Frontal zones, temperature gradient and depth characterize the foraging habitat of king penguins at South Georgia

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ABSTRACT: Investigating the responses of marine predators to oceanographic structures is of key importance for understanding their foraging behaviour and reproductive success. Using Global Positioning System (GPS) and Time-Depth-Temperature-Recorder (TDR) tags, we investigated how king penguins breeding at South Georgia explore their foraging area over the summer season in both the horizontal and vertical dimensions. We determined how horizontal habitat use may relate to different Antarctic Circumpolar Current (ACC) frontal zones and associated thermal structuring of the water column. To study the penguins' use of the water column, we examined foraging niches defined by temperature, temperature gradient and depth, and explored the importance of these thermal properties for prey pursuit. King penguins foraged within the Polar Front (PF) and its southern edges during incubation, and the Antarctic Zone (AAZ) and Southern ACC Front (SACCF) during brooding. Foraging niches became more distinct with the advancing summer season, defined by strong thermal gradients at shallow depths in the AAZ, and weak gradients at greater depths in the SACCF. These niches indicate foraging in the sub-thermocline Winter Water (WW) in the AAZ, and in deep WW and Circumpolar Deep Water (CDW) at the SACCF. The influence of different ACC frontal zones in the area to the north of South Georgia appears to provide for a horizontally and vertically segregated environment. The presence of optional foraging areas and niches close to the colony clearly play an important role in these king penguins' foraging success.

KEY WORDS: *Aptenodytes patagonicus* · Hydrological structure · Antarctic Circumpolar Current · Temperature gradient · Foraging niche · Seabird

INTRODUCTION

The behaviour and distribution of marine predators are generally thought to be determined by the location of their prey, but influenced by specific time and energy constraints. Prey distribution is strongly influenced by the structure of the marine environment (Owen 1981, Franks 1992), which is determined by physical properties such as temperature and temperature gradient. They govern the concentration of nutrients in the water column (Lima et al. 2002), which in turn influence the distribution and abun-

dance of planktonic organisms and, hence, higher trophic levels including the prey of apex predators (Owen 1981, Lutjeharms 1985, Schneider 1990). Surface features such as oceanographic fronts arise from where different water masses meet (Schneider 1990), and are, therefore, locations where different habitats as well as strong physical gradients occur in a spatially restricted area. Such a heterogeneous environment may be crucial for the existence of distinct foraging niches for predators.

King penguins are one of the most important avian consumers in the Southern Ocean (Woehler 1995).

They feed mainly on myctophids (Cherel & Ridoux 1992, Olsson & North 1997), mesopelagic fish that are generally associated with particular water masses or temperature ranges (Hulley 1981, Kozlov et al. 1991, Collins et al. 2012, Fielding et al. 2012), as well as with fronts and related oceanographic features (Brandt et al. 1981, Kozlov et al. 1991, Pakhomov et al. 1996, Rodhouse et al. 1996). Among diving birds, king penguins are able to forage at depths of over 300 m (Charrassin et al. 2002), and are known to use thermal discontinuities for foraging (Charrassin & Bost 2001). However, we still have little detailed understanding about how these predators may explore the thermal structure of the water column in different marine environments, and how habitat use may be adjusted depending upon changing constraints.

King penguins experience changing time and energy constraints over the summer breeding season (Charrassin et al. 2002, Halsey et al. 2010). During incubation (December to February), each parent alternately incubates and then returns to sea to restore its body reserves in 2 to 3 wk long foraging trips (Bost et al. 1997). After hatching, chick rearing (February to March) causes increased energy demand since the chick must be provisioned regularly (Charrassin et al. 1998). It is likely that changes in foraging behaviour reflect how these predators access the most profitable oceanographic structures according to their time and energy constraints. In this context, the thermal structuring of the foraging area and the presence of different foraging niches may play an important role (Charrassin & Bost 2001).

South Georgia is situated within the Antarctic Circumpolar Current (ACC), the most pronounced feature of the Southern Ocean circulation (Rintoul et al. 2001). It includes 3 major deep-reaching fronts, from north to south, the SubAntarctic Front (SAF), the Polar Front (PF) and the southern ACC Front (SACCF) (Orsi et al. 1995). The PF is an important foraging area for incubating king penguins at South Georgia (Trathan et al. 2008, Scheffer et al. 2010). However, there is no information on how changing breeding constraints may affect foraging behaviour, and how this may relate to local oceanography. For king penguins, foraging areas close to the SACCF have not yet been considered, despite the key role of this front for the Scotia Sea ecosystem (Thorpe et al. 2002, 2004, Ward et al. 2002, Murphy et al. 2004) and its close proximity to the breeding colonies at South Georgia. We know very little about features in the vertical dimension that may restrict efficient foraging for diving predators such as king penguins, or how this may relate to any changing constraints for these birds. Identifying such features and their association with different oceanographic areas may increase our understanding of how horizontal habitat use by diving predators is related to their exploration of the water column. This may be of importance in the context of environmental change, and any future potential effects on king penguin populations (Le Bohec et al. 2008, Forcada & Trathan 2009, Péron et al. 2012).

We investigated how king penguins breeding at South Georgia explore their available foraging area over the summer season in the horizontal and vertical dimensions. Using a combination of Global Positioning System (GPS) tracking and time-depth-temperature recorders (TDR), we addressed the question of how horizontal habitat use may relate to different ACC frontal zones and associated thermal structuring of the water column, and how diving behaviour, presumably targeting particular niches in the water column, changed accordingly. The results are discussed in the context of environmental variability and the potential vulnerability of diving predators such as king penguins to future environmental change.

MATERIALS AND METHODS

Study area, study period and device deployments

The study was conducted at the Hound Bay king penguin breeding colony on the northeast coast of South Georgia (54.23° S, 36.15° W) during the austral summers of 2005 to 2006 and 2006 to 2007. In total, 17 adult breeding king penguins were tagged: (1) during incubation in December 2005 to January 2006 (Early Incubation, n = 4, female), (2) during late incubation in January to February 2007 (Late Incubation, n = 4, unknown sex) and (3) during brooding (n = 9, unknown sex). Brooding birds were subsequently distinguished into Brooding I and Brooding II based on behaviour (see 'Results').

The horizontal movements of penguins were tracked by Track-Tag GPS loggers (Navsys; further details of Track-Tag are available at www.navsys. com/Products/tracktag.htm), which require only 60 ms to store raw GPS data. Devices were programmed to record positions at 60 s intervals and were equipped with a saltwater switch to delay acquisition while birds were under water. Loggers, with batteries and housing, weighed 55 g (<0.5% of body mass) and measured 35 × 100 × 15 mm (<0.7% of the cross sectional area of the body). Diving behaviour was recorded by TDR (Wildlife Computers). TDR devices

were programmed to record depth and water temperature at 1 s intervals when wet. Recordings during surface periods were halted by a saltwater switch and resumed when the bird restarted diving. The resolution of depth recordings was 0.5 m. TDRs weighed 30 g (<0.25 % of body mass) and measured 15 × 100 × 15 mm (Mk9) and 10 × 90 × 20 mm (Mk7) (<0.5 % of the cross sectional area of the body). Of the 17 penguins equipped with GPS devices, 13 of them had Mk9 TDR with external fast-responding temperature sensors, 2 had Mk7 TDR and 2 were without TDR devices. Devices were attached using methods modified from Wilson et al. 1997. All devices were recovered after a single foraging trip (varying between 5 and 23 d). In 2007, all tracked birds were weighed before leaving for sea and after their return to land to determine body mass gain during the foraging trips.

