

Fine-scale foraging cues for African penguins in a highly variable marine environment

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ABSTRACT: Breeding seabirds often need to locate prey in spatially confined search areas on short temporal scales. Ocean physical features such as thermoclines are used as foraging cues since they concentrate and thus increase the likelihood of locating prey. However, in highly variable environments, it is less well understood how these features act as foraging cues. African penguins *Spheniscus demersus* foraging in Algoa Bay, South Africa, were fitted with GPS-TD loggers to determine the cues they use to locate prey on fine temporal (<24 h) and spatial (<100 km) scales in a bay with changing thermal properties. African penguins showed a preference for cooler surface waters associated with upwelling, avoiding warm surface waters associated with the Agulhas Current. Thermocline presence and characteristics were an important foraging cue; penguins consistently foraged at and below the thermocline even though its depth and gradient shifted over time. Dive ascent and descent rates were quicker in the presence of thermoclines with strong gradients, which form a distinct separation between the warm upper mixed layer and the cooler lower layer. Foraging dives occurred predominantly below the thermocline, while search dives occurred around the thermocline depth. Penguins dived deeper in search of prey when there was no thermocline. Our results demonstrate that top predators can cope with highly variable environments by adjusting their search strategy to target environments suited to their main prey.

KEY WORDS: Foraging ecology · Thermocline variability · GPS tracking · Dive behaviour · Top predator

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INTRODUCTION

The energetics of breeding seabirds constrain them to locate prey in as short a time or as small an area as possible (Alonzo et al. 2003, Weimerskirch 2007). Understanding the behaviour of marine top predators when locating patchy and scarce food resources in the open ocean remains a fundamental component in their conservation (Costa et al. 2012). The oceans can appear to be largely featureless compared to terrestrial ecosystems, but they are highly heterogeneous with a network of features that provide a navigable environment. Features such as eddies, fronts, currents, upwelling cells, and thermo-

clines not only define this landscape but also have the ability to concentrate biological resources, including producers and consumers (Pakhomov et al. 1994, Hunt et al. 1999, Pollard et al. 2002). Thus, it is not surprising that top predators are strongly associated with these features and use them to locate prey patches on short temporal and spatial scales, especially when providing for offspring (Charrassin & Bost 2001, Nel et al. 2001, Hyrenbach et al. 2006, Cotté et al. 2007, Bost et al. 2009).

Seabird life histories, characterized by long life spans and late maturation, have evolved to cope with this heterogeneous ocean landscape, low prey availability and often long commutes between foraging

and breeding areas (Lack 1968, Ricklefs 1990). These birds have evolved a suite of strategies to increase the probability of locating scarce and patchy prey distributions. For instance, many breeding seabirds, especially long-range foragers such as albatrosses and the larger penguins, use sea surface temperature (SST) gradients to locate meso-scale (100–1000 km) ocean physical features such as eddies, fronts, and upwelling zones that advect nutrients to the euphotic zone from deep waters (Cotté et al. 2007, Trathan et al. 2008, Kappes et al. 2010).

Sea temperature cues are not confined to horizontal space. Temperature gradients through the water column can also concentrate prey and act as foraging cues for diving seabirds (Charrassin & Bost 2001, Takahashi et al. 2008, Kokubun et al. 2010, Scheffer et al. 2010, 2012, Pelletier et al. 2012). Thermoclines are rapid changes in water temperature with depth due to stratification of surface waters, and typically form the boundary between the surface mixed layer and deeper layers. Nutrient advection from nutrient rich, deeper water is limited across the thermocline because of different water densities (Fiedler 2010) potentially concentrating prey around thermoclines (Hansen et al. 2001). The inhibition of nutrient movement across the thermocline is particularly acute for persistent and strong thermoclines (Gray & Kingsford 2003), and their ecological importance has been well documented for many top predators (Charrassin & Bost 2001, Biuw et al. 2007, Takahashi et al. 2008, Kokubun et al. 2010, Kuhn 2011, Scheffer et al. 2012). Predator foraging depth is often dependent on thermocline depth (Takahashi et al. 2008). King penguins *Aptenodytes patagonicus* forage preferentially within and below the thermocline where prey is concentrated by the cold surface mixed layer (Charrassin & Bost 2001), and inter-annual differences in the foraging behaviour of thick-billed murres *Uria lomvia* have been attributed to the position and structure of the thermocline (Takahashi et al. 2008, Kokubun et al. 2010).

At finer spatial scales (1–100 km) it is less well understood how predators find patchily distributed prey because physical cues tend to be ephemeral, and thus the location of prey less predictable. For example, most studies only consider dive behaviour in relation to vertical thermal structure in environments that are relatively stable or compare diving in different conditions. Little is known about how marine predators use a thermocline as it changes in position and structure through time. Furthermore, few studies are able to predict how such a dynamic thermocline affects the behaviour of diving seabirds

under a range of conditions. Top predators do, however, show behavioural plasticity by adjusting their foraging behaviour to that of their prey and changing environments (Embling et al. 2012, McIntyre et al. 2014). At fine scales there are considerable lags between physical processes, their associated increase in primary production and the subsequent response by intermediate prey species (Durant et al. 2007). This is especially concerning for short-ranged seabirds, which are bound by energetic or reproductive constraints. These birds are able to spend less time and cover less area when searching for prey, effectively reducing their ability to encounter scattered prey patches (Weimerskirch 2007).

African penguins *Spheniscus demersus* are short-range predators that typically forage within 10 to 50 km of their colonies when breeding (Wilson 1985, Pichegru et al. 2009). They are endemic to southern Africa and have experienced severe population decreases over the last century, with the most rapid decrease occurring over the last decade, in part due to declines in their main prey species (Crawford et al. 2008, 2011). In South Africa alone, a 60% decrease in the number of breeding birds since 2004 has resulted in the species being up-listed from 'Vulnerable' to 'Endangered' (Crawford et al. 2011, Birdlife International 2013) and has attracted powerful conservation efforts (Pichegru et al. 2010, 2012).

In order to effectively conserve African penguins, it is necessary to gain a better understanding of their habitat use and behaviour in relation to the processes that govern local productivity and prey distribution. Islands in Algoa Bay, South Africa, are the eastern-most breeding colonies and now host close to half of the global population (Rand 1963, Crawford et al. 2009, 2011). Penguins breeding in Algoa Bay face considerable challenges in locating prey, as the bay is known for its high degree of environmental variability with thermal conditions changing on scales of kilometers and days (Schumann et al. 2005). Frequent low-pressure storms in winter drive a deep, mixed upper layer (Hunter 1982) and extensive easterly winds in summer drive upwelling of cool water at Port Alfred, located 100 km further east (Goschen & Schumann 1988). Cool waters entering the bay from the Port Alfred upwelling cell form thermoclines that are advected towards the surface where they are confronted by warmer, wind-mixed surface waters (Goschen & Schumann 1990, Roberts 2010).

In this paper we predict that the characteristics of thermoclines and cool surface waters associated with

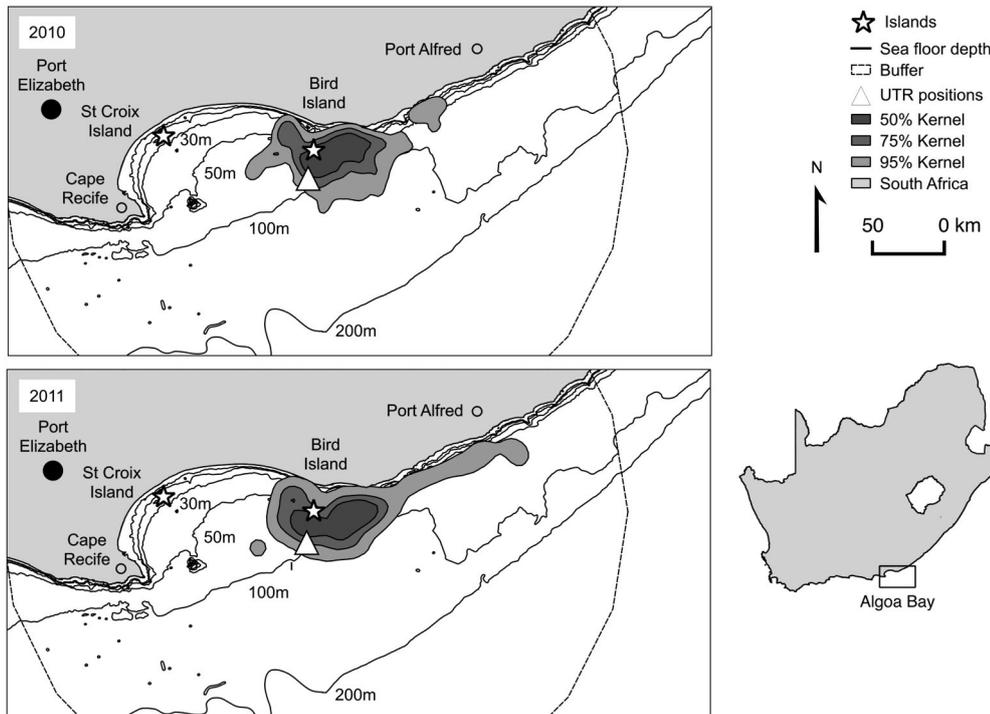


Fig. 1. Locations of main African penguin breeding colonies on Bird Island (east) and St Croix (west) Islands, in Algoa Bay on the south coast of South Africa. Kernel density estimates are shown for penguins deployed with GPS-temperature depth (TD) loggers during the May–July 2010 (top panel) and March–June 2011 (bottom panel) breeding seasons. UTR: underwater temperature recorder

upwelling are important foraging cues for African penguins as their prey show preference for cooler surface waters (Barange et al. 2005). Warm waters from the Agulhas Current occasionally intrude into Algoa Bay over the narrow continental shelf and are likely to drive prey deeper; thus, in the presence of warm surface waters and deeper thermoclines penguins are predicted to dive deeper in search of prey. However, these oceanographic processes together with meteorological influences create a heterogeneous marine environment that is almost always undergoing changes in its thermal structure (Schumann et al. 2005). This system therefore provides an ideal situation for understanding how a short-ranged marine predator utilizes a changing landscape to locate prey that occurs at temporally varying densities and is often patchily distributed (Coetzee et al. 2008).

MATERIALS AND METHODS

GPS tracking African penguins

African penguins provisioning small chicks (2–3 wk old) on Bird Island, Algoa Bay (33.841°S, 26.286°E; Fig. 1), were tracked during 2 successive austral autumns (May–July 2010 and March–April 2011) using GPS-TD loggers (earth & Ocean Technologies) consisting of a GPS recorder combined with a time-

depth recorder (size = 96 × 39 × 26.5 mm). Each penguin was tracked for 1 trip before loggers were removed, and the same bird was not tracked again within the same season. The loggers were attached to the lower dorsal section of the bird using waterproof Tesa® tape (Pichegru et al. 2010). The loggers recorded latitude and longitude (to 0.001 min of latitude and longitude) every 1 min to an accuracy of less than 10 m (Ryan et al. 2004). The GPS-TD loggers carried pressure (recording depth to the nearest 0.1 m; Ryan et al. 2007) and temperature sensors, both of which recorded at 1 s intervals. The GPS-TD temperature probe has a resolution of ~0.03 K and can detect a 90% change in temperature in ~2 s (earth & Ocean Technologies calibration certificates).

Dive analyses were conducted in MT Dive software (Jensen Software Systems), with a dive defined as a descent to depths >3 m to distinguish between diving and porpoising (Wilson & Wilson 1990, Pichegru et al. 2010). Tracks were visualized in QGIS (QGIS Development Team 2015) and only complete tracks were selected for analysis (tracks with no positional data for >25% of the trip duration were excluded). GPS signals are lost underwater, thus a GPS position was inferred for each dive by linear extrapolation between the 2 closest GPS positions (before and after the dive) based on the start time of each dive and time of each GPS position. Only dives with an inferred position within 500 m of a GPS fix were included in habitat selection analyses.

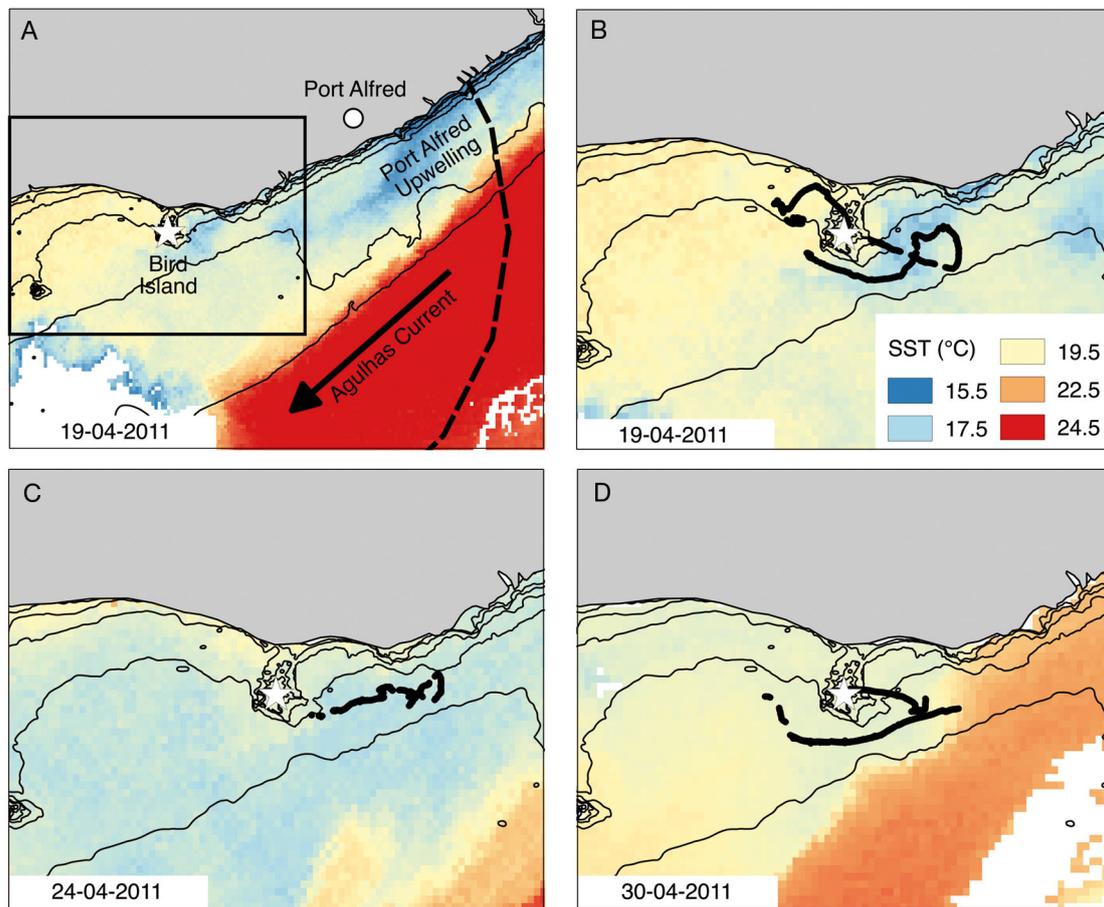


Fig. 2. Variation in sea surface temperature (SST) within the foraging area of breeding African penguins from Bird Island, South Africa (white star). (A) Area containing zones of upwelling and Agulhas Current, and the penguin foraging area (inset). (B–D) Track of 1 bird foraging superimposed on SST on the day of its foraging trip. (A,B) Upwelling originates east of Port Alfred and flows into the eastern section of Algoa Bay, (D) an intruding wedge of warm water from the Agulhas Current later replaces these cool upwelled waters

Habitat use in relation to surface and bottom features

We utilized SST and chl *a* recorded by the MODIS satellite platform (www.afro-sea.org.za), which records daily averages at a 1×1 km scale, to determine the thermal and chl *a* habitat preