

Combined influence of meso-scale circulation and bathymetry on the foraging behaviour of a diving predator, the king penguin (*Aptenodytes patagonicus*)

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ABSTRACT

Investigating the responses of marine predators to environmental features is of key importance for understanding their foraging behaviour and reproductive success. In this study we examined the foraging behaviour of king penguins breeding at Kerguelen (southern Indian Ocean) in relation to oceanographic and bathymetric features within their foraging ambit. We used ARGOS and Global Positioning System tracking together with Time–Depth–Temperature-Recorders (TDR) to follow the at-sea movements of incubating and brooding king penguins. Combining the penguin behaviour with oceanographic data from the surface through satellite data and at depth through in-situ recordings by the TDRs enabled us to explore how these predators adjusted their horizontal and vertical foraging movements in response to their physical environment. Relating the observed behaviour and oceanographic patterns to local bathymetry lead to a comprehensive picture of the combined influence of bathymetry and meso-scale circulation on the foraging behaviour of king penguins.

During both breeding stages king penguins foraged in the area to the south-east of Kerguelen, where they explored an influx of cold waters of southern origin interacting with the Kerguelen Plateau bathymetry. Foraging in the Polar Front and at the thermocline was associated with high prey capture rates. However, foraging trip orientation and water mass utilization suggested that bathymetrically entrained cold-water features provided the most favourable foraging locations. Our study explicitly reports the exploration of bathymetry-related oceanographic features by foraging king penguins. It confirms the presence of Areas of Ecological Significance for marine predators on the Kerguelen Plateau, and suggests the importance of further areas related to the cold-water flow along the shelf break of the Kerguelen Plateau.

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1. Introduction

The foraging behaviour of marine predators is dependent upon the horizontal and vertical distribution of their prey (Hunt, 1990). Prey distribution is, in turn, influenced by the physical properties of the water column, including such factors as temperature and temperature gradient (Owen, 1981; Franks, 1992; Acha et al., 2004), factors which also help characterize different water masses

within the ocean. Thus, the horizontal and vertical patterns of water mass distribution govern prey distribution in terms of species composition and prey patch properties such as patch size and density (Collins et al., 2008, 2012; Saunders et al., 2013, 2014). At-sea studies on marine predators have shown that oceanographic structure as well as its stability plays a crucial role for predators, influencing their horizontal and vertical movements when seeking prey (Costa et al., 2010; Scheffer et al., 2010; Péron et al., 2012). Until now however most studies have been focused on the influence of hydrological features on the animals' behaviour (Bost et al., 2009). Few studies have investigated the combined influence of bathymetry and hydrology.

Bathymetry impacts oceanographic patterns through its steering effect on horizontal and vertical circulation (Moore et al., 1999; Gille et al., 2004; Roquet et al., 2009; Park et al., 2008b, 2014). Such interaction of oceanographic circulation with

Abbreviations: PFZ, Polar Frontal Zone; PF, Polar Front; AAZ, Antarctic Zone; SACC, Southern Antarctic Circumpolar Current Front; FTC, Fawn Trough Current; SML, Surface Mixed Layer; TH, Thermocline; WW, Winter Water; CDW, Circumpolar Deep Water; BMG, body mass gain.

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bathymetric features can lead to upwelling of nutrients and organic matter (Gill, 2002; Sokolov and Rintoul, 2007), resulting in enhanced productivity in these locations (Genin, 2004; White et al., 2007; Morato et al., 2009). Pronounced bathymetric features such as seamounts, canyons or shelf breaks have been reported to attract various marine predators for foraging (Worm et al., 2003; seabirds: Thompson, 2007; Morato et al., 2008; Ribic et al., 2008; Amorim et al., 2009; marine mammals: Gill, 2002; Friedlaender et al., 2006; Kaschner, 2007; turtles: Santos et al., 2007; pelagic fish: Litvinov, 2007). Studies on diving predators indicate that the animals direct their foraging effort at depth into specific water masses associated with such bathymetric steering and upwelling (Costa et al., 2008, 2010; Muelbert et al., 2013), potentially targeting profitable prey resources associated with these features.

The Kerguelen area supports one of the largest shelf systems in the Southern Ocean. Due to the high levels of productivity in the surrounding waters and given its relative isolation within the Southern Ocean, the Kerguelen Plateau hosts very high abundances of marine predators, including penguins, petrels and seals (Weimerskirch et al., 1989; Hindell et al., 2011). The Kerguelen Plateau is one of the major bathymetric obstructions to the eastward flow of the Antarctic Circumpolar Current (ACC), significantly steering and channelling most of the deep-reaching ACC flow (Park et al., 2008b, 2014; Sokolov and Rintoul, 2009a). The steering effects of the Plateau bathymetry may lead to increased spatial stability in oceanographic processes (Charrassin et al., 2004), creating oceanographic features of high predictability in close proximity to various seabird and seal breeding colonies (Cherel and Weimerskirch, 1995; Guinet et al., 2001; Bost et al., 2002). These characteristics highlight the importance of the Kerguelen Plateau as a site of great interest to study in detail the role of interactions between bathymetry and hydrology for top-predator behaviour.

The most prominent oceanographic features in the Kerguelen area are the Polar Front (PF) and the Fawn Trough Current (FTC), both of which are part of the ACC. The PF marks the boundary between cold waters of Antarctic origin and the warmer Polar Frontal Zone waters, and is traditionally defined as the northernmost extent of Winter Water (WW) of temperatures <2 °C (see Park et al., 2014 for an extensive review of PF definitions, particularly in the Kerguelen Plateau area). Based on these subsurface characteristics, the PF and other ACC fronts can be identified from Sea Surface Height (SSH) signatures at the ocean surface derived from qualitative changes in vertical oceanographic profiles, which are closely linked to the biological habitat zones associated with the fronts (Venables et al., 2012). The PF crosses the northern Kerguelen Plateau just south of Kerguelen (Park et al., 2014; see Fig. 1), wraps anticyclonically around the island from the south-east, and then continues south-eastwards along the east of the Kerguelen Plateau (Park et al., 2014). The FTC is a strong current along the southern edge of the northern Kerguelen Plateau, representing an important part of the ACC flow (Park et al., 2008b; Roquet et al., 2009). Most of the FTC is deflected south-eastwards by the Chun Spur, a pronounced bathymetric feature at the south-eastern end of the northern Kerguelen Plateau. However, a part of the shallower waters (corresponding to the cold Winter Water (WW) layer, ~100 m depth) is advected northwards across the Chun Spur (Park et al., 2008b, 2009; Roquet et al., 2010), forming a cold-water subsurface tongue along the eastern Plateau shelf break, extending up to the latitude of Kerguelen (Charrassin et al., 2004; Park et al., 2008b; van Wijk et al., 2010; see Fig. 1). The rugged bathymetry of the Kerguelen Plateau leads to upwelling of this cold WW flow along the eastern Kerguelen Plateau shelf break (Park et al., 2008b; van Wijk et al., 2010). Because of its unique characteristics of cold waters of Antarctic Zone origin, these waters from the FTC can be clearly distinguished from the warmer surrounding waters (Park et al., 2009; Roquet et al., 2010).

King penguins are important avian predators breeding at Kerguelen (Bost et al., 2013), comprising an estimated 342 000 breeding pairs, rapidly increasing (Chamaillé-Jammes et al., 2000; Bost et al., 2013, the last estimate dating of 1999). They rely mainly on myctophids (Myctophidae: lantern fish) (Cherel and Ridoux, 1992; Olsson and North, 1997; Bost et al., 2002), mesopelagic fish with the species preyed upon by king penguins generally associated with particular water masses or temperature ranges (Hulley, 1981; Kozlov et al., 1991; Saunders et al., 2014) as well as with fronts and eddies (Brandt et al., 1981; Pakhomov et al., 1996; Rodhouse et al., 1996). King penguins are known to explore their foraging habitat in a non-random way, targeting large- and mesoscale surface features such as fronts and eddies (Cotté et al., 2007; Trathan et al., 2008; Bost et al., 2009; Scheffer et al., 2010) as well as specific water masses and thermal features within the water column (Charrassin and Bost, 2001; Scheffer et al., 2012).

In the Kerguelen area, previous studies have shown that king penguins during the brood and crèche stages forage in areas close to the shelf break to the south-east of the island (Charrassin et al., 2002b; Pütz, 2002; Bost et al., 2011; Hindell et al., 2011), where they explore the subsurface tongue of cold water originating from the FTC (Charrassin et al., 2002b, 2004). However, we still have no detailed knowledge about how the penguins use such bathymetrically entrained oceanographic features for foraging, particularly during incubation where birds have the time to explore areas at greater distances from the colony.

In this study we investigated the foraging behaviour of king penguins breeding at Kerguelen in relation to oceanographic features within their foraging range, particularly regarding the importance of bathymetrically entrained features. Using Argos and GPS telemetry together with TDR tracking devices, we studied the penguins' detailed surface and diving behaviour during incubation and brooding. Combining the behavioural data with bathymetry, remote-sensing (Sea Surface Height) and in-situ (water temperature from the TDR sensors) data, we investigated how the birds' surface and diving behaviour related to oceanographic features in the horizontal and vertical dimension arising from the interaction between oceanographic circulation at meso-scales (10s–100s of kilometres) with bathymetry.

2. Material and methods

2.1. Study area, study period and device deployments

Our study took place at the Ratmanoff king penguin breeding colony on the east coast of Kerguelen Island (49.24°S, 70.55°E). The Ratmanoff colony is one of the largest breeding colonies at Kerguelen, comprising more than 70 000 of the estimated 342 000 breeding pairs at the island (Bost et al., 2013). Fieldwork was conducted during the austral summers of 1997/98 and 1998/99 and all those between 2005/06 and 2010/11, generally between January and March and on incubating and brooding birds. In total 84 adult king penguins were tagged, 31 during the incubation and 53 during the brood stage.

The horizontal movements of king penguins were tracked using two types of device: (1) Argos Platform Terminal Transmitters (PTT Kiwisat 90 g; and (2) Fastloc GPS loggers (Sirtrack, NZL; 127 g) configured to record positions at 60 s intervals and equipped with a saltwater switch to delay acquisition while birds were under water. This later type was used since the season 2009/2010.

Diving behaviour was recorded with time-depth recorders attached to the same penguins (Mk9 devices; Wildlife Computers, Redmond, USA) with fast-responding external temperature sensors, enabling us to investigate penguin diving behaviour in relation to their hydrological environment at depth. The TDR

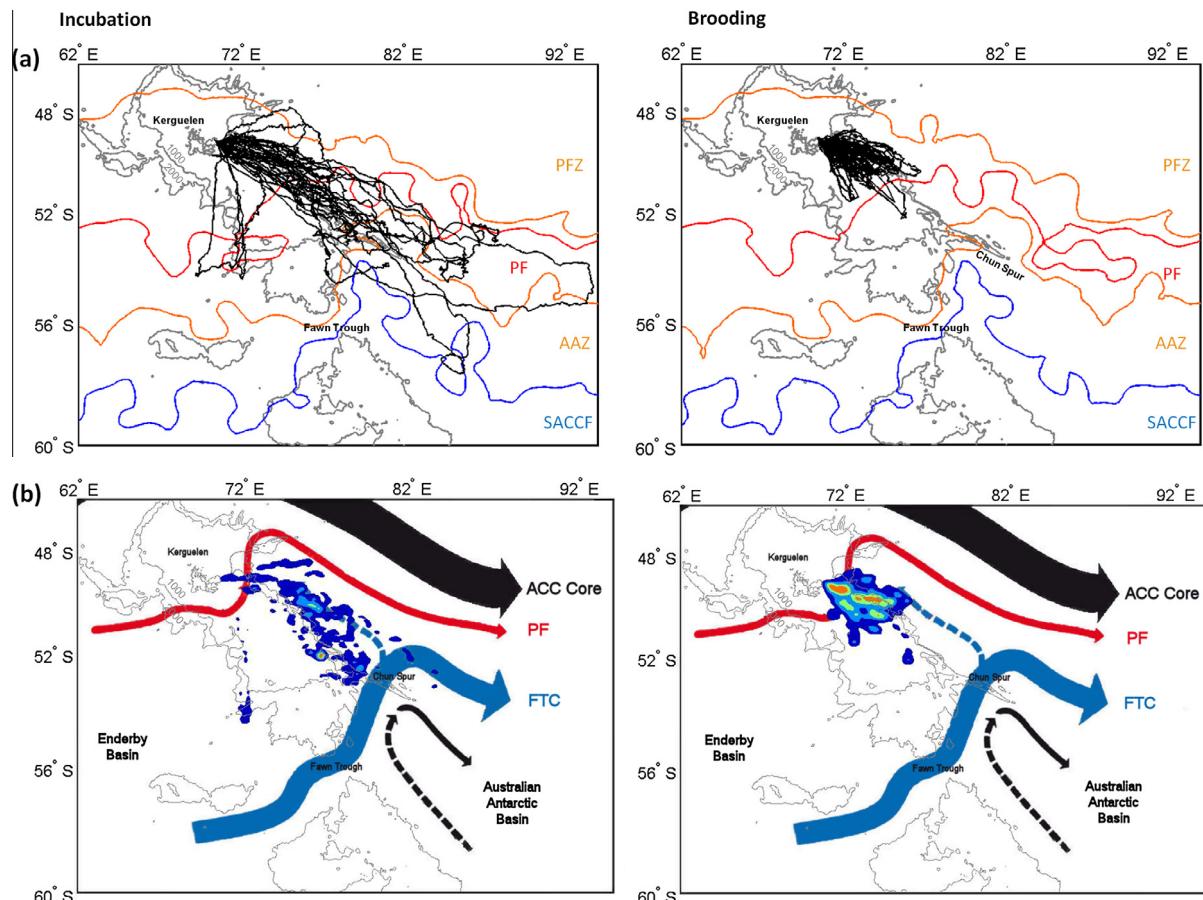


Fig. 1. Tracks and foraging zones of king penguins breeding at Kerguelen during incubation and brood. a – Most likely tracks estimated by the state space model from the raw tracking data. Grey contours show bathymetry at 0, 1000 and 2000 m depth. Coloured contours indicate frontal positions from SSH signatures, calculated as the mean positions over the trip period of all tracked birds. Abbreviations of frontal zones: PFZ – Polar Frontal Zone; PF – Polar Front; AAZ – Antarctic Zone; SACC – Southern ACC Front. The PF is shown as its mean summer signature contour (red) with its northern and southern limits (orange) following Venables et al. (2012). b – Kernel densities of king penguin foraging locations in relation to main oceanographic features and bathymetry of the Kerguelan Plateau. a – Incubation; b – Brooding. Contours encompass 5%, 25%, 50% and 75% of the foraging location distributions. Grey contours show bathymetry at 0, 1000 and 2000 m depth. Arrows show main oceanographic features in the foraging area following Park et al. (2008b). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Overview of study birds equipped with GPS, Argos and/or TDR devices with successful data retrieval.

Year	Incubation	Brooding
1998	–	15 Argos only
1999	4 Argos only	8 Argos only
2006	3 Argos + Mk9	6 Argos + Mk9 1 Argos only
2007	2 Argos + Mk9	5 Argos + Mk9
2008	2 Argos + Mk9 1 Argos only 1 Mk9 only	1 Argos + Mk9
2009	–	4 Argos + Mk9 9 Mk9 only
2010	9 Argos only 2 Mk9 only	–
2011	3 GPS + Mk9 4 Mk9 only	4 GPS only
Total birds equipped	31	53

devices were programmed to record depth and water temperature at 1 s intervals. They weighed 30 g in air and measured 15 × 100 × 15 mm (<0.5% of the cross sectional area of the body).

In total 38 birds were equipped with Argos and 7 with GPS devices only, and 26 with both Argos/GPS and TDR. A summary of the number of tracked birds and device types deployed in the different study years is given in Table 1.

Devices were attached using methods modified from (Wilson et al., 1997). All devices were recovered after a single foraging trip (varying between 5 and 51 days, some trip durations were unknown during 2010 as birds did not return, but deserted their breeding attempt in the unusual and extreme conditions encountered that year). Study birds were weighed before leaving for sea and after their return to land, to determine body mass gain (BMG) during the foraging trip.

2.2. Environmental data

2.2.1. Bathymetry, slope and Sea Surface Height (SSH) data

In our analyses, we used the Smith and Sandwell Global Seafloor Topography from Satellite Altimetry and Ship Depth Soundings (NOAA and Scripps Institution of Oceanography) (Smith and Sandwell, 1997) at a spatial resolution of 2' × 2'. More details are available at http://gcmd.nasa.gov/records/GCMD_SIO_NOAA_SEAFLOORTOPO.html. Bathymetric slope was calculated as the maximum slope value within a 5 × 5 moving window of grid cells across the bathymetry grid.

We also used absolute dynamic topography (ADT) delayed time (DT) data from Aviso (www.aviso.oceanobs.com). Data were available at a spatial resolution of 1/3° × 1/3° and at a weekly temporal resolution. ACC fronts and zones were defined based on SSH signatures following Venables et al. (2012), where frontal SSH

signatures were defined based on qualitative changes in vertical profile characteristics. These frontal signatures were defined based on the Scotia Sea, but are considered to be valid for other locations of the Southern Ocean (Venables et al., 2012).

2.2. Vertical temperature data and definition of different water masses

Vertical temperature values were obtained from the external TDR Mk9 sensor data attached to the foraging penguins. TDR Mk9 temperature sensors provide high accuracy data (accuracy $0.1\text{ }^{\circ}\text{C} \pm 0.05\text{ }^{\circ}\text{C}$, Simmons et al., 2009), and were therefore used for determining the properties of the water column encountered during penguin dives. For each dive, temperature data that were recorded during the descent and ascent phases were projected onto a vertical axis corresponding to the maximum depth of the dive and averaged at 1 m depth intervals. This resulted in regularly gridded temperature data in the vertical plane, and facilitated calculation of the average potential differences in the water column properties encountered during the descent and ascent phases of the dive. A 5 m moving average filter was then applied to the temperature profiles, allowing for correction of any potential measurement errors from the TDR temperature sensors without smoothing out thermal discontinuities in the water column. 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. Based on the regularly gridded temperature profiles we calculated the vertical water temperature gradient for each depth point; this was estimated as the temperature difference between 25 m above and 25 m below the given depth point. As the penguin behaviour is likely to be impacted by prey distribution and not directly by the water column properties we chose a relatively large depth window to take into account potential effects of changes in water column properties on prey distribution in adjacent layers above and below a certain depth. For example, prey might aggregate not only directly at the point of a strong thermal gradient, but also in layers just above and below the thermocline. We therefore chose this relatively large depth window of 25 m above and below a given point to include the potential importance of changes in water column properties on the surrounding points. 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 $>$ maximum depth – 25 m). The resulting possible bias in gradient values may only impact the depth range between the maximum depth range of a dive and 25 m above, as dives shallower than 50 m were not considered for analyses of foraging behaviour (see Section 2.3.3). A temperature gradient of +1 thus corresponds to a temperature increase of $1\text{ }^{\circ}\text{C}$ per 50 m depth, -1 to a temperature decrease of $1\text{ }^{\circ}\text{C}$ per 50 m.

To identify water masses from the water characteristics encountered by the penguins in the water column we defined five water masses Surface Mixed Layer (SML), Thermocline (TH), Winter Water (WW), cold WW (WWc) and Circumpolar Deep Water (CDW) based on water temperature (T), temperature gradient ($\text{grad}T$) and depth (D) recorded by the TDR devices. Firstly the temperature gradient was used to identify water masses characterized by distinct thermal gradient properties, with the TH defined as waters of $\text{grad}T$ stronger than $-0.5\text{ }^{\circ}\text{C}/50\text{ m}$ (based on visual inspection of TDR depth-temperature profiles), and the upper layer of CDW (modified CDW) as waters of positive $\text{grad}T$ arising from the meeting of cold WW with the warmer CDW (Gordon et al., 2000). Water masses of weaker $\text{grad}T$ were then distinguished based on water temperature. SML and WW were defined as waters of neutral or weak negative $\text{grad}T$ ($\text{grad}T > -0.5\text{ }^{\circ}\text{C}/50\text{ m}$) above

and below the TH, respectively, with temperature ranges of $>2\text{ }^{\circ}\text{C}$ (SML), $0.5\text{--}2\text{ }^{\circ}\text{C}$ (WW) and $<0.5\text{ }^{\circ}\text{C}$ (WWc) based on water temperatures reported for the area explored by our study penguins (Park et al., 2008b, oceanographic sections B and C). Finally, a depth threshold of 100 m (based on visual inspection of depth-temperature profiles) was applied as an additional criterion to clearly distinguish CDW from the potential occurrence of positive $\text{grad}T$ in the SML due to surface heating and turbulence. In summary the different water masses were defined as follows: SML: $\text{grad}T > -0.5$; $T \geq 2$; $D \leq 100\text{ m}$; TH: $\text{grad}T \leq -0.5$; WW: $-0.5 < \text{grad}T \leq 0$; $0.5 < T < 2$; WWc: $-0.5 < \text{grad}T \leq 0$; $T \leq 0.5$; CDW: $\text{grad}T > 0$; $D > 100\text{ m}$.

Based on these definitions a specific water mass was assigned to each depth grid point of each dive. The resulting dataset thus consisted of temperature, temperature gradient and water mass profiles on a regular 1 m depth grid for each dive.

2.3. Data analysis

Data analyses were performed using Matlab (The MathWorks, Inc., MA 01760-2098, USA), and R (R Development Core Team, 2012) for the state space models. Dive parameters from the TDR data were calculated with the custom-made software MultiTrace (Jensen software systems, Laboe, Germany). Analysis of penguin foraging behaviour in relation to horizontal and vertical oceanography was carried out on the dataset for which simultaneous Argos/GPS and TDR recordings were available (see Table 2 for details).

2.3.1. Deriving spatial patterns of the water column structure in the foraging area from the TDR temperature sensor data

From the in-situ TDR temperature data we assessed the fine-scale structure of the horizontal and vertical habitat in the foraging area explored by king penguins. From the vertical water mass profiles of all available TDR recordings we determined the shallowest depth of WW occurrence in the water column (WW upper limit), and projected this onto a latitude-longitude grid based on the dive locations (see Section 2.3.3 for the calculation of dive coordinates). Horizontal interpolation of WW upper limits between the dive locations was carried out using linear interpolation. The resulting maps allowed visualization of spatial changes in the structure of the water column in the areas explored by king penguins as well as relationships between oceanographic structure at depth with bathymetry and surface oceanographic features determined from SSH.

2.3.2. Analysis of surface behaviour

GPS data were downloaded from each device and decoded into GPS locations using manufacturer-supplied software (Sirtrack Fastloc software, version 1.5.0.2). Following the manufacturer's instructions, we excluded locations from the analysis when residual error values were greater than 30 or fewer than 6 satellites were used for location calculation (Sirtrack, 2010). Argos data were processed with state-space models (Jonsen et al., 2003, 2005) in order to estimate the most probable locations taking into account measurement errors. The process model of the state space model uses transition equations based on correlated random walk models to estimate the most probable locations of an animals' path, while the observation model discriminates between different behavioural states for each estimated location. As the observation model of the state-space model did not lead to a clear distinction of behavioural modes into travel and foraging with our data, we used First-Passage Time analysis in order to detect area-restricted search behaviour from the GPS and the estimated Argos locations. First Passage Time provides a measure of the time an animal takes to cross a virtual circle of a radius r that is moved along

Table 2

Trip parameters and body mass gain for king penguins during incubation and brood. Additional *n*-values in () are given where the number of sampled birds was different from the number of GPS/Argos-tracked birds (e.g. if penguins only equipped with TDR were included in the calculation of trip duration and body mass gain). Values represent mean ± standard error.

Year	Month	<i>n</i>	Trip duration (days)	Trip length (km)	Max. dist. from colony (km)	Body mass gain (kg)	Body mass gain/day
<i>Incubation</i>							
1998		0					
1999	Jan	4	18.95 ± 1.48	1242.5 ± 118.03	481.13 ± 47.73	3.1 (<i>n</i> = 1)	0.17 (<i>n</i> = 1)
2006	Jan	3	21.19 ± 1.89	1433.17 ± 26.73	459.64 ± 47.98	No data	No data
2007	Feb	2	18.99 ± 2.74	1645.66 ± 163.82	634.85 ± 78.07	2.25 ± 1.35	0.11 ± 0.06
2008	Feb	3	31.39 ± 1.01	2311.76 ± 141.27	813.68 ± 106.69	2.8 ± 0.26	0.09 ± 0.01
2009		0					
2010	Feb	9	39.02 ± 2.56 (<i>n</i> = 11)	3021.17 ± 389.64	991.98 ± 152.67	3.96 ± 0.21	0.11 ± 0.01
2011	Feb	3	23.86 ± 1.28 (<i>n</i> = 7)	1476.4 ± 161.67	515.48 ± 24.41	4.24 ± 0.28 (<i>n</i> = 7)	0.18 ± 0.01 (<i>n</i> = 7)
Mean ± SE		24	27.69 ± 2.01	2091.08 ± 2.08	717.24 ± 72.60	3.16 ± 0.21	0.12 ± 0.01
<i>Brooding</i>							
1998	Feb	15	8.58 ± 0.52 (<i>n</i> = 25)	710.12 ± 68.72	244.55 ± 24.74	1.86 ± 0.17 (<i>n</i> = 25)	0.23 ± 0.03 (<i>n</i> = 25)
1999	Feb	8	8.90 ± 1.6	738.69 ± 81.5	280.82 ± 33.14	2.03 ± 0.35 (<i>n</i> = 4)	0.3 ± 0.09 (<i>n</i> = 4)
2006	Feb	7	8.57 ± 0.87	682.98 ± 81.08	244.24 ± 31.60	2.3 ± 0.22	0.3 ± 0.04
2007	Feb	5	9.59 ± 0.54	967.26 ± 77.53	299.56 ± 14.25	2.65 ± 0.26	0.28 ± 0.04
2008	Feb	1	11.2	901.41	308.82	2.3	0.21
2009	Feb	4	11.36 ± 1.33 (<i>n</i> = 11)	717.23 ± 113.55	289.96 ± 45.28	2.62 ± 0.12 (<i>n</i> = 11)	0.25 ± 0.03 (<i>n</i> = 11)
2010		0					
2011	Feb	4	9.23 ± 0.72	674.27 ± 39.48	249.37 ± 19.49	1.73 ± 0.27	0.19 ± 0.04
Mean ± SE		44	9.34 ± 0.51	741.95 ± 34.66	263.38 ± 12.33	2.07 ± 0.12	0.24 ± 0.02

its track, assuming that high First Passage Time corresponds to area-restricted search behaviour (Fauchald and Tveraa, 2003). For each location we assigned SSH, bathymetry and bathymetry slope values by searching for the geographically nearest value within the corresponding environmental dataset.

Kernel densities of foraging locations of incubating and brooding penguins were computed on latitude and longitude using a Gaussian Kernel (Matlab kde2d function, Botev et al., 2010). Locations at distances <30 km from the colony were excluded from the kernel density estimation to reduce the colony bias on the spatial distribution of the penguins. The kernel densities of tracks with combined GPS/Argos and TDR data available were then overlaid on the main oceanographic and bathymetric features to assess potential associations of foraging with oceanography and bathymetry in areas where analysis of penguin foraging behaviour in relation to horizontal and vertical oceanography was carried out.

For each bird, we calculated trip duration, distance covered, maximum distance from the colony and the furthest latitude south and east reached. Exact departure and return times from and to the island were determined from the TDR data for birds with Argos/GPS and TDR devices, and from field observations and visual inspection of surface tracks arriving at the colony for Argos/GPS data only.

2.3.3. Analysis of diving behaviour

A zero offset correction was applied on the dive data to correct for surface drift in the TDR pressure sensors. Only dives deeper than 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., 2002a).

2.3.3.1. Calculation of dive parameters. Diving behaviour was analysed by calculating the following dive parameters: dive duration, post-dive interval duration, duration and start depth of the bottom phase (the time between the first and last wiggle or dive step deeper than 75% of the maximum dive depth, following Halsey et al., 2007) and the number of wiggles per dive. Wiggles were defined as deviations of >1 m depth with an absolute vertical instant >0, and are considered to represent a proxy of feeding success during the penguins' dives (Bost et al., 2007). Furthermore, we determined

the broadness index calculated as bottom duration: dive duration following Halsey et al. (2007), indicating the proportion a dive spent in the bottom (foraging) phase. From the TDR temperature sensor data, we determined the temperature at the start of each bottom phase, indicating the temperature where prey pursuit started.

2.3.3.2. Interpolation of oceanographic and bathymetric parameters for each dive. Exact sunrise and sunset times were calculated as described in Scheffer et al. (2010) based on nautical definitions of sunrise and sunset (twilight hours defined as the sun being geometrically 12° below the horizon) (US Naval Observatory Astronomical Applications Department). Geographical coordinates of the start of each dive were interpolated based on time from the GPS and the estimated Argos location data, assuming straight line travel and constant speed between 2 location points (Weavers, 1991). For each dive location we assigned SSH, bathymetry and slope values by searching for the geographically nearest value within the corresponding environmental datasets. Dive locations were then assigned to ACC frontal classes (PFZ, PF, AAZ, SACC) defined in Venables et al. (2012) based on the SSH value previously assigned to each dive location. Dive locations were further assigned to bathymetry classes defined by depth and slope. Bathymetry classes were defined as shelf (depth ≤ 1000 m), shelf break (depth > 1000 m, slope ≥ 0.2) and offshore (depth > 1000 m, slope < 0.2) following visual inspection of a 3-dimensional map of the Northern Kerguelen Plateau bathymetry in Park et al. (2008b). Setting the shelf depth limit to 1000 m ensured that deep troughs on the Plateau were assigned to the shelf class.

