth wiggles,

Table 1

Trip parameters for chinstrap penguins studied in a colony on King George Island, Antarctica, in the austral summers of 2006/2007, 2009/2010, and 2014/2015.

Year	Trip parameters		
	Number of trips (number of birds)	Trip duration (h)	Maximum distance from colony (km)
2007	22 (18)	9.55 ± 4.86	16.16 ± 10.06
2010	13 (11)	11.62 ± 4.62	21.64 ± 10.28
2015	26 (19)	9.91 ± 4.59	14.97 ± 6.70
^a Model used	GLMM (G) with LRT		GLMM (G) with LRT
Statistics and <i>P</i> value	$\chi^2 = 0.81, P = 0.667$		$\chi^2 = 1.75, P = 0.418$

^a GLMM: generalized linear mixed model; G: gamma error distribution was used in the models; LRT: likelihood ratio test.

Table 2

Dive parameters for chinstrap penguins studied in a colony on King George Island, Antarctica, in the austral summers of 2006/2007, 2009/2010, and 2014/2015.

Year	Dive parameters				
	Number of dives	Frequency of dives during trip (h ⁻¹)	Dive depth (m)	Dive duration (s)	Number of depth wiggles per dive
2007	4904	24.78 ± 6.56	29.15 ± 6.59	70.51 ± 8.99	5.08 ± 0.88
2010	2245	16.33 ± 4.74	37.01 ± 10.60	80.98 ± 13.09	3.78 ± 0.32
2015	4512	19.34 ± 5.72	33.90 ± 12.71	76.68 ± 17.79	5.82 ± 1.18
^a Model used	GLMM (G) with LRT		GLMM (G) with LRT	^b GLMM (G) with LRT	^b GLMM (G) with LRT
Statistics and <i>P</i> value	$\chi^2 = 7.41, P = 0.025^*$		$\chi^2 = 9.19, P = 0.010^*$	$\chi^2 = 21.39, P < 0.001^*$	$\chi^2 = 27.36, P < 0.001^*$

Dive depth, dive duration, and number of depth wiggles per dive were obtained repeatedly for each bird, therefore they are presented as the mean ± SD of averaged values for each bird.

*Significant difference between the years.

^a GLMM: generalized linear mixed model; G: gamma error distribution was used in the models; LRT: likelihood ratio test.

^b Dive depth was included as a fixed effect in the model.

respectively), followed by the Bransfield Strait slope zone. In 2015, the number of depth wiggles was highest in the Bransfield Strait slope zone, followed by the Seamount zone (Table 3). Among ARS zones determined by FPT analyses, 28.6%, 40.5%, and 23.7% of ARS zones occurred in the Seamount zone in 2007, 2010, and 2015, respectively (we counted ARS zones if some part of the ARS occurred within the Seamount zone). In 2007 and 2010, both the number of dives and the number of depth wiggles that occurred within ARS zones was highest in the Seamount zone, followed by the Bransfield Strait slope zone (Table 3). However, in 2015 the number of dives that occurred within ARS zones was highest in the Bransfield Strait slope zone followed by the Seamount zone (Table 3).

The observed number of dives in the Seamount zone exceeded those expected from the relative size of the 95% kernel boundary area and distance from the colony in all years (Table 3; χ^2 test, $P < 0.001$). The observed number of depth wiggles in the Seamount zone also exceeded those expected in all years (Table 3; χ^2 test, $P < 0.001$). Similarly, the observed number of dives or depth wiggles in the Bransfield Strait slope zone exceeded those expected in all years (Table 3), but were closer to the expected values compared with the Seamount zone (for example, the observed and expected number of depth wiggles was not significantly different in 2010, χ^2 test, $P = 0.148$). In contrast, the observed number of both dives and depth wiggles was lower than those expected in the King George Island shelf and Maxwell Bay zones in all 3 years (Table 3; χ^2 test, all