Oceanography of the study area

South Georgia is a sub-Antarctic island situated within the path of the ACC, with the PF to the north and the SACCF close to the island (Fig. 1). In contrast to most other king penguin breeding colonies which are located north of the PF (Bost et al. 2009), South Georgia is situated south of the PF. The PF is commonly defined as the location where cold Antarctic subsurface waters sink below warmer sub-Antarctic waters (Deacon 1933), corresponding to the northernmost extent of the subsurface temperature minimum, <2°C near 200 m depth (Belkin & Gordon 1996). The flow regime close to South Georgia is dominated by the SACCF, which loops anticyclonically around the South Georgia peri-insular shelf before retroflecting north of the island (Orsi et al. 1995, Thorpe et al. 2002, Meredith et al. 2003) at ~36° W. The SACCF flow is rich in nutrients (Ward et al. 2002), and hosts high biomass of zooplankton (Murphy et al. 2004). The Antarctic Zone (AAZ) is situated between the PF and the SACCF; it is characterized by the meeting of cold Antarctic waters and warmer surface waters from the PF. A complex eddy field has been described in the AAZ north of South Georgia as well as a warm-core anticyclonic circulation at around 52° S, 35° W (Meredith et al. 2003). Recent definitions of ACC fronts and zones in terms of Sea Surface Height (SSH) allow the identification of such features from altimetry data (Sokolov & Rintoul 2009, Venables et al. 2012), and the assignation of specific thermal profiles to frontal zones (Venables et al. 2012). In the Scotia Sea, the vertical structure of the water column includes the Surface Mixed Layer (SML), and the underlying cold Winter Waters (WW) originating from the previous winter mixed layer. The SML and WW are separated by a thermocline, a strong vertical temperature gradient of variable extent and intensity. Below the WW layer (from ~250 to 300 m), temperatures rise towards 2°C, characterizing the Circumpolar Deep Water (CDW).
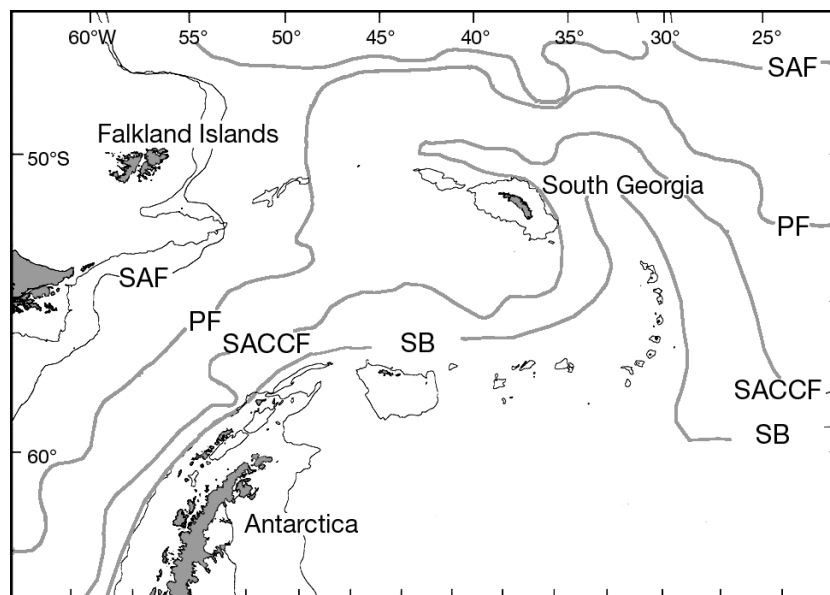

Fig. 1. South Georgia and the Antarctic Circumpolar Current (ACC) frontal positions in the Scotia Sea. Fronts: thick grey lines; 500 m and 1000 m isobaths: dark grey. Frontal positions from Orsi et al. (1995). SAF: Sub-Antarctic Front; PF: Polar Front; SACCF: Southern ACC Front; SB: Southern ACC Boundary

Oceanographic data

SSH data

Changes in SSH encountered by the penguins over their foraging trips were analyzed using Aviso (www.aviso.oceanobs.com) absolute dynamic topography (ADT) data. We used Near-real time (NRT) data available at a higher temporal resolution than the delayed time (DT) products. Data were available at a spatial resolution of 1/3° × 1/3° and a biweekly temporal resolution. SSH values at each dive location were estimated by searching for the geographically nearest value within the corresponding dataset.

Vertical temperature data

Vertical temperature values were obtained from the external Mk9 sensor data after applying appropriate temperature correction factors from the device calibration data sheets (Wildlife Computers). Mk7 temperature data were not used due to long response times of the internal temperature sensors. Mk9 temperature sensors provide high quality data (accuracy 0.1°C ± 0.05°C, Simmons et al. 2009), and were, therefore, used for determining the properties of the water column encountered during the penguins' dives. To compensate for the surface heating effect by direct sun exposure and penguin body temperature on the temperature sensors (McCafferty et al. 2007), temperature values collected between 0 and 10 m were replaced by the value measured at 10 m depth during the ascent. The vertical water temperature gradient for each recorded depth point was also calculated; this was estimated as the temperature difference between 25 m above and 25 m below the given depth point. Temperature gradients near to the depth extremes of a dive were calculated using the maximal depth range possible (limited by the surface for points <25 m depth, and by the maximal dive depth for points >max. depth 25 m). The resulting possible bias in gradient values may only affect the depth range between the maximum depth range of a dive and 25 m above, as dives <50 m were not considered for analyses of foraging behaviour (see Data analysis). A temperature gradient of 1 thus corresponds to a temperature increase of 1°C per 50 m depth, −1 to a temperature decrease of 1°C per 50 m.

Data analysis

Data analyses were performed using Matlab (MathWorks) and the custom-made software Multi-Trace (Jensen software systems).

Analysis of surface and diving behaviour

GPS data were filtered to remove positions with navigation class >2, where class categories were 0: good, 1: altitude aided, 2: marginal position dilution of precision, and 3: bad. For each bird, we calculated trip duration, distance covered, max. distance from the colony and the furthest latitude south reached. Exact departure and return times from and to the island were determined from the TDR data. A foraging zone coefficient (FZC) was calculated as the total trip length (km) divided by the max. distance from the colony (km) (modified from Guinet et al. 1997, Hull et al. 1997), indicating the degree of directness or looping of a foraging trip.

A zero offset correction was applied on the dive data. Only dives >50 m depth were used for analysis, as they were considered to represent the majority of king penguins foraging dives (Pütz et al. 1998, Charrassin et al. 2002). Diving behaviour was analysed by calculating the following dive parameters: dive depth, dive duration, bottom duration (the time between the first and last wiggle or dive step deeper than 75% of the maximum dive depth, following Halsey et al. 2007), the number of wiggles (deviations >1 m of depth with an absolute vertical instant >0) as a proxy of feeding success (Bost et al. 2007) and broadness index (bottom duration:dive duration, indicating the proportion of a dive used for the bottom period, see Halsey et al. 2007 for more details). Furthermore, we determined the total vertical distance travelled per day, the dive frequency, the percentage of submerged time compared to the total time at sea, and the percentage of submerged time spent at depths >150 m as proxies of foraging effort. As king penguins are visual feeders and essentially forage during the daylight and twilight hours (Bost et al. 2002), night dives were excluded from the analyses. Exact sunrise and sunset times were calculated as described in Scheffer et al. 2010. Geographical coordinates at the start of each dive were interpolated based on time from the GPS data, assuming straight line travel and constant speed between 2 location points (Weavers 1992).

Principal Component Analysis (PCA) was carried out on 15 variables characterizing foraging behaviour (surface movements and diving behaviour, see Table 1 for the complete listing of all PCA variables), allowing identification of the main variables accounting for differences in foraging behaviour as well as behavioural groupings of birds. Dive parameters among grouped birds were compared using Kruskal-Wallis statistics as tests for normality failed (Jarque Bera test) and transformations did not help the data to conform to the normality assumption. When significant differences were found among groups, an all pairwise multiple comparison (Dunn's method) was performed to determine the groups that differed from the others.