2.3.3.3. Detailed analysis of foraging phases at depth in relation to water column properties, frontal zones and bathymetry. Detailed use of the water column by the penguins while foraging was analysed by considering the bottom phase of the dives, which is thought to be the most important phase for prey capture (Charrassin et al., 2002a; Simeone and Wilson, 2003; Ropert-Coudert et al., 2006; Bost et al., 2007). Based on the vertical grid of water masses properties compiled for each dive (see Section 2.2.2), we determined the accumulated bottom time spent in different water masses for each dive, calculated as the summed bottom times spent at each

1 m depth interval during the dive. We evaluated the penguins' exploration of different water masses during bottom periods using the following analyses and plots:

1. Maps of the ambient water temperature at the start of the dive bottom periods overlaid on bathymetry and frontal zones allowed visualization of spatial patterns in water properties explored during prey pursuit in relation to bathymetry and surface oceanographic features. Comparison with maps of the start depths of dive bottom periods allowed examining if the penguins adjusted their dive depths to the oceanographic context (for example if locations of colder bottom start temperatures coincided with deeper dive bottom periods). The start temperatures and start depths of dive bottom periods were projected onto a latitude-longitude grid based on the dive locations. Horizontal interpolation of dive parameters between the dive locations was carried out using linear interpolation.
2. Changes in water mass exploration during bottom periods in relation to ACC fronts and bathymetry were analysed considering SSH, depth and slope for incubating and brooding birds. Kernel densities of accumulated dive bottom times in relation to SSH and depth were computed for the different water masses, illustrating how the exploration of water masses changed with SSH and bathymetry for incubating and brooding king penguins.
3. The foraging performance of king penguins in the different frontal and bathymetry zones as well as in the different water masses was assessed based on the number of wiggles in relation to dive cycle time (dive duration + post-dive interval) in locations where foraging was identified from surface movements, indicating the efficiency of a foraging dive in terms of prey pursuit events per unit of dive time.

2.3.4. Statistics

Comparisons of dive parameters among breeding stages, frontal and bathymetry zones as well as among the different water masses explored were carried out using Kruskal-Wallis tests 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. Linear regression was used to analyse the relation of body mass gain with foraging trip duration. Pearson's correlation coefficients were computed to determine if significant correlation existed between start depths and start temperatures of dive bottom periods as tests for data normality failed.

3. Results

3.1. Foraging trip orientation in relation to bathymetry and oceanography

All foraging trips made by king penguins were oriented to the south or south-east of Kerguelen, with birds of different breeding stages showing different foraging trip characteristics (Table 2) and targeting areas of differing bathymetric and oceanographic properties (Figs. 1 and 2). Incubating birds undertook extended foraging trips to the south and east along the shelf break of the Northern Kerguelen Plateau and into offshore areas, reaching PFZ, PF, AAZ and rarely SACCW waters (Figs. 1a and 2a; Table 2). Brooding birds undertook shorter foraging trips on the Kerguelen Plateau shelf or towards the shelf break, exploring exclusively PF waters (Figs. 1a and 2a; Table 2).

Foraging locations identified from surface movements in the combined Argos/GPS and TDR dataset coincided with areas influenced by the cold-water subsurface current along the south-eastern shelf break of the Northern Kerguelen Plateau, and with the area in proximity of the northern Chun Spur for birds during incubation (Fig. 1b). Foraging areas for brooding birds were mostly located over the Northern Kerguelen Plateau shelf and shelf break to the south-east of the island, with the outermost foraging locations reaching areas impacted by the cold-water subsurface current (Fig. 1b).

3.2. Body mass gain (BMG)

Incubating birds had higher levels of total body mass gain (BMG), whereas brooding birds showed higher mass gains per day (Table 2). Daily BMG decreased with foraging trip duration for both incubating and brooding birds (Incubation: $R^2 = 0.31$, Brooding: $R^2 = 0.3$) (Fig. 3). Brooding birds showed higher BMG for short foraging trips, but with a steep decrease with increasing trip duration.

3.3. Frontal positions and water column structure in the foraging area

The PF identified from its mean SSH summer signature crossed the Northern Kerguelen Plateau in south-west to north-east direction to the south of Kerguelen, and then continued in south-eastward direction to the east of the Kerguelen Plateau (Figs. 1a, 4, 6 and 7). The SSH signature for the AAZ and SACCW followed the south-eastern edge of the Kerguelen Plateau along the 2000 m depth contour of the Fawn Trough canyon. After the Fawn Trough canyon, the AAZ and SACCW showed northward extensions, with the AAZ reaching over the Chun Spur to the eastern side of the Kerguelen Plateau. The upper limit of the WW reached its shallowest depths of around 50 m in proximity of the south-eastern shelf break to the north and northwest of the Chun Spur and in the influx area of AAZ waters (Fig. 4a). Cold WW in the water column explored by penguins was restricted to areas to the north-west of the Chun Spur (Fig. 4b).

3.4. Diving behaviour and water column exploration

3.4.1. Diving behaviour during incubation and brood

The depth at which the bottom phase of the dives started increased significantly from incubation to brood (131.2 ± 2.8 m and 148.4 ± 6.8 m, respectively; Fig. 5a), whereas there was no significant change in broadness index (indicating the proportion of bottom time during a dive) between the two breeding stages (0.28 ± 0.02 and 0.28 ± 0.03 , respectively; Fig. 5b) (Kruskal-Wallis-Test, $p = 0.01$).

3.4.2. Exploration of the water column during dive bottom periods in relation to bathymetry and frontal zones

Incubating and brooding birds explored the SML, TH, WW, cold WW and CDW during the bottom periods of their dives (Fig. 2b). Water mass exploration during the dive bottom periods changed with SSH and bathymetry (Figs. 2b, 6 and 8a). The dive bottom start temperature decreased towards the south-east, with coldest temperatures occurring along the south-east shelf break of the Kerguelen Plateau and to the north of the Chun Spur for incubating birds (Fig. 6a), and just offshore the Kerguelen Plateau shelf break for brooding birds (Fig. 6b). Start depths of dive bottom periods were deeper in areas of coldest bottom start temperatures (Pearson's R : -0.48 for incubation, -0.62 for brood, $p = 0$, where 1 is total positive correlation, 0 is no correlation, and -1 is total negative correlation) (Fig. 7). The exploration of different water masses at depth in relation to SSH and bathymetry showed similar

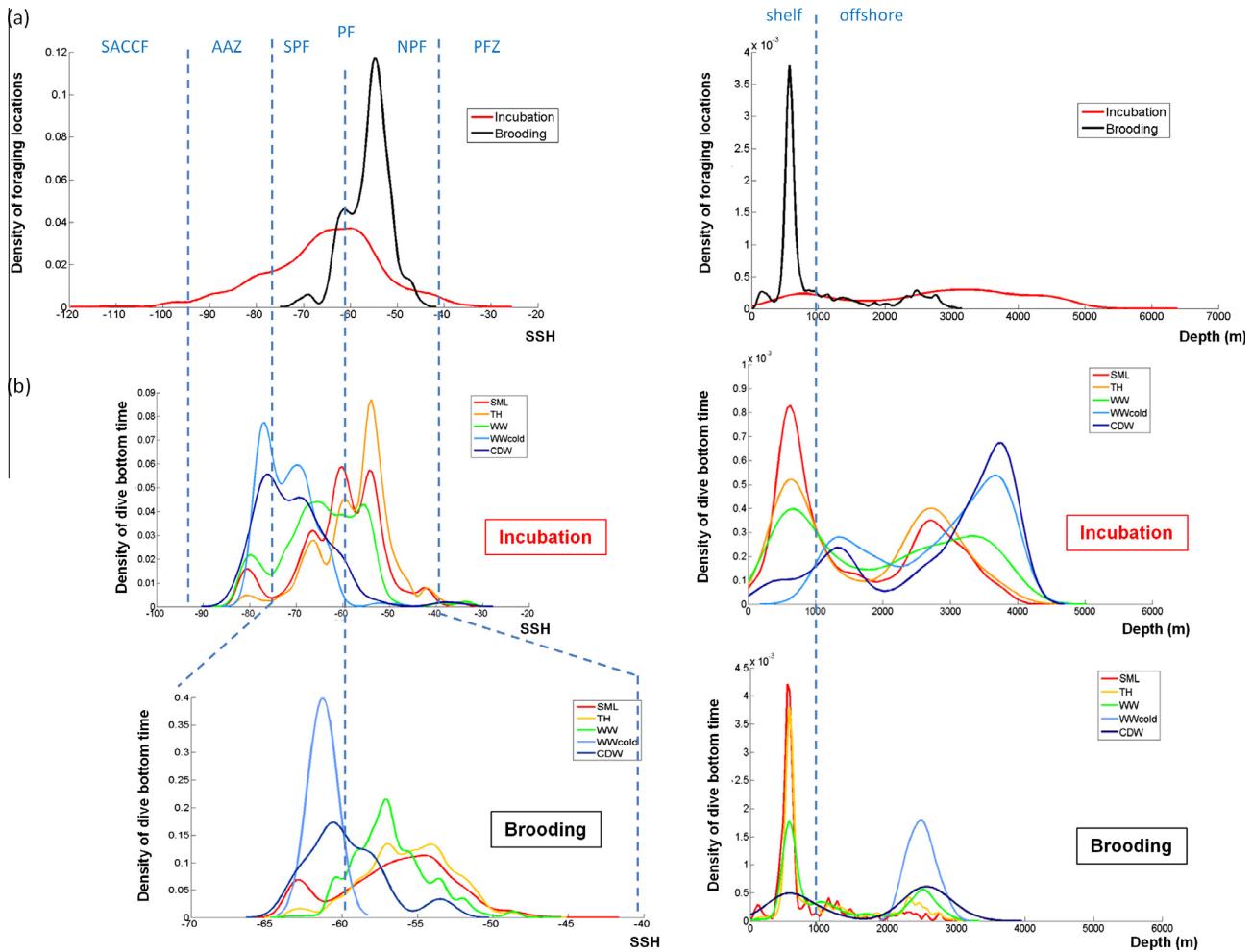


Fig. 2. Density distributions of king penguin foraging locations and water masses exploration in relation to frontal zones and bathymetry. a – Density distributions of foraging locations of incubating (red) and brooding (black) birds in relation to SSH (indicating frontal zones) and depth. b – Density distributions of accumulated dive bottom times of incubating and brooding penguins spent in different water masses in relation to SSH and depth. Abbreviations of frontal zones: PFZ – Polar Frontal Zone; PF – Polar Front; NPF – northern PF area; SPF – southern PF area (NPF and SPF define the areas between the mean PF position and its northern and southern limit, respectively); AAZ – Antarctic Zone; SACCF – Southern ACC Front. Frontal definitions are based on SSH signatures from Venables et al. (2012). Abbreviations of water masses: SML – Surface Mixed Layer; TH – Thermocline; WW – Winter Water; WWc – cold Winter Water <0.5°C; CDW – Circumpolar Deep Water. For details on the water masses definitions see Section 2.2.2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

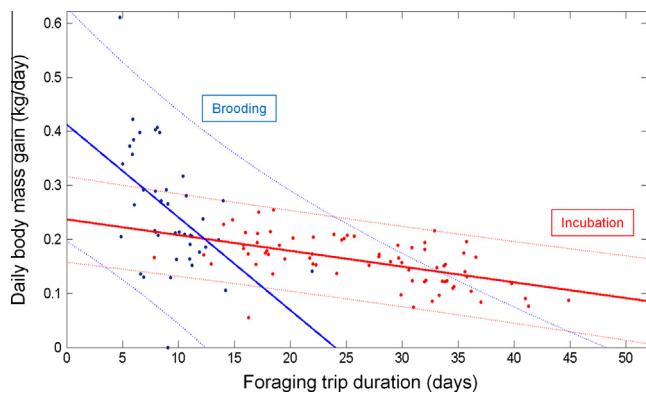


Fig. 3. Daily body mass gain (BMG) of incubating (red) and brooding (blue) king penguins in relation to foraging trip duration. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

patterns for incubating and brooding birds (Fig. 2b). SML and TH exploration mostly occurred in the northern PF area (waters between the mean summer PF signature and its northern limit)

as well as on the Kerguelen Plateau shelf, and declined towards more southern signatures. WW exploration peaked in intermediate SSH signatures, while cold WW and CDW exploration clearly increased towards the southernmost SSH signatures (AAZ for incubation, southern PF area for brooding) and in areas off the Kerguelen Plateau shelf. When looking at the importance of the different water masses in frontal (PFZ, PF, AAZ) and bathymetry (shelf, shelf break, offshore) zones, differences in water mass exploration were most apparent with SSH for incubating birds, and with bathymetry for brooding birds (Fig. 8a). In general, the exploration of the SML during dive bottom periods decreased and the WW and CDW exploration increased from the PFZ to the AAZ for incubating birds, and from shelf to offshore areas for brooding birds.

3.4.3. Dive efficiency in relation to bathymetry and frontal zones

Dive efficiency in terms of wiggle numbers per dive cycle time changed with frontal and bathymetry zones for incubating and brooding birds (Fig. 8b). Relative wiggle numbers were highest in the PFZ/PF and on the shelf, and lowest in the AAZ and in offshore areas for incubating and brooding birds, respectively (incubation in SSH classes: PFZ 2.11 ± 0.05 ; PF 1.95 ± 0.01 ; AAZ 1.67 ± 0.02 ; brood-

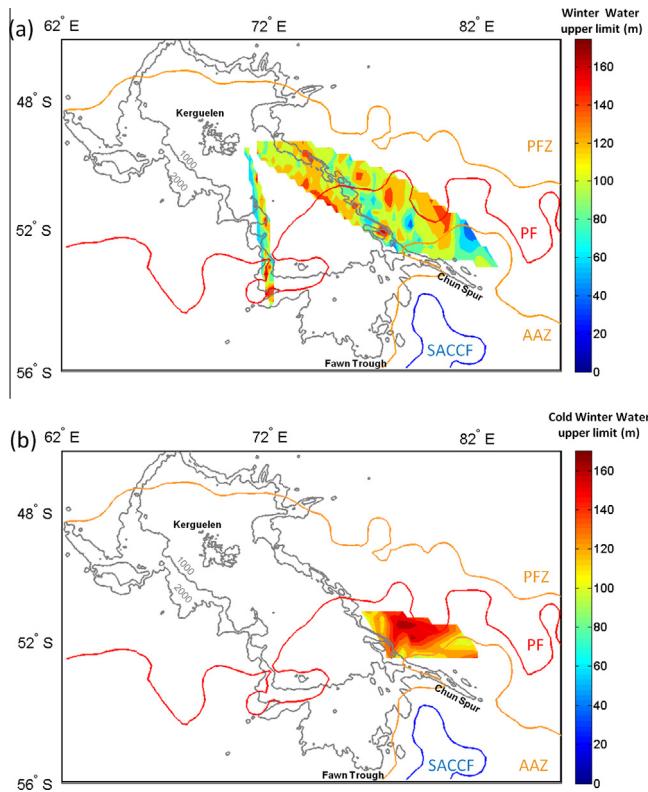


Fig. 4. Maps of water column structure and frontal zones in the foraging area of king penguins. Colouring shows Winter Water (WW) upper limit in the water column from TDR temperature sensor data: a – WW (0.5–2 °C), and b – Cold WW (<0.5 °C). Grey contours show bathymetry at 0, 1000 and 2000 m depth. Coloured contours indicate frontal positions from SSH signatures, calculated as the mean positions over the trip period of all tracked birds with TDR devices. Abbreviations of frontal zones: PFZ – Polar Frontal Zone; PF – Polar Front (shown as its mean summer signature contour in red, with its northern and southern limits in orange); AAZ – Antarctic Zone; SACC – Southern ACC Front. The PF is shown as its mean summer signature contour (red) with its northern and southern limits (orange) following Venables et al. (2012). NPF and SPF define the areas to the north and south of the mean PF position, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

in bathymetry classes: shelf 1.84 ± 0.02 ; shelf break 1.43 ± 0.04 ; offshore 1.46 ± 0.04 ; Kruskal–Wallis-Test, $p = 0.01$.

3.4.4. Dive efficiency in different water masses

The number of wiggles per dive cycle time showed differences depending upon which water masses were targeted during the dive bottom periods (Fig. 9). For incubating birds, relative wiggle numbers were highest during exploration of the TH, and showed significantly reduced values for all others water masses (SML 2.05 ± 0.03 ; TH 2.28 ± 0.02 ; WW 1.63 ± 0.01 ; WWcold 1.45 ± 0.04 ; CDW 1.21 ± 0.04 ; Kruskal–Wallis-Test, $p = 0.01$). Brooding birds showed highest relative wiggle numbers in the SML, and lowest in WW (SML 1.96 ± 0.04 ; TH 1.87 ± 0.03 ; WW 1.63 ± 0.01 ; WWcold: no dive bottom periods; CDW 1.51 ± 0.01 ; Kruskal–Wallis-Test, $p = 0.01$).

4. Discussion

Our study investigated the detailed foraging behaviour of a key diving predator in relation to its oceanographic environment, with particular focus on the importance of bathymetrically entrained oceanographic features. Our results provide a comprehensive picture of how the animals use their marine habitat at the ocean

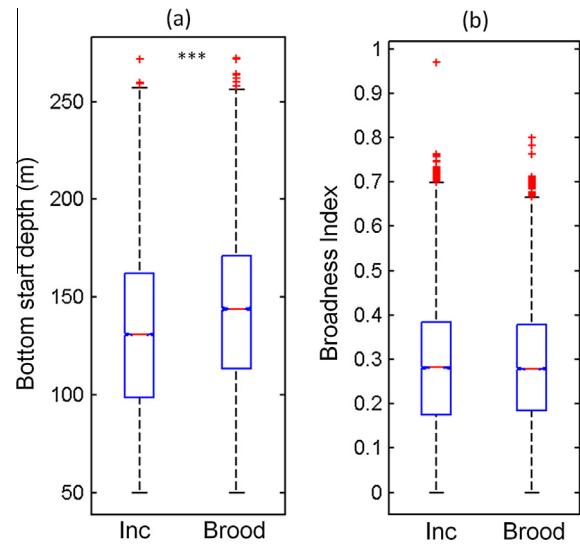


Fig. 5. Changes in king penguin diving behaviour from incubation to brood. a – bottom start depth; b – broadness index. *** indicates significant differences to the other water masses with $p = 0.01$ (Kruskal–Wallis Test).

surface and at depth, and identifies key oceanographic features for king penguins and potentially other marine predators breeding at the Kerguelen Plateau.

4.1. Oceanographic patterns in the area to the south-east of Kerguelen

4.1.1. Frontal positions

The spatial patterns of the oceanography and frontal positions found in our study area were consistent with general circulation patterns in the Kerguelen area described by a number of previous studies (Orsi et al., 1995; Moore et al., 1999; Park et al., 2008b, 2009, 2014; Park and Vivier, 2011; Sokolov and Rintoul, 2009a; Roquet et al., 2009; van Wijk et al., 2010). The PF crossing the Northern Kerguelen Plateau in south-west to north-east direction to the south of Kerguelen was consistent with positions reported in Park et al. (2008b, 2014). The slight mismatch in our PF position to the east of Kerguelen compared to the position showed in Park et al. (2008b) may be related to the fact that definitions and property values for a given front may not be consistent all along its circumpolar path (Belkin and Gordon, 1996). This means that applying a static criterion validated in one location may lead to different results in other locations (Orsi et al., 1995). The identification of frontal signatures associated with the FTC were in agreement with those reported by Park et al. (2009) and Park and Vivier (2011), where waters assigned to the AAZ and SACC in our study were identified as the SACC.

4.1.2. Spatial patterns in water mass distribution used by foraging king penguins

Spatial patterns in water mass distribution were consistent with the circulation patterns reported in previous studies. Shallowest WW depths (of around 50 m) mapped by king penguins in our study corresponded to the cold-water flow to the north of the Chun Spur area and along the south-eastern Kerguelen Plateau shelf break (Charrassin et al., 2002b, 2004; Park et al., 2008b, 2009; Roquet et al., 2010; van Wijk et al., 2010). Mapping the temperatures and depths at the start of prey pursuit phases during the penguins' dives showed the tracking of the cold-water flow by foraging king penguins during both incubation and brood. Cold WW exploration by king penguins was limited to the area of the AAZ northward loop over the Chun Spur, where the influx of the coldest

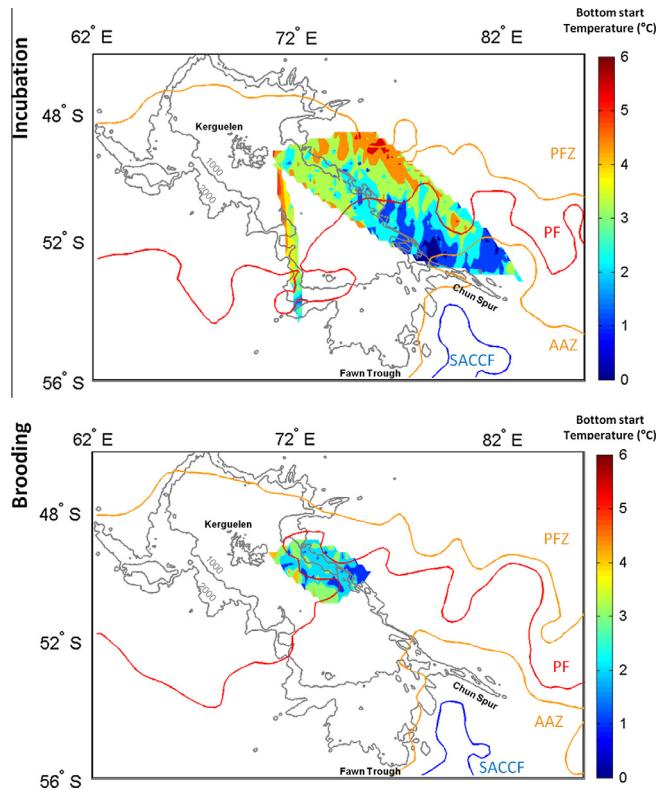


Fig. 6. Maps of water temperatures at the start of the dive bottom period of a – incubating and b – brooding birds. Grey contours show bathymetry at 0, 1000 and 2000 m depth. Coloured contours indicate frontal positions from SSH signatures, calculated as the mean positions over the trip period of tracked birds with TDR devices. Abbreviations of frontal zones: PFZ – Polar Frontal Zone; PF – Polar Front (shown as its mean summer signature contour in red, with its northern and southern limits in orange); AAZ – Antarctic Zone; SACC – Southern ACC Front. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

waters of southern origins across the northern Chun Spur (Park et al., 2008b, 2009; Roquet et al., 2010) may lead to the occurrence of cold WW at depths available to king penguins.

4.2. Foraging behaviour in relation to oceanography and bathymetry

The consistent south-east orientation of foraging trips towards the cold-water sub-surface current originating from the FTC highlights the importance of this feature for foraging king penguins during incubation and brooding. Myctophids may become more available by latitude and depth through the northward advection and upwelling of FTC waters along the Kerguelen Plateau, and may aggregate at thermal gradients in the water column (Hulley, 1981; Kozlov et al., 1991; Pakhomov et al., 1996). Our study underlines the local importance of the FTC subsurface current and its interaction with bathymetry for king penguins at Kerguelen during incubation and brooding (Charrassin et al., 2002b, 2004).

4.2.1. Exploration of the cold-water subsurface current from the FTC

4.2.1.1. Foraging zones of incubating birds. During their extensive trips, incubating birds mainly foraged along the south-eastern side of the Kerguelen Plateau as well as in the north-western vicinity of the Chun Spur area. Exploration of the cold-water tongue from its origin at the Chun Spur until the latitude of Kerguelen during dive bottom periods and deeper dives associated with the exploration of the cold water masses suggests that strong foraging

relationships exist with this feature. Foraging over the area between the northern Chun Spur and the Heard-McDonalds Island Trough was associated with the exploration of cold water masses. These locations have been shown to be important pathways of southern waters flowing onto the Kerguelen Plateau and into the area to the east of Kerguelen as the cold-water subsurface tongue (Park et al., 2008b). Rugged bathymetry and seamounts may enhance upwelling of these cold waters, as indicated by shallow WW depths encountered by king penguins just downstream of the FTC flow crossing the Chun Spur. Myctophids associated with the cold waters of Antarctic origin may thus become accessible to king penguins in such locations of potential upwelling, while spatial stability of these bathymetrically entrained structures may provide for predictable and reliable foraging locations. Coldest water temperatures, highest WW proportions and the encounter of cold WW and CDW of Antarctic origin during bottom periods of the dives coincide with these areas of cold-water influx from the FTC over the Chun Spur in the AAZ, suggesting that birds may direct their foraging into features related to such flows. Deeper dive bottom periods associated with the exploration of cold waters at depth suggest adaptation of diving behaviour by the penguins to reach these waters associated with the cold-water influx from the FTC. Similar exploration of the cold-water influx over the shallow and rugged bathymetry in areas near the Chun Spur may occur in king penguins breeding at Heard Island as well as in macaroni penguins breeding at Kerguelen and Heard Island from the apparent coincidence of their foraging locations with areas of the FTC cold-water flow potentially interacting with the Kerguelen Plateau (Hindell et al., 2011; Thiebot et al., 2014).

4.2.1.2. Foraging zones of brooding birds. The foraging areas used by brooding birds were mainly located over the Kerguelen Plateau between the island and the shelf break, corresponding to the trips made by brooding king penguins reported in previous studies (Koudil et al., 2000; Bost et al., 2002, 2011; Charrassin et al., 2002b, 2004; Hindell et al., 2011). In this area, the subsurface cold-water current appears to be steered onto the shelf towards the island of Kerguelen (Charrassin et al., 2002b, 2004), potentially by upwelling at the abrupt escarpment (between the 1000 to 3000 m isobaths) oriented in the north-south direction just to the east of Kerguelen (Charrassin et al., 2004). Such cold-water flow onto the Plateau may generate strong thermal gradients at relatively shallow depths, where myctophids may aggregate. High proportions of SML and TH exploration during dive bottom periods indicate the target of prey resources associated with such vertical thermal gradients and the adjacent SML layer in shelf areas. In shelf break and offshore waters, low water temperatures and high proportions of WW encountered while increasing the depth of dive bottom periods indicate the exploration of prey resources associated with the cold-water subsurface current.

4.2.2. Foraging adjustments to breeding constraints

During the brooding stage, king penguins foraged in areas closer to the colony at greater depths. In other breeding locations, similar patterns of changes in surface and diving behaviour have been reported for king penguins during the brood stage. At Crozet, both incubating and brooding birds target similar foraging areas, but considerably increase their travel and dive effort in terms of surface speed and dive depth during brooding (Charrassin and Bost, 2001; Charrassin et al., 2002a). At South Georgia, brooding king penguins undertake shorter foraging trips to closer foraging areas than during incubation, indicating less travel effort (Scheffer et al., 2012). However, when compared to brooding penguins at Kerguelen, birds at South Georgia often dive to significantly greater depths and reduce the dive bottom times when foraging closest to the colony (Scheffer et al., 2012), indicating that these birds may reach their

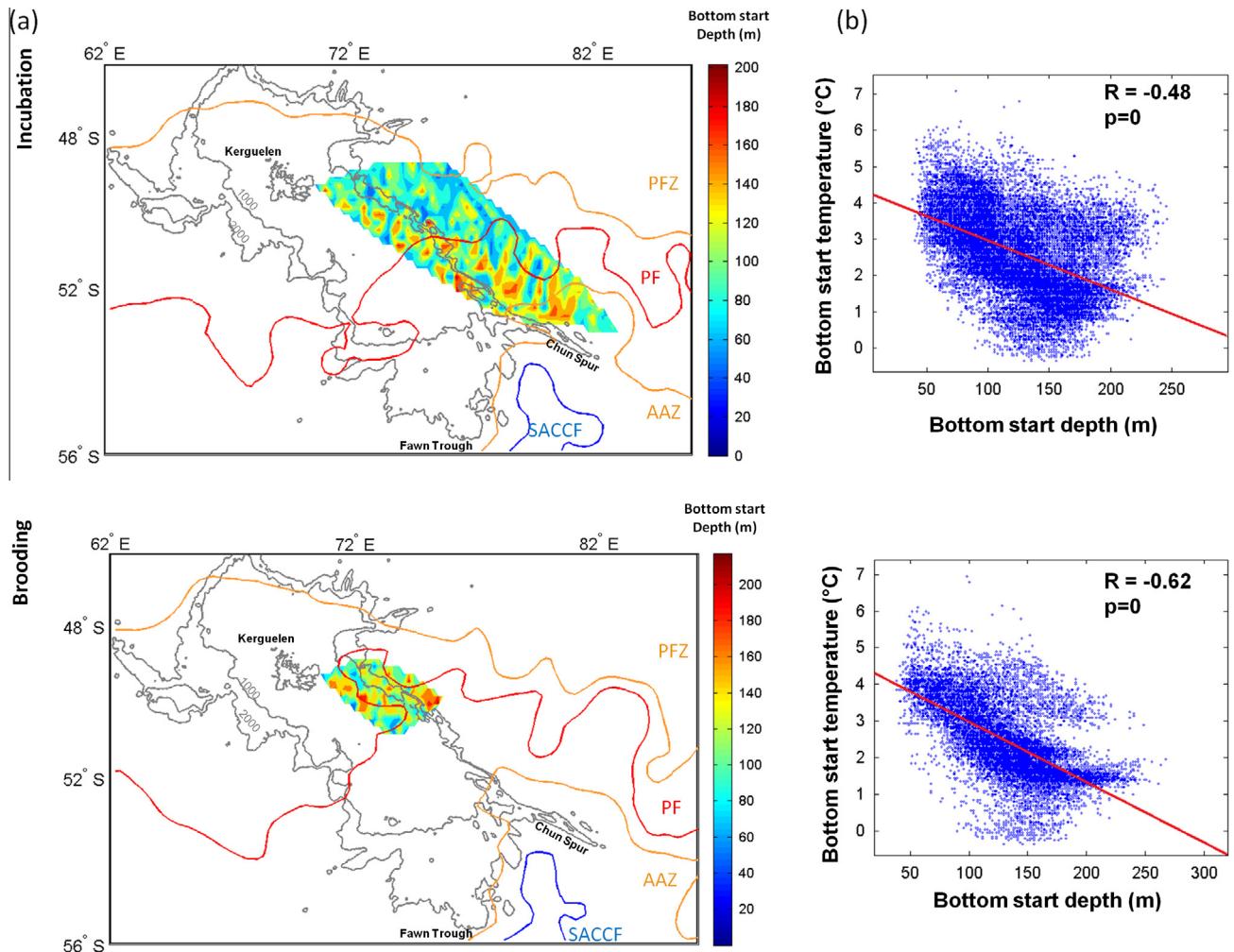


Fig. 7. Start depths of king penguins dive bottom periods, and relations with dive bottom temperatures. a – Maps of start depths of dive bottom periods of incubating and brooding birds. Grey contours show bathymetry at 0, 1000 and 2000 m depth. Coloured contours indicate frontal positions from SSH signatures, calculated as the mean positions over the trip period of tracked birds with TDR devices. Abbreviations of frontal zones: PFZ – Polar Frontal Zone; PF – Polar Front (shown as its mean summer signature contour in red, with its northern and southern limits in orange); AAZ – Antarctic Zone; SACC – Southern ACC Front. b – Correlation between start depths and start temperatures of the dive bottom periods for incubating and brooding king penguins. R values are Pearson's correlation coefficients, where 1 is total positive correlation, 0 is no correlation, and -1 is total negative correlation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

physiological dive limits (Halsey et al., 2010). At Kerguelen, short foraging trips with only a moderate increase in dive effort and constant proportions of dive bottom times during brooding indicate that the FTC influx along the Kerguelen Plateau shelf may allow horizontal and vertical foraging adaptation to breeding constraints with only moderate increases in physiological efforts.

High daily BMG of brooding birds but a rapid decrease in BMG with increasing trip duration suggests that prey resources in proximity of the colony may allow profitable foraging for relatively short periods, but may be less profitable for longer trip durations. Prey resources on the Kerguelen Plateau shelf may be of high temporal and spatial small-scale variability due to enhanced vertical mixing by tidal forces (Mongin et al., 2008; Park et al., 2008a) and the lack of aggregative effects of pronounced oceanographic features over the Plateau (Park et al., 2008b). This may lead to increased search times for prey patches and therefore less profitable foraging trips in terms of catch per unit effort (CPUE), with lower BMG of birds spending long times exploring these resources. Marine predators with lesser time constraints such as incubating penguins appear to target areas of potentially higher stability of oceanographic features and associated prey resources, such as cold water flows steered by the pronounced bathymetric features in the

Chun Spur area, and to a lesser extent offshore PF areas characterized by the structuring effects of large- and mesoscale oceanographic features (Lima et al., 2002). Shallower dive bottom periods and higher BMG during incubation indicate increased foraging efficiency in terms of CPUE similar to patterns reported in Shaffer et al. (2003) for albatrosses under different breeding constraints. This suggests the area immediately to the north-west of the Chun Spur to be an important foraging region for king penguins, allowing for profitable foraging.

4.2.3. Importance of the Polar Front (PF)

The majority of king penguins foraging occurred in areas of PF surface signature. Although this may be related to the immediate proximity of the PF to the Kerguelen breeding colony, significantly higher foraging dive performances in terms of wiggle frequencies compared to the AAZ indicate favourable foraging conditions in the PF for king penguins. Myctophids have been found to be highly accessible at the PF in terms of reduced depth and high densities (Sabourenkov, 1991; Pakhomov et al., 1994), potentially due to their aggregative behaviour at the strong horizontal and vertical thermal gradients in the water column (Kozlov et al., 1991) arising from the juxtaposition of Antarctic and Subtropical water masses.

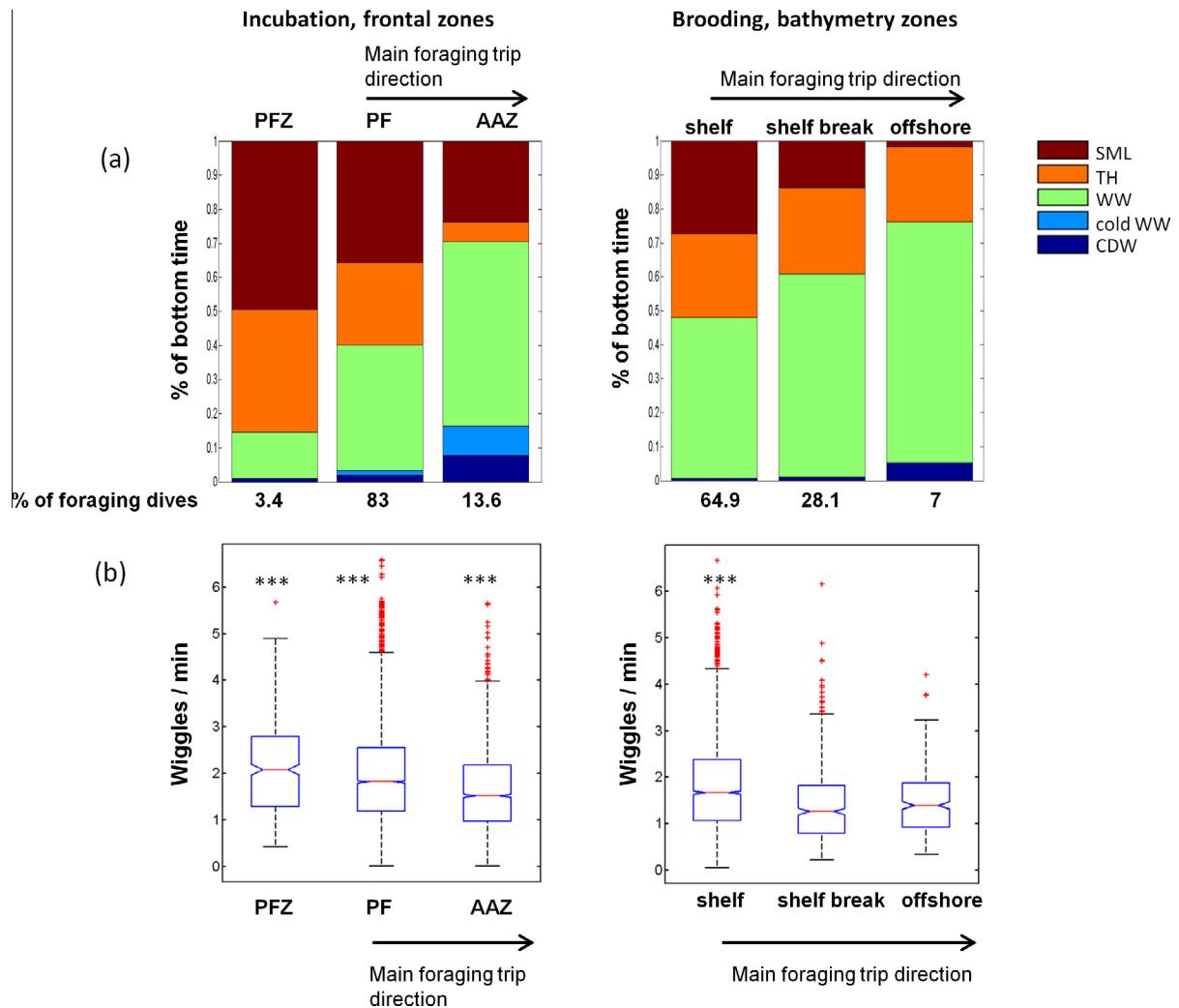


Fig. 8. Diving behaviour of king penguins in different frontal and bathymetry zones. a – Water masses targeted during bottom periods, and b – wiggle frequency per unit of dive cycle time in different frontal zones for incubating birds, and in different bathymetry zones for brooding birds. Wiggle frequencies include only dives occurring in foraging locations identified from surface movements. The arrow indicates the main foraging trip direction from the colony to the outermost locations of the trip. Percentages of foraging dives in (a) are relative to the total number of foraging dives of the corresponding breeding stage. *** in (b) indicates significant differences to the other zones with $p = 0.01$ (Kruskal–Wallis Test). Frontal zones are defined based on SSH signatures, and bathymetry zones based on depth and slope. For details on the definition of the frontal and bathymetry zones as well as the different water masses see Section 2. Abbreviations of frontal zones: PFZ – Polar Frontal Zone; PF – Polar Front; AAZ – Antarctic Zone. Abbreviations of water masses: SML – Surface Mixed Layer; TH – Thermocline; WW – Winter Water; WWcold – cold Winter Water <0.5C; CDW – Circumpolar Deep Water.

Such shallow and dense prey aggregations may occur in areas of PF signature, and may allow efficient foraging dives with high prey capture rates for king penguins. Our study therefore emphasizes the importance of the PF for foraging king penguins regarding individual foraging dive efficiency in terms of prey capture rates per unit of dive time, confirming previous studies on other Southern Ocean marine predators (Bost et al., 2009; Thiebot et al., 2011) and king penguins in different breeding locations (Bost et al., 1997; Guinet et al., 1997; Sokolov et al., 2006; Trathan et al., 2008; Scheffer et al., 2010; Péron et al., 2012).

4.2.4. Importance of the thermocline

In the water column, the Thermocline (TH) appeared to provide the most favourable foraging feature for king penguins at Kerguelen, indicated by the highest wiggle frequencies per unit of dive cycle time of incubating birds when targeting prey in this layer. During the austral summer, the TH is the layer of one of the most pronounced thermal gradients in the ocean, resulting from the juxtaposition of warm SML and cold WW. Discontinuities in physical water column properties at the TH results in biomass accumulation

and enhanced biological activity (Thomas and Emery, 1988; Lima et al., 2002), which may lead to dense aggregations of higher trophic levels such as myctophids at this layer (Hulley, 1981; Kozlov et al., 1991; Pakhomov et al., 1996). The TH (and possibly adjacent layers of the SML) may therefore host profitable prey aggregations at relatively shallow depths, allowing highly efficient foraging in terms of prey capture rates. Our results of the penguins dive performance in different water masses were consistent with spatial patterns of foraging efficiency, with highest wiggle frequencies occurring in the PF and shelf areas where most intense SML and TH exploration took place during prey pursuit phases (see Fig. 8).

The importance of the TH has already been reported for king penguins in other breeding locations, where birds target prey associated with or close to thermal discontinuities in the water column at Crozet (Charrassin and Bost, 2001) and South Georgia (Scheffer et al., 2012). The TH also influences the diving behaviour of various marine predators (elephant seal: Boyd and Arnbom, 1991; Biuw et al., 2007), and other diving birds (murrels: Takahashi et al., 2008; little blue penguins: Ropert-Coudert et al., 2009; Pelletier

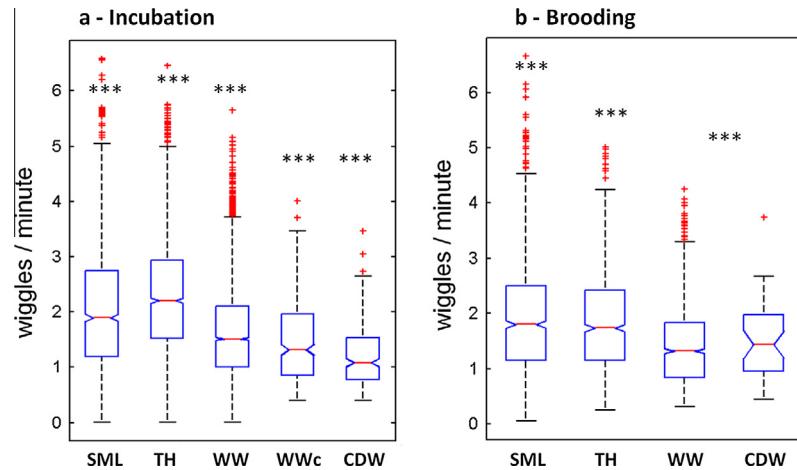


Fig. 9. Dive efficiency of king penguins in different water masses for a – incubating and b – brooding birds. Wiggle frequencies include only dives occurring in foraging locations identified from surface movements. *** indicates significant differences to the other water masses with $p = 0.01$ (Kruskal-Wallis Test). *** situated between two water masses indicates no significant difference between these groups, but significant differences occurring with the other water masses. Abbreviations of water masses: SML – Surface Mixed Layer; TH – Thermocline; WW – Winter Water; WWc – cold Winter Water <0.5°C; CDW – Circumpolar Deep Water. For details on the water masses definitions see Section 2.2.2.

et al., 2012). Our study confirms the key importance of the TH for foraging king penguins at Kerguelen in terms of highest prey capture rates at the individual dive scale.

4.2.5. Importance of bathymetry-related oceanographic processes

While the highest foraging dive performances in terms of prey catch rates were associated with SML and TH exploration in PF/PFZ and shelf areas, only a few foraging trips were oriented into oceanic PF waters but rather towards areas along the Kerguelen Plateau shelf break characterized by strong interaction of oceanographic circulation with bathymetry, where the birds increased WW exploration. Shallow prey aggregations in the TH and SML may allow for high prey capture rates per unit of dive time at the individual dive scale. However, topographically complex landscapes such as the shelf break and areas near the Chun Spur may lead to spatially localized and stable micro-niches in terms of oceanography and associated prey resources (Bouchet et al., 2014). Such conditions may allow for shorter search times for prey patches, and therefore increase foraging profitability in terms of CPUE on the foraging trip scale. Enhanced prey availability through upwelling of nutrients (Carter and Gregg, 2002; Genin, 2004), and/or prey of different energy content associated with deeper and colder waters may further increase foraging profitability for king penguins in these locations of oceanographic circulation interacting with pronounced bathymetry. Common patterns of foraging trip orientation towards areas where such cold water masses may become available through bathymetry-induced steering, and increased dive effort (deeper dive bottom periods) associated with the exploration of these cold waters shown by both incubating and brooding birds while adjusting foraging trip duration to changing breeding constraints underlines the importance of bathymetry-related oceanographic features for the foraging animals.

The importance of bathymetrically entrained oceanographic features such as canyons, steep slopes or seamounts to marine predators has been suggested for a number of species in the Southern Ocean (Costa et al., 2008, 2010; Ribic et al., 2008; Muelbert et al., 2013) as well as in more temperate regions (Worm et al., 2003; Thompson, 2007; Morato et al., 2008, 2010; Amorim et al., 2009). Our study provides evidence for similar behaviour in king penguins. Comparison with the diving behaviour of Southern Elephant Seals at the Antarctic Peninsula (Costa et al., 2008, 2010; Muelbert et al., 2013) suggests similarities in the exploration

of water masses of southern origin in locations where these waters may become more accessible to the animals through steering effects of bathymetry. As a detailed analysis of combined behaviour and oceanography, our study adds information on how diving predators may explore such features related to bathymetric steering at the ocean surface and at depth.

The use of bathymetry-related oceanographic structures by king penguins is contrasting to behaviour in other breeding locations such as South Georgia or Crozet, where dynamic oceanographic features such as eddies and fronts have been identified to be the main foraging features during incubation and brood (Bost et al., 1997; Cotté et al., 2007; Trathan et al., 2008; Scheffer et al., 2010, 2012). Such different behavioural patterns may reflect the species' adaptation to environments characterized by different oceanographic processes, the Kerguelen Plateau dominated by the direct effects of its pronounced shallow bathymetry (Park et al., 2008b, 2014), and the more oceanic systems at South Georgia and Crozet characterized by dynamic features (Trathan et al., 1997; Thorpe et al., 2002; Meredith et al., 2003; Murphy et al., 2007).

While remotely sensed oceanographic parameters such as SSH and SST have been shown to play a role in habitat modelling for king penguins and other marine predators at Kerguelen (Bost et al., 2011; Hindell et al., 2011), they have been found to explain only parts of the animals' behaviour (Hindell et al., 2011). In our study, SSH signatures allowed us to identify the PF and the immediate FTC influx over the Chun Spur as well as changes in the penguins' diving behaviour associated with the different frontal zones. However, surface signatures did not fully reflect the northward extension of the cold-water subsurface flow along the Kerguelen Plateau shelf break, which appears to be a key feature for foraging king penguins. Taking into account the penguins' detailed behavioural adaptation to oceanographic features at the surface and within the water column, our methods may be complementary to other existing studies on the foraging behaviour of king penguins. This may particularly be valid for areas characterized by important interactions of oceanographic circulation with bathymetry, where surface features might not sufficiently reflect oceanographic patterns explored by the animals. However, we suggest the cold-water influx over the Chun Spur identified from remote sensing data as an important descriptor of the foraging landscape of king penguins breeding at Kerguelen. Foraging trips of king

and macaroni penguins as well as Antarctic fur seals breeding at Kerguelen or Heard Island into areas near the Chun Spur (Goldsworthy et al., 2010; Staniland et al., 2010; Hindell et al., 2011; Thiebot et al., 2014) indicate that our results may also be of importance for other marine predators foraging in areas characterized by the steering effects of the Kerguelen Plateau bathymetry on oceanographic patterns.

4.3. Areas of Ecological Significance (AES) at the Kerguelen Plateau

The high intra- and interannual consistency in foraging trip orientation of brooding king penguins to the south-east of the island towards the shelf break shown in our study and in previous work (Bost et al., 2002; Charrassin et al., 2002b, 2004), and the identification of an Area of Ecological Significance (AES) at the Kerguelen Plateau (Hindell et al., 2011) underlines the importance of this area for king penguins and other marine predators breeding at Kerguelen. Similarly, the foraging areas of incubating king penguins appear to exhibit a high level of spatial consistency close to the subsurface cold-water flow along the south-eastern shelf break. Our study provides complementary information to the AES already identified (Hindell et al., 2011), as it augments information about areas of high significance for foraging king penguins, particularly during the incubation stage. These areas may also be of importance for other marine predators breeding on the Kerguelen Plateau, whose foraging areas coincide with areas of the subsurface cold-water current close to its origin at the Chun Spur (Antarctic fur seals, macaroni and king penguins breeding at Heard Island), or with locations further upstream towards Kerguelen (black-browed albatrosses) (Hindell et al., 2011).

5. Conclusion

Our study shows the exploration of oceanographic features related to the interaction of mesoscale circulation with pronounced bathymetry by foraging king penguins. Foraging trip orientation and diving behaviour towards the exploration of cold water masses in locations of oceanographic circulation interacting with the Kerguelen Plateau suggest the importance of such bathymetrically entrained features for king penguins during the incubation and brooding stage. In this context, the cold-water flow and potentially associated upwellings of FTC along the Kerguelen Plateau shelf break and waters in areas near the Chun Spur appear to play a key role for the animals' foraging. Our study provides evidence to previous claims that king penguins explore bathymetrically entrained oceanographic features for foraging. This is contrasting to behaviour in other breeding locations such as South Georgia or Crozet islands where the birds mainly explore more dynamic features such as fronts and eddies.

While thermocline and surface mixed layer exploration in PF and shelf areas was associated with highest prey capture rates at the individual dive scale, the exploration of cold-water features in locations of strong bathymetric steering appeared to increase foraging efficiency in terms of CPUE on the foraging trip scale. This might be related to higher stability of oceanographic features and associated prey resources in such locations, which may allow for shorter search times for prey patches.

We show how interactions of oceanography with bathymetry may help in understanding the foraging behaviour of a key marine predator at the Kerguelen Plateau. This is important knowledge for the prediction of foraging habitats for upper trophic-level marine predators at the Kerguelen Plateau, which is essential for conservation measures. Comparison with other studies suggests that our findings may also be true for other marine predators breeding at the Kerguelen Plateau (black-browed albatrosses, fur seals, king

and macaroni penguins breeding at Heard Island) who appear to explore similar areas for foraging. Our study confirms the AES on the Kerguelen Plateau shelf identified by Hindell et al. (2011), and further suggests the importance of the area immediately to the north-west of the Chun Spur.

However, while bathymetry consists of static features, oceanographic patterns and associated biological processes are characterized by temporal and spatial variability (Sokolov and Rintoul, 2009b; van Wijk et al., 2010; Dragon et al., 2011; Saunders et al., 2013, 2014; Park et al., 2014). Therefore, an important next step would be to assess how variability in hydrological processes impact oceanographic features in the identified key foraging areas, and how the penguins respond to such changes. This may allow gaining a more complete picture of how these animals adjust foraging to their environment.

Author contributions

CAB designed the experiments; AS and CAB carried out the fieldwork; CAB supervised the experiments in the field; AS performed the analysis of the data; JE provided help with the environmental data analysis; AS, CAB and PT wrote the paper.

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