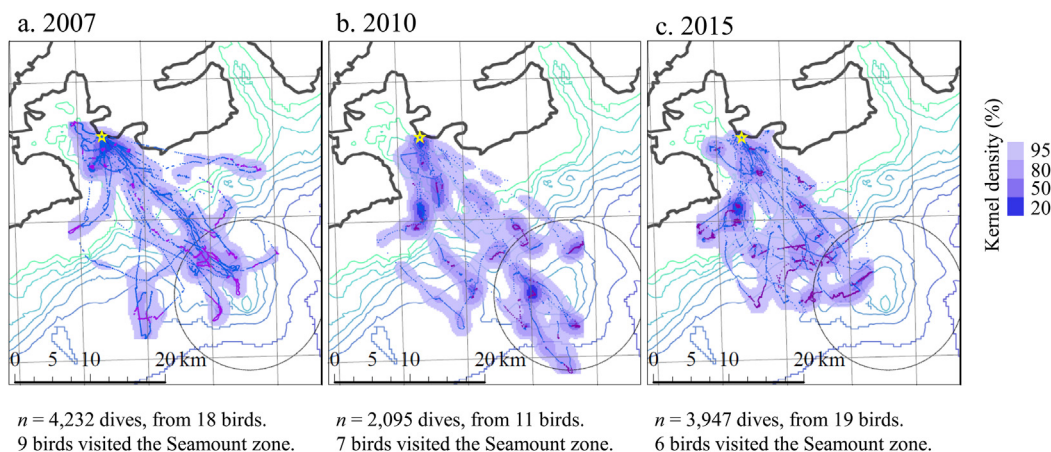


Fig. 3. Tracks and kernel density of diving locations for chinstrap penguins in (a) 2006/2007, (b) 2009/2010, and (c) 2014/2015 austral summers. Blue dots and lines are raw tracks, and thick purple dots and lines show the location of dives in area-restricted search (ARS) zones (See Section 2.5. Analyses of foraging habitat in Materials and methods for determination of ARS zones). 95%, 80%, 50%, and 20% kernel boundary areas are shown. The areas enclosed by the 95% kernel boundary contours and the distance from the colony were used to set a null hypothesis for habitat preference (See Section 2.5 Analyses of foraging habitat). The black circles shown in each panel indicate the boundary of the Seamount zone.

Table 3
Foraging habitat use of chinstrap penguins. Five habitat zones were defined by bathymetry. The areas enclosed by the 95% kernel boundary area, the observed and expected number of dives and depth wiggles, and the observed number of dives and depth wiggles in area-restricted search (ARS) zones are shown. Note that a relatively higher number of dives and depth wiggles were observed in the Seamount zone compared to the number expected from the size of the area and distance from the colony.

	Subregions determined by bathymetry					Total
	Shelf		Submarine valley	Bransfield strait		
	King George island	Nelson island	Maxwell bay	Slope	Seamount	
95% kernel boundary area						
2007	48.2 km ² (14.5%)	21.7 km ² (6.5%)	52.6 km ² (15.8%)	132.6 km ² (39.8%)	77.6 km ² (23.3%)	332.6 km ²
2010	21.5 km ² (5.5%)	35.8 km ² (9.1%)	49.2 km ² (12.6%)	149.9 km ² (38.2%)	135.7 km ² (34.6%)	392.1 km ²
2015	30.1 km ² (8.9%)	46.0 km ² (13.6%)	54.3 km ² (16.1%)	152.2 km ² (45.1%)	54.9 km ² (16.3%)	337.4 km ²
Observed number of dives						
2007	731 (17.3%)	177 (4.2%)	1058 (25.0%)	1090 (25.8%)	1176 (27.8%)	4232 dives by 18 birds
2010	73 (3.5%)	248 (11.8%)	413 (19.7%)	605 (28.9%)	756 (36.1%)	2095 dives by 11 birds
2015	269 (6.8%)	756 (19.2%)	775 (19.6%)	1393 (35.3%)	754 (19.1%)	3947 dives by 19 birds
^aExpected number of dives						
2007		239 (5.6%)	1570 (37.1%)	832 (19.6%)	355 (8.4%)	4232 dives
2010		216 (10.3%)	753 (36.0%)	530 (25.3%)	309 (14.7%)	2095 dives
2015		444 (11.2%)	1461 (37.0%)	968 (24.5%)	249 (6.3%)	3947 dives
Observed number of depth wiggles						
2007	3530 (17.1%)	897 (4.3%)	5474 (26.5%)	5168 (25.0%)	5591 (27.1%)	20,660 wiggles
2010	172 (2.1%)	1031 (12.8%)	1626 (20.2%)	2223 (27.6%)	2994 (37.2%)	8046 wiggles
2015	1515 (6.9%)	4748 (21.8%)	3350 (15.3%)	7352 (33.7%)	4861 (22.3%)	21,826 wiggles
^aExpected number of depth wiggles						
2007	6035 (29.2%)	1167 (5.6%)	7665 (37.1%)	4059 (19.6%)	1734 (8.4%)	20,660 wiggles
2010	1103 (13.7%)	831 (10.3%)	2892 (35.9%)	2035 (25.3%)	1185 (14.7%)	8046 wiggles
2015	4563 (20.9%)	2455 (11.2%)	8077 (37.0%)	5353 (24.5%)	1378 (6.3%)	21,826 wiggles
^bObserved number of dives in ARS zones						
2007	49 (4.8%)	44 (4.3%)	201 (19.5%)	201 (19.5%)	535 (51.9%)	1030 dives by 17 birds
2010	0 (0.0%)	59 (9.6%)	80 (13.1%)	158 (25.8%)	316 (51.5%)	613 dives by 11 birds
2015	41 (3.4%)	255 (21.3%)	67 (5.6%)	436 (36.5%)	397 (33.2%)	1196 dives by 19 birds
^bObserved number of depth wiggles in ARS zones						
2007	331 (5.6%)	296 (5.0%)	1358 (22.9%)	1161 (19.6%)	2790 (47.0%)	5936 wiggles
2010	0 (0.0%)	252 (8.8%)	377 (13.2%)	768 (27.0%)	1451 (50.9%)	2848 wiggles
2015	315 (4.0%)	1750 (22.1%)	335 (4.2%)	2750 (34.7%)	2767 (35.0%)	7917 wiggles

^a We assumed that the number of dives or the number of depth wiggles was proportional to the relative size of the 95% kernel boundary area and inversely proportional to the distance from the colony in each of the five zones (See Section 2.5. Analyses of foraging habitat in Material and methods).

^b Definition and determination of ARS zones are described in Section 2.5. Analyses of foraging habitat in Materials and methods.

$P < 0.001$). The relationship between the observed and expected number of dives and depth wiggles was variable in the Nelson Island shelf zone according to the variation between the years (Table 3).

Satellite imagery showed that chlorophyll *a* concentrations were different among the five zones in each year (Fig. 4; GLM with LRT, $\chi^2 = 18.28$, $P = 0.001$ for 2007, $\chi^2 = 38.64$, $P < 0.001$ for 2010, and $\chi^2 = 57.97$, $P < 0.001$ for 2015). The Seamount zone had the highest chlorophyll *a* concentrations in each year. The chlorophyll *a* concentrations were also different among the three years in each zone (Fig. 4; GLM with LRT, $\chi^2 = 452.82$, $P < 0.001$), with the lowest concentration in 2010 followed by 2015 and 2007.

3.3. Diet

Stomach contents were collected from 16, 6, and 5 birds in 2007, 2010, and 2015, respectively. The average food mass was 558.7 ± 223.0 g, 304.8 ± 182.7 g, and 249.3 ± 135.8 g in 2007, 2010, and 2015, respectively. The main prey was Antarctic krill *Euphausia superba* (% wet mass, $99.8 \pm 0.5\%$ for 2007, $99.8 \pm 0.2\%$ for 2010, $99.8 \pm 0.6\%$ for 2015). Other prey types including two Antarctic silverfish *Pleurogramma antarcticum*, three Antarctic silverfish and an amphipod, and one Antarctic silverfish were found in 2007, 2010, and 2015 respectively. Stomach contents were obtained from 3, 4, and 1 GPS-tracked birds that visited the Seamount zone in 2007, 2010, and 2015, respectively. Their main prey was also Antarctic krill (% wet mass, >98%). The other prey items were Antarctic silverfish (% wet mass, 0–1.7%) and amphipods (% wet mass, 0–0.1%).

4. Discussion

This GPS-tracking study demonstrated that chinstrap penguins from King George Island often foraged in areas associated with a seamount. The Seamount zone hosted a larger number of dives and depth wiggles during dives compared to other zones, considering the relative size of the 95% kernel boundary within each zone and distance from the colony (Table 3). The high number of depth wiggles and ARS dives (Table 3) suggests that the foraging effort of the penguins was high in the Seamount zone. Furthermore, our results suggest that the Seamount zone was consistently important as a foraging hotspot used by chinstrap penguins over three different years.

Seamounts have been considered important static features that affect the foraging behavior and distribution of marine predators (Hyrenbach, 2000; Hazen et al., 2013). Previous studies have shown that a variety of Antarctic marine predators frequently use areas around large seamounts and submarine banks (at scales of 100–1000 km) as important foraging habitats (Barlow and Croxall, 2002; Lea et al., 2008; Hindell et al., 2011). However, the importance of small-scale to meso-scale seamounts (about 10 km) for foraging predators has only been recognized recently, since the foraging behavior of predators has been tracked with high-resolution GPS loggers (Maxwell et al., 2012; Wakefield et al., 2012). Maxwell et al. (2012) demonstrated that seamounts at a scale of 10 km directly create foraging hotspots for northern elephant seals because benthic fish aggregate on top of the seamounts. However, in the present study the seamount appears to have had an indirect influence on penguin foraging through

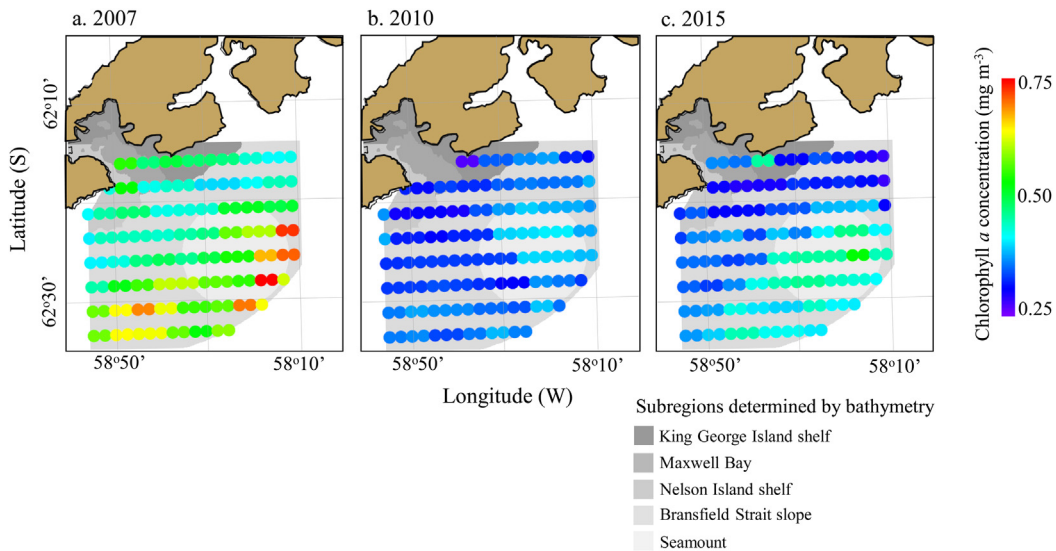


Fig. 4. Chlorophyll *a* concentration in the foraging area of chinstrap penguins in each of the three study years, obtained by satellite imagery from NOAA (See Section 2.2. *Environmental setting*). Filled circles with the color spectrum show the chlorophyll *a* concentration in each location. Gray colors indicate the subregions determined by bathymetry.

physical and biological processes, because the penguins only dived to 30–40 m (Table 2), which was well above the top of the seamount (700 m below the sea surface).