Analysis of horizontal and vertical habitat use

The horizontal habitat use of king penguins was analysed with respect to trip orientation relative to

Table 1. Principal component analysis of the foraging parameters. Component loadings of the different variables

Variable	PC1 (75.7%)	PC2 (21.8%)
Dive depth	0.1717	0.1133
Dive duration	0.0551	0.0456
Bottom duration	−0.0868	−0.2066
No. wiggles/dive	−0.0613	−0.3846
Dive frequency	−0.0812	−0.2237
% time submerged	0.0498	−0.0957
% time submerged >150 m	0.5444	0.3738
No. wiggles:time submerged	−0.0718	−0.5024
No. wiggles:bottom duration	0.0217	−0.1862
Depth range index	−0.0336	−0.1832
Broadness index	−0.1306	−0.2522
Vertical distance:day	0.1422	−0.0198
Trip duration	−0.4662	0.3432
Trip length	−0.487	0.2627
Max. distance from colony	−0.3902	0.1557

the different ACC fronts. The ACC fronts and zones were defined based on SSH signatures following Venables et al. (2012). The penguin's vertical habitat use was analysed with respect to the exploration of depth and thermal properties of the water column relative to the ACC fronts. We considered the bottom phases of dives, which is thought to be the most important phase for prey capture (Charrassin et al. 2002, Simeone & Wilson 2003, Ropert-Coudert et al. 2006). Kernel density estimations of bottom periods of the different foraging groups were computed on SSH and depth using a Gaussian Kernel. These were then overlaid on the vertical thermal structure of different ACC frontal zones following Venables et al. 2012. This allowed us to analyse the penguins' use of the water column with respect to depth and thermal structures relative to frontal zones.

Detailed use of the water column by the penguins while foraging was analysed by considering depth, temperature and temperature gradient during the bottom periods of the dives. Analyses were carried out on data with a resolution of 1 Hz. Contour plots of bottom periods of dives >50 m on depth – temperature gradient and temperature – temperature gradient axes allowed us to evaluate the penguins' use of the water column, and to identify the target of different water masses by the different foraging groups. To identify water masses from the water characteristics targeted by the penguins, we defined 4 water masses based on water temperature (T) and temperature gradient (gradT): thermocline waters (T ≥ 1.5; gradT < 0), WW in proximity ≤25 m of the

thermocline (T < 1.5; gradT < 0), WW deeper than 25 m below the thermocline (T < 1.5; gradT ≥ 0), CDW (T ≥ 1.5; gradT ≥ 0).

Wiggles occurrence and influencing factors

As wiggles are good proxies of prey capture attempts in penguins (Takahashi et al. 2004, Bost et al. 2007, Hanuise et al. 2010), we examined water characteristics where wiggles occurred, with respect to temperature and temperature gradient. We used logistic regression models to quantify relationships between water properties and the occurrence of wiggles for individual as well as for grouped birds. For the regression models, we included temperature and temperature gradient data for dives >50 m depth with a temporal resolution of 1 s, after testing for noncorrelation using Pearson's correlation coefficient. The predictor of wiggles occurrence was a combination of the water temperature, the values and the absolute values of the temperature gradient, taking into account the direction of the gradient as well as its intensity. To evaluate model discrimination performances between wiggle presence and absence, we used risk score plots (Royston & Altman 2010). Risk score plots allowed us to graphically compare the densities of the risk score (linear predictor) in the event and no-event group (occurrence and nonoccurrence of wiggles). The overlap of the risk score densities determined the discrimination performance of the model: the larger the overlap, the weaker the discrimination.

RESULTS

Identification of different foraging groups

We distinguished 4 foraging groups characterized by differences in breeding stage as well as foraging characteristics (Fig. 2, Tables 1, 2 & 3). The groups were Early Incubation (n = 4), Late Incubation (n = 4), Brooding I (n = 3) and Brooding II (n = 4). The PCA of foraging parameters showed the separation of the 4 foraging groups, and allowed the identification of the main variables accounting for the differences (Fig. 2, Table 1). The first principal component was mainly explained by the horizontal and vertical distances travelled. These variables separated the Brooding II from the Incubation groups, with the Brooding I birds spread out in between. Brooding II birds were characterized by the shortest horizontal (Table 2) and
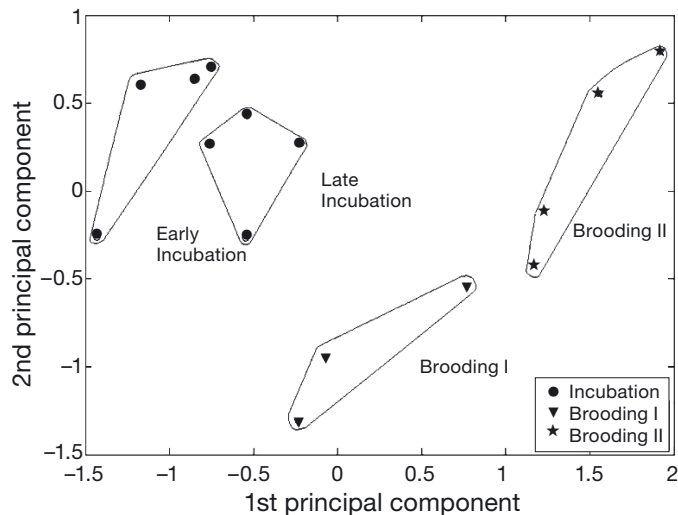
Fig. 2. *Aptenodytes patagonicus*. Principal component analysis of the foraging parameters in the different foraging groups. Component loadings of the variables are listed in Table 1

and Brooding II groups. Brooding I birds were characterized by a dominant bottom phase, high wiggle numbers and a high dive frequency (Table 3). Brooding II birds showed the deepest and longest dives with the shortest bottom periods (Table 3). Broadness index was highest for Brooding I birds and lowest for Brooding II birds (Table 3). A main variable influencing both principal components was the proportion of dive time spent at depths >150 m, separating the Brooding II birds from the Incubation and Brooding I groups (Fig. 2, Table 1).

Trip orientation and foraging areas

All trips were oriented to the north towards the SACCF, AAZ and PF waters, with birds of different breeding stages targeting different foraging areas (Fig. 3) and showing different foraging trip characteristics (Table 2). Early Incubation birds undertook the most extended foraging trips, where increased SSH values indicated PF and Polar Frontal Zone (PFZ) waters. Late Incubation birds targeted areas at the southern edge of the PF and in the AAZ.

longest daily vertical (Table 3) distances travelled. The second principal component was mainly loaded with variables of underwater foraging behaviour, separating the Brooding I birds from the Incubation

Table 2. *Aptenodytes patagonicus*. Trip parameters for individual birds in the different foraging groups (FZC = foraging zone coefficient)

Bird ID	Date of deployment and recovery	Trip duration (d)	Trip length (km)	Max. distance from colony (km)	Min.° S reached	FZC
Early Incubation						
8	23.12.2005–13.01.2006	19.9	2077	642	49.84	3.2
9	28.12.2005–18.01.2006	19.5	2291	522	49.77	4.4
10	30.12.2005–17.01.2006	16.4	1880	520	49.83	3.6
11	30.12.2005–23.01.2006	23.2	2510	537	49.73	4.7
Mean ± SE		19.7 ± 1.4	2190 ± 136	556 ± 29	49.79 ± 0.03	4.0 ± 0.3
Late Incubation						
C5	02.02.2007–20.02.2007	17.3	1585	435	50.77	3.7
C7	02.02.2007–2.02.2007	20.3	1506	409	50.72	3.7
C9	03.02.2007–26.02.2007	23.2	1690	558	51.82	3.0
C10	03.02.2007–17.02.2007	13.4	1150	445	50.40	2.6
Mean ± SE		18.6 ± 2.1	1483 ± 117	462 ± 33	50.93 ± 0.31	3.2 ± 0.3
Brooding I						
H5	09.02.2007–17.02.2007	6.1	610	234	52.55	2.6
H9 (no TDR)	12.02.2007–19.02.2007	6.2	559	227	52.5	2.5
P3	18.02.2007–01.03.2007	9.1	925	317	51.67	3.1
P5	18.02.2007–28.02.2007	7.0	822	346	51.32	2.9
Mean ± SE		7.1 ± 0.7	729 ± 87	281 ± 30	52.01 ± 0.31	2.8 ± 0.1
Brooding II						
H3	09.02.2007–16.02.2007	5.1	491	190	52.98	2.6
H6 (no TDR)	10.02.2007–16.02.2007	5.5	490	159	53.04	3.1
P4	18.02.2007–25.02.2007	6.0	517	163	53.50	3.2
P10	27.02.2007–04.03.2007	4.8	430	112	53.44	3.9
T4	28.02.2007–06.03.2007	5.5	629	247	52.20	2.4
Mean ± SE		5.4 ± 0.2	512 ± 33	174 ± 22	53.03 ± 0.23	3.0 ± 0.3

Table 3. *Aptenodytes patagonicus*. Dive parameters for individual birds in the different foraging groups. KW = Kruskal Wallis test with p < 0.001. Dunn's test was performed with p < 0.05. The foraging groups show significant differences from others as indicated (all: all other foraging groups; Inc: Early & Late Incubation; BI: Brooding I; BII: Brooding II). VD = vertical distance

Bird ID	Dive depth (m)	Dive duration (s)	Bottom duration (s)	Wiggles per dive	Broadness index	Total VD (km d^{-1})	Total dives per day	% of time sub-merged >150 m
Early Incubation								
8	117.8	246.5	61.6	6.3	0.26	306.5	268.5	2.3
9	130.2	259.0	73.1	8.0	0.28	306.2	209.4	4.7
10	129.0	287.4	92.2	9.1	0.32	266.1	171.0	3.5
11	126.0	260.5	82.6	12.4	0.32	301.8	583.0	3.4
Mean ± SE	125.7 ± 2.8	263.3 ± 8.6	77.4 ± 6.6	9.0 ± 1.3	0.30 ± 0.02	295.1 ± 9.7	308.0 ± 93.8	3.5 ± 0.5
Late Incubation								
C5	134.2	246.8	61.9	10.5	0.25	310.1	412.5	4.1
C7	128.8	260.9	73.3	7.4	0.28	315.1	249.7	4.1
C9	144.1	258.6	54.1	7.1	0.21	297.7	261.3	4.6
C10	122.5	251.4	57.8	5.7	0.23	364.2	361.5	3.1
Mean ± SE	132.4 ± 4.6	254.4 ± 3.3	61.8 ± 4.1	7.7 ± 1.0	0.24 ± 0.02	321.8 ± 14.6	321.2 ± 39.4	4.0 ± 0.3
Brooding I								
H5	145.1	256.0	70.9	9.7	0.28	434.8	327.3	6.4
P3	118.0	249.8	96.2	14.6	0.39	317.1	254.2	2.0
P5	111.3	239.0	81.0	10.4	0.34	333.6	355.4	2.1
Mean ± SE	124.8 ± 10.3	248.3 ± 4.7	82.7 ± 7.4	11.6 ± 1.5	0.33 ± 0.03	361.8 ± 36.8	312.3 ± 30.2	3.5 ± 1.4
Brooding II								
H3	163.8	272.2	57.9	8.8	0.21	432.2	294.2	8.4
P4	201.9	308.4	52.1	6.5	0.17	377.5	249.0	10.8
P10	183.4	288.8	55.5	5.3	0.19	437.6	199.0	12.7
T4	175.8	294.2	68.1	11.4	0.24	424.9	366.4	9.6
Mean ± SE	181.2 ± 8.0	290.9 ± 7.5	58.4 ± 3.4	8.0 ± 1.3	0.20 ± 0.01	418.0 ± 13.8	277.2 ± 35.5	10.4 ± 0.9
KW & Dunn's test	all	BI-BII	BI-BII	BI	BI-BII	Inc-BI&BII	BII	BII

Brooding birds undertook shorter trips into areas south of the PF. Brooding I birds showed highly directed foraging trips into AAZ waters, indicated by low FZC values. Brooding II birds were characterized by less directed foraging trips into the SACCF or its northern boundary.

Vertical habitat use

Penguins in the different foraging groups showed differing use of the water column in the various ACC zones (Fig. 4), targeting different depths, water temperatures and temperature gradients during the bottom periods of the dives (Fig. 5). Early Incubation birds foraged in the SACCF, the AAZ, the PF and occasionally in PFZ waters, and explored a broad temperature range of −1 to 6°C, with temperature gradients between 0.5 and −3°C per 50 m. The thermocline and WW appeared to be the most important water masses for bottom times, but there was no clear concentration of bottom times in specific parts of the water column. Late Incubation birds foraged in the

SACCF and in the AAZ until the southern edge of the PF. Bottom periods were directed into waters of −0.5 to 2°C and temperature gradients of up to −4°C per 50 m. Shallow and deep WW were the most targeted water masses. Brooding I birds showed highly focused targeting of shallow waters of strong thermal gradients in the AAZ. Bottom periods were directed into similar conditions to those of Late Incubating birds, but more focused on strong gradients in shallow WW. Brooding II birds concentrated their foraging activity in SACCF waters, where they dived to depths of 100 to 300 m. Bottom periods occurred in a restricted range of temperature and temperature gradient of −0.5 to 2°C and −0.5 to 0.5°C per 50 m, respectively. This indicates the target of deep WW and CDW.

Wiggles occurrence and influencing factors

For incubating birds, the correlations between wiggle occurrence and water properties were generally weak when considered over an entire foraging trip.

(a) Early Incubation 2005/06 (n = 4)

(b) Late Incubation 2007 (n = 4)

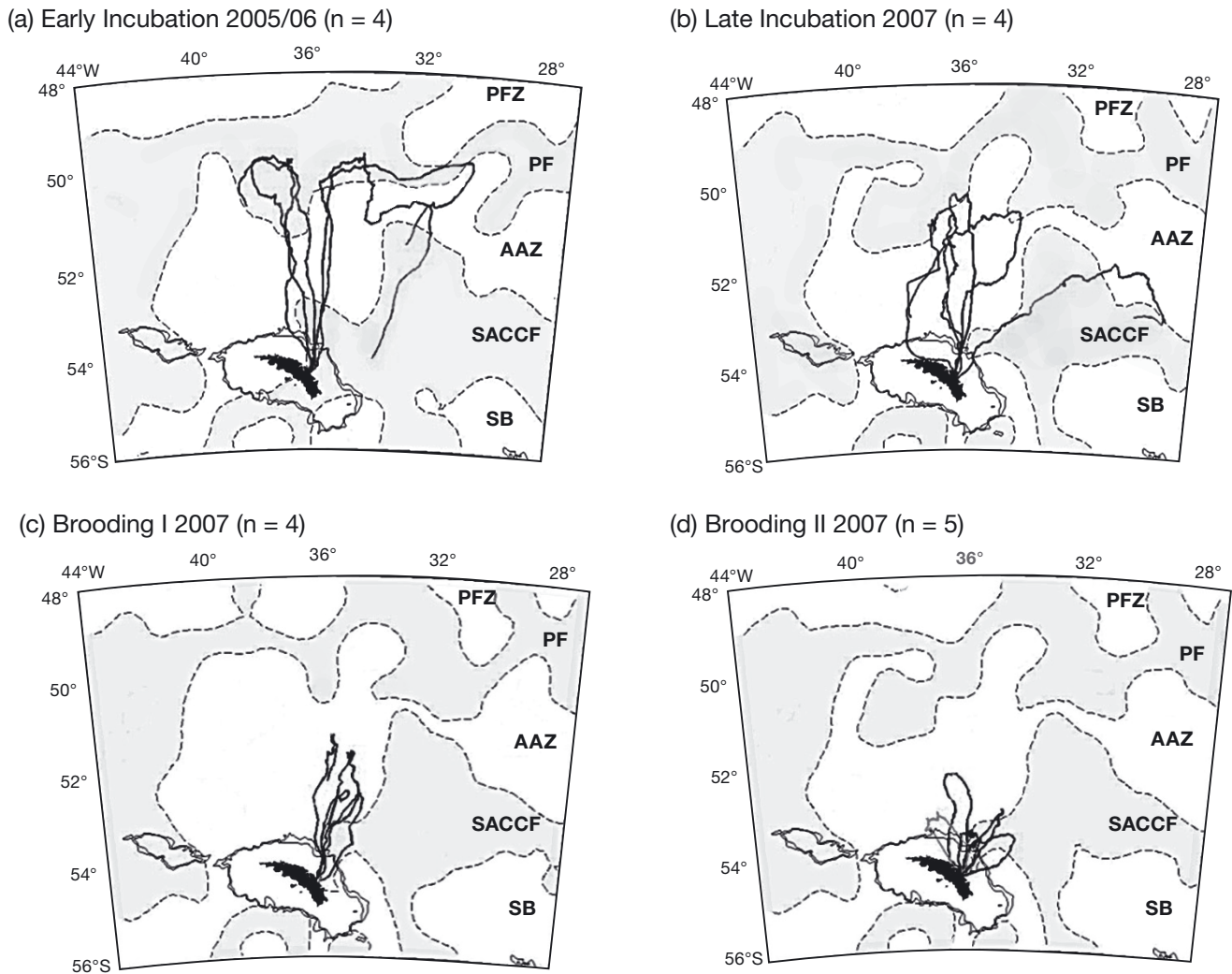(c) Brooding I 2007 (n = 4)

(d) Brooding II 2007 (n = 5)

Fig. 3. *Aptenodytes patagonicus*. Tracks of GPS-equipped individuals (a–d) from South Georgia during summer 2005 to 2006 and summer 2007 with the major ACC fronts in the Scotia Sea. Incomplete tracks are due to tag memory limitations or insufficient time at the surface to collect GPS satellite ephemerides. Frontal zones are based on Sea Surface Height (SSH) definitions from Venables et al. (2012). Frontal positions shown on the maps correspond to the mean positions over the trip period of the corresponding foraging group. PFZ: Polar Frontal Zone; PF: Polar Front; AAZ: Antarctic Zone; SACCF: Southern ACC Front; SB: Southern ACC Boundary

In the PFZ, low water temperature appeared to play a more important role for wiggles occurrence than the temperature gradient (Fig. 6 a,b). The logistic regression model showed that wiggle occurrence was greater at negative water temperature gradients for Brooding I birds, and increasing with positive gradient for Brooding II birds (Fig 6c,d). Correlations were stronger for Brooding I than for Brooding II birds. Risk score plots indicated better model discrimination performances for conditions of wiggles absence than of wiggles presence for all birds, and reduced performances for grouped birds compared to the analysis of single birds.

Body mass gain of tracked penguins

Brooding II birds had highest body mass gains per day as well as in relation to horizontal and vertical distances travelled. Brooding I birds showed higher mass gains per day and distances travelled than the Incubation group (Table 4).

DISCUSSION

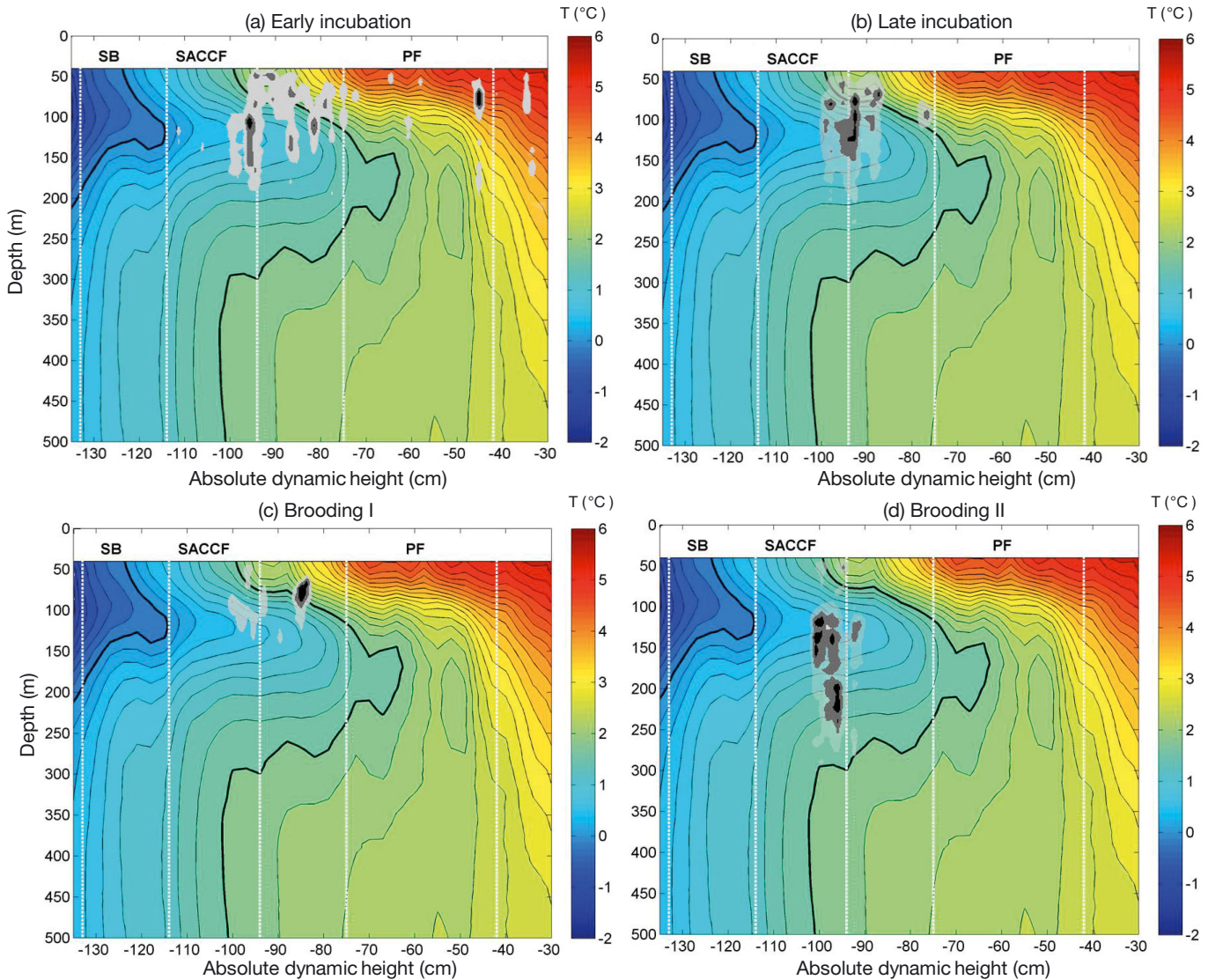This is the first study to investigate how a deep diving avian marine predator changes its foraging

Fig. 4. *Aptenodytes patagonicus*. Kernel densities of bottom times for the different foraging groups (a–d). Density contours encompass 20, 50 and 90% of the bottom time distributions. Temperature profiles on SSH and depth with ACC front limitations from Venables et al. (2012)

behaviour and habitat use at a fine spatial scale, both vertically and horizontally. The major features of our study are: (1) King penguin foraging behaviour showed different horizontal and vertical patterns over the summer season, presumably in response to changing energetic constraints related to their breeding phase. Foraging trips during incubation extended to the PF, whereas brooding birds foraged exclusively south of the PF in AAZ and SACCF waters. (2) Diving behaviour was correlated with the thermal structure of the water column, with the vertical temperature gradient and depth appearing to play important roles for the separation of different vertical foraging niches. (3) Structure in the hydrological environment south of the PF may allow foraging strat-

egy adjustment in relation to changing constraints, and may offer important flexibility for king penguins in the context of environmental variability.

Foraging areas in relation to frontal zones

Areas used for foraging by king penguins changed over the course of the summer season. Birds explored the PF during early incubation and the waters between the PF and the SACCF later in the summer season. For seabirds, changes in foraging trip duration at different times of the breeding cycle are known to occur and are thought to be the result of changing time constraints arising from the need to supply the chick
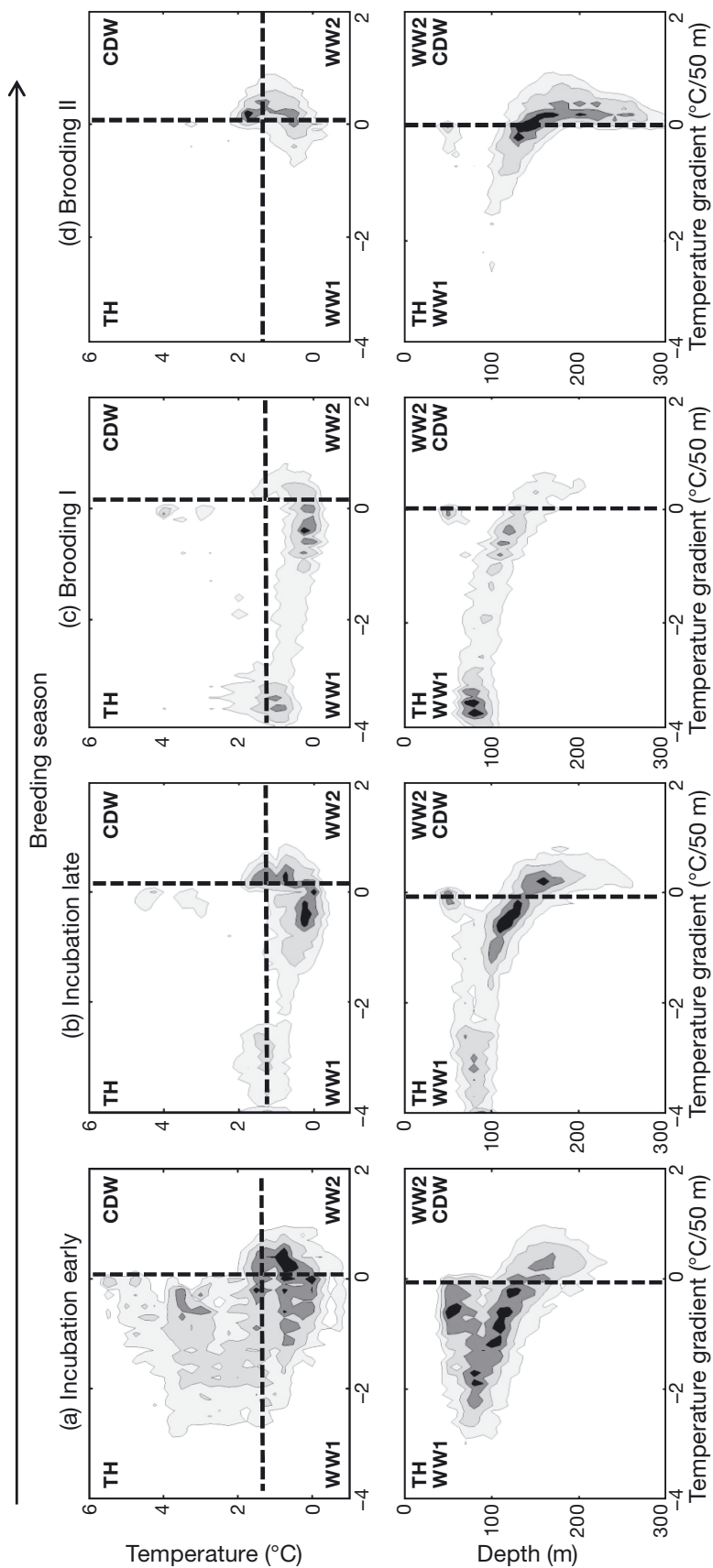
Fig. 5. *Aptenodytes patagonicus*. Environmental niches in the water column targeted by different foraging groups (a–d). Plotted are bottom times of all dives >50 m on temperature, temperature gradient and depth axes. Contours encompass 10, 25, 50 and 90% of the bottom times of each foraging group. Dotted lines = limits of the water column characteristics used for the definition of the water masses (see Material and Methods). TH = thermocline; WW1 = shallow winter water close to the thermocline; WW2 = deeper winter water; CDW = circumpolar deep water

with food (Bost et al. 1997, Charrassin et al. 1999, Lescroël & Bost 2005). However, in contrast with the situation at South Georgia, king penguins breeding at other locations have not been reported as changing their foraging areas between incubation and brooding (Bost et al. 1997, Guinet et al. 1997, Sokolov et al. 2006). The accessible region to the north of South Georgia is influenced by 2 major ACC fronts, both representing potential areas of increased mesoscale variability (Trathan et al. 1997, 2000, Moore et al. 1999b, Thorpe et al. 2002, Meredith et al. 2003), and, therefore, the possibility of alternative foraging locations for marine predators. The role of the PF has already been reported for king penguins breeding at South Georgia (Trathan et al. 2008, Scheffer et al. 2010) and at other locations (Bost et al. 1997, 2009, Moore et al. 1999a, Charrassin & Bost 2001, Sokolov et al. 2006). At South Georgia, the AAZ and SACCF appear to provide alternative foraging areas closer to the colony. It may allow short foraging trips with low travel costs for birds with high time and energy constraints, as shown by brooding birds, and may, therefore, play a key role for king penguins.

The importance of the SACCF for the Scotia Sea ecosystem has been emphasised in previous studies (Thorpe et al. 2002, 2004, Ward et al. 2002, Murphy et al. 2004;) due to nutrient enrichment resulting in increased phyto- and zooplankton development, possibly resulting in increased myctophid densities associated with these more productive waters. In the AAZ, the meeting of Antarctic waters with warmer PFZ waters as well as the presence of SACCF eddies
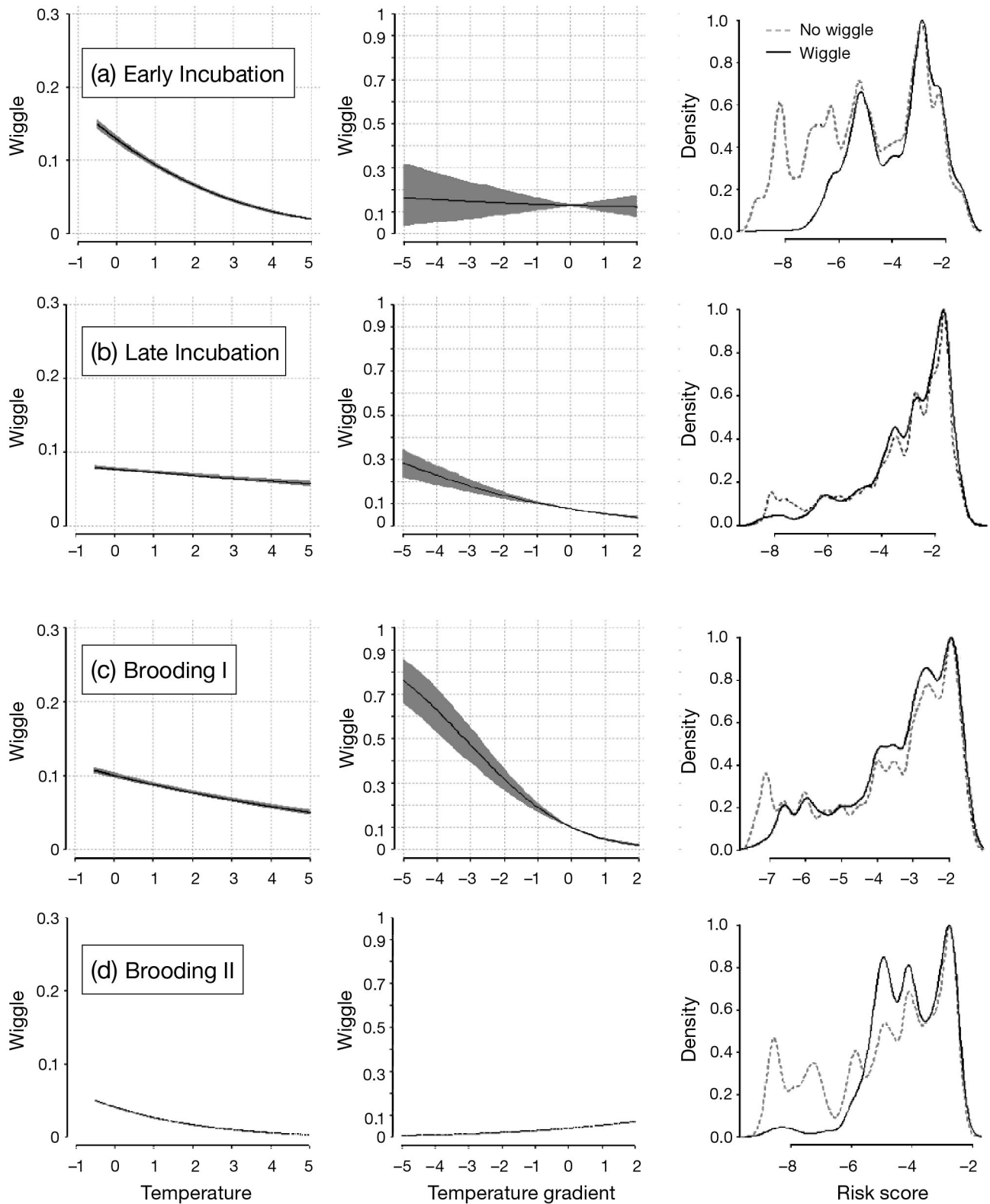
Fig. 6. *Aptenodytes patagonicus*. Wiggles occurrence as a function of water temperature and temperature gradient, and corresponding risk score plots for model discrimination performance. Output of the logistic regression model and risk score plots for (a) 1 Early Incubation and (b) 1 Late Incubation bird. Early Incubation includes data from only within PF and PFZ waters, Late Incubation includes data from the entire trip. (c,d) Model output and risk score plot for (c) 1 Brooding I and (d) 1 Brooding II bird

Table 4. *Aptenodytes patagonicus*. Body mass at start and end of foraging trips as well as total body mass gain per day and per distance travelled for individuals tracked in 2007. HD = horizontal distance; VD = vertcal distance

Bird ID	Start weight (kg)	End weight (kg)	Mass gain		
			(kg d^{-1})	(kg per 100 km HD)	(kg per 100 km VD)
Late Incubation					
C5	11.4	15.4	0.23	0.25	0.07
C7	11.4	17.0	0.28	0.34	0.09
C9	11.0	14.2	0.14	0.19	0.05
C10	11.8	14.6	0.21	0.24	0.06
Mean ± SE	11.4 ± 0.2	15.3 ± 0.6	0.21 ± 0.03	0.26 ± 0.04	0.07 ± 0.01
Brooding I					
H5	13.8	15.8	0.33	0.33	0.08
H9	13.8	16.9	0.50	0.55	no TDR
P3	12.1	15.1	0.33	0.32	0.10
P5	14.1	17.0	0.42	0.35	0.12
Mean ± SE	13.5 ± 0.5	16.2 ± 0.4	0.39 ± 0.04	0.39 ± 0.06	0.10 ± 0.01
Brooding II					
H3	14.0	16.8	0.55	0.57	0.13
H6	13.0	15.8	0.51	0.57	no TDR
P4	13.8	15.9	0.35	0.41	0.09
P10	12.0	14.5	0.46	0.58	0.10
T4	15.1	17.9	0.58	0.44	0.14
Mean ± SE	13.6 ± 0.5	16.0	0.49 ± 0.04	0.51 ± 0.04	0.12 ± 0.01

(Thorpe et al. 2002, Meredith et al. 2003) may create areas of strong thermal gradients, where myctophids may aggregate (Brandt et al. 1981, Kozlov et al. 1991). Reduced vertical mixing in the AAZ compared to adjacent frontal areas may increase the stability of such thermal structures, therefore favouring associated prey patches (Spear et al. 2001).

King penguins have already been reported to use mesoscale oceanographic features for non-random directed foraging during incubation at South Georgia (Trathan et al. 2008, Scheffer et al. 2010) and at Crozet islands (Cotté et al. 2007). Seasonal changes between foraging areas associated with different larger-scale oceanographic features of elevated mesoscale activity support the hypothesis that king penguin alter their foraging behaviour at different spatial and temporal scales.

Targeted foraging niches in the water column

Our detailed analysis of the time spent at the bottom of the dives, relative to frontal zones and to thermal structures in the water column, allowed us to determine the water masses explored by king penguins over the summer season, and how birds adjust their foraging niches according to breeding constraints.

During December and January, incubating birds foraged in the SACCF, the AAZ and the PF, and targeted various thermal structures at different depths in the water column. Enhanced vertical mixing in frontal areas (Spear et al. 2001) may lead to increased spatial and temporal variability in thermal structures and associated prey resources. Such dynamic prey distributions may be reflected by the less consistent targeting of specific depth-temperature-gradient patterns of birds foraging in the PF compared to in the AAZ, and only weak correlation of wiggle occurrence with specific temperature gradients.

Late Incubation and Brooding I birds mainly foraged in AAZ waters. Brooding I birds targeted shallow WW in close proximity to the thermocline, and wiggles occurrence was correlated with strong thermal gradients. The importance of sub-thermocline prey aggregations has already been reported for dolphins (Scott & Chivers 2009), tuna (Schaefer et al. 2007) and sunfish (Cartamil & Lowe 2004), and appears to be confirmed for king penguins foraging in the AAZ. Collins et al. (2008, 2012) found that certain myctophid species can be present at shallow depths during daytime in the AAZ in the area to the north of South Georgia. Strong thermal gradients of high stability may represent suitable conditions for stable myctophid aggregations at shallow depths, which have been reported previously associated with warm-core rings in the Gulf Stream (Conte et al. 1986) and in the equatorial Atlantic Ocean, with tuna

also exploiting these aggregations (Marchal & Le-bourges 1996, Bard et al. 2002). The diving behaviour of Brooding I birds may indicate the presence of such permanent myctophid layers at shallow depths of 70 to 110 m in the Scotia Sea, even though this has so far only been reported from more temperate regions. However, this hypothesis remains speculative as independent prey data was not available for our study.

Brooding II birds showed significantly deeper dives than the other groups, mainly targeting waters with weak positive temperature gradients at the transition between deep WW and CDW in the SACCF. High body mass gains despite increased dive depths and reduced bottom times suggest increased foraging efficiency in these deep waters. Deep and long dives reported from king penguins at Crozet in autumn (Charrassin et al. 1998, 2002, Halsey et al. 2010) suggest seasonal changes in targeted prey similar to those observed at South Georgia for Brooding II birds. At Crozet, king penguins appear to compensate increased costs for deeper dives in autumn by longer bottom times (Charrassin et al. 2002, Halsey et al. 2010). At South Georgia, king penguins seem to be able to increase foraging efficiency at the bottom of dives. The foraging area targeted by Brooding II birds may provide particular conditions of highly profitable prey resources at great depths, potentially enhanced by the higher nutrient content in areas with the SACCF influx into the Scotia Sea (Ward et al. 2002).

Thermal structure of the water column and foraging

The thermal structure of the water column and depth appeared to play a crucial role for the separation of foraging niches and the expression of different foraging patterns, especially with increasing constraints on the animals. Relative water structures have been suggested to play an important role for vertical movements of other diving predators such as tuna and billfish (Brill et al. 1993, Brill & Lutcavage 2001), sunfish (Cartamil & Lowe 2004), dolphins (Scott & Chivers 2009) and basking sharks (Sims et al. 2005). Foraging tuna and associated tropical seabirds have been reported to be more abundant in non-frontal areas characterized by lower vertical mixing and higher stability of vertical thermal structures (Owen 1981, Spear et al. 2001). King penguins are diving predators that target similar prey; they may, therefore, rely on the same criteria for favourable foraging habitats and show similar affinity with well structured waters, possibly reflected by targeting distinct niches in non-frontal or border areas by brooding birds. In addition to the importance of frontal zones for Southern Ocean marine predators (Bost et al. 2009), non-frontal or boundary areas with a higher stability of vertical thermal structures may also play a key role for diving predators such as king penguins, especially when constraints limit flexible travel times and behavioural adaptations to dynamic conditions at fronts.

The vertical temperature gradient appeared to be a main factor for foraging niche adjustment and explaining differences in prey pursuit behaviour (wiggle occurrence). Thermal gradients are locations of enhanced biological activity (Thomas & Emery 1988, Lima et al. 2002), resulting in the accumulation of biomass for various trophic levels, ranging from planktonic organisms to mesopelagic fish and ultimately upper trophic level predators. Being one of the most pronounced vertical temperature gradients in the ocean, the thermocline has already been suggested as an important feature for king penguins at Crozet (Charrassin & Bost 2001) as well as for other marine predators foraging in the Southern Ocean (Boyd & Arnbom 1991, Biuw et al. 2007) and in more temperate regions (Cayre & Marsac 1993, Kitagawa et al. 2000, Spear et al. 2001, Weng et al. 2009, Sepulveda et al. 2010). Our study underlines the crucial role of the thermocline for foraging king penguins breeding at South Georgia. It also demonstrates the possibility that king penguins have alternate efficient foraging strategies for exploiting water masses where thermal gradients do not seem to be the main factor governing prey distribution.

Our regression models have revealed some insights into the effect of thermal properties of the water column on king penguins foraging. However, variable regression coefficients between individual birds as well as the prevalence of Brooding I and Brooding II patterns on identical trip departure dates underline the fact that foraging strategies might not only relate to particular environmental conditions. Behavioural plasticity and individual factors (Svanback & Bolnick 2005, Sargeant et al. 2007) such as detailed breeding constraints, fitness and prior experience may also play a role. Lower model performances for wiggle presence than absence may result from the fact that favourable foraging conditions for king penguins are not only determined by the thermal structure of the water column, but may also be influenced by other factors governing prey distribution in a given environment such as stochastic processes and prey behaviour.

King penguins' foraging and environmental variability

Foraging behaviour of king penguins breeding at South Georgia appears to be structured both horizontally and vertically. Penguins targeted different foraging areas depending on their breeding constraints, and adjusted their foraging activity in the water column. So far such strong habitat selection and the presence of alternative foraging niches have not been reported for king penguins from other locations. Patterns described from Crozet suggest changes in foraging characteristics over the summer season similar to those described at South Georgia, with shortening of foraging trips and increasing dive depths. However, penguins in both the incubation and brooding stage target the PF, and foraging patterns appear less diverse than those of king penguins at South Georgia with respect to trip characteristics, diving behaviour and the targeting of distinct niches in the water column (Charrassin et al. 1998, 2002, Charrassin & Bost 2001). This may suggest that alternative foraging areas closer to the colony, as reported from South Georgia, are not available at Crozet.

For king penguins breeding north of the PF (i.e. Crozet, Marion Island), the geographically nearest profitable myctophid aggregations may be found at accessible depths mostly at the PF and its northern edges, as myctophid species targeted by king penguins are known to increase in depth northwards of the PF (S. Fielding pers. comm.). This means that penguins breeding in these locations may depend to a higher degree on the PF. Predicted declines of king penguins due to environmental variability (Barbraud et al. 2008, Le Bohec et al. 2008, Péron et al. 2012) and in case of shifts in the PF may, therefore, only relate to areas where the animals are highly dependent on the PF due to the lack of alternative foraging areas. Such predictions might be of lesser value for king penguins breeding at South Georgia.

King penguins at South Georgia appear to be able to exploit profitable prey resources at the southern edge and south of the PF, either in terms of reduced depth in the AAZ or of increased profitability per catch effort at the bottom in SACCF waters. The area south of the PF may offer an elevated degree of foraging habitat segmentation to king penguins, as other structures than the PF may provide for profitable prey resources at accessible depths. King penguins from Heard Island, also located south of the PF, appear mainly to forage in the area to the east of the island (Moore et al. 1999a, Wienecke & Robertson 2006), a location influenced by the southern branch of the PF and the Fawn Trough current (Roquet et al. 2009, van Wijk et al. 2010). Foraging in areas outside or at the southern boundaries of the PF, areas characterized by cold water masses, may produce similar patterns to those at South Georgia. However, studies from Heard Island provide no information on diving behaviour in relation to the thermal structure of the water column, or on segregation of foraging areas.

Oceanography at South Georgia is known to be influenced by ENSO (El Niño – Southern Oscillation) and SAM (Southern Annular Mode) as well as more direct atmospheric processes (Trathan & Murphy 2002, Meredith et al. 2008). However, different time lags between these events and the response in oceanography at South Georgia occur (Meredith et al. 2008), as well as temporal variation in the connections within the Scotia Sea ecosystem (Murphy et al. 2007). Our study includes reports of only one season per foraging group. Therefore, it remains open as to whether the patterns observed are a constant element in the foraging strategy of king penguins breeding at South Georgia, or whether they are a response to particular conditions during our study years. Nevertheless, the oceanographic patterns observed during our study appear to be consistent with general patterns described in the area to the north of South Georgia (Trathan et al. 1997, 2000, Thorpe et al. 2002, Meredith et al. 2003, Brandon et al. 2004). Also, the temporal and spatial scales of the oceanographic features considered exceed the duration of the tracked foraging trips. Low sample sizes of the different foraging groups may raise questions about conclusions on general behavioural patterns at a population level. Even so, the foraging patterns observed during brooding indicate the presence of optional foraging niches close to shore at South Georgia, allowing foraging of potentially increased efficiency, at least in some years. This might also play a key role in potential responses of king penguins to environmental changes (Forcada & Trathan 2009), as optional foraging niches may allow them to better adjust foraging behaviour in response to the prevailing oceanographic conditions.

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