Small-scale to meso-scale (about 10 km) seamounts have been suggested to enhance the food availability for predators through physical processes that affect vertical distribution of nutrients and prey (seamounts in general, Pitcher et al., 2007; submarine moraine banks around South Georgia used by albatrosses, Wakefield et al., 2012). In the present study area, the Bransfield Current flows from southwest to northeast along the slope of Bransfield Strait, with an approximate flow rate of 0.5 m s^{-1} and a maximum thickness of 800 m (Zhou et al., 2006; Sangrà et al., 2011). The Orca Seamount, located in the middle of the current system, likely induces local upwelling secondary to tidal mixing and turbulence (White et al., 2007). The locally elevated chlorophyll *a* around the Seamount zone (Fig. 4) suggests such local upwelling might enhance the availability of Antarctic krill near the subsurface around the seamount, as krill are advected by the Bransfield Current system (Ichii et al., 1998; Catalán et al., 2008). Indeed, locally elevated krill abundance was reported around the Orca Seamount by a previous study of fine-scale krill distribution (Kalinowski, 1984).

In the present study, chinstrap penguins concentrated their foraging efforts in the seamount zone, but did forage elsewhere (Table 3). It appears that chinstrap penguins might use the Seamount zones more intensively in years with less prey availability. In 2010, when prey availability was low compared with the other 2 years, inferred from the deeper dive depth, less frequent dives and depth wiggles, and relatively low chlorophyll *a* (Table 2, Fig. 4), penguins used the Seamount zones most frequently among the 3 years (Table 3). The Orca Seamount is located about 25 km from the colony (Fig. 1), which is near the outer boundary of the chinstrap penguin foraging area (Fig. 3). In contrast, penguins performed less frequent dives or depth wiggles than expected in the King George Island shelf and Maxwell Bay zones, which are closer to the colony (Table 3). During breeding season, conspecific/congeneric foraging efforts increase near the colonies, possibly resulting in prey depletion (Forero et al., 2002). The Seamount may provide a distant, but static, foraging hotspot for land-based diving predators during the breeding season, even though the degree of utilization does change inter-annually, possibly as a result of

fluctuation in prey availability near the colony.

Similar to the Orca Seamount, several other small-scale to meso-scale (about 10 km) seamounts with volcanic origin exist in the Bransfield Strait (Schreider et al., 2014). During summer, the Bransfield Strait region provides important foraging habitats for several types of predators such as central place foragers including shorter-ranging *Pygoscelis* penguins and longer-ranging Antarctic fur seals (Ichii et al., 2007), flying seabirds (Santora and Reiss, 2011), as well as migrants (e.g., cetaceans; Santora et al., 2010; Santora et al., 2014). Further multi-species and/or multi-location studies on foraging behavior with high resolution GPS-depth information would allow the identification of local foraging hotspots associated with small-scale to meso-scale bathymetric features. Bransfield Strait is an area of increasing importance for krill fisheries (Kawaguchi et al., 2006). Information on foraging hotspots associated with small-scale to meso-scale bathymetric feature is essential for effective marine spatial planning. This information would be particularly relevant to short-ranging central place foragers, because they can not easily move to further alternative areas without sacrificing energy delivered to their offspring.

In conclusion, this multi-year study showed that breeding chinstrap penguins often foraged in areas associated with a small-scale to meso-scale seamount, in Bransfield Strait, Antarctica. This is possibly because the seamount increases the availability of Antarctic krill owing to a bathymetry-driven upwelling phenomenon. Seamounts located near the coast offer short-ranging marine predators consistent foraging hotspots across years, and are of great importance in terms of marine conservation.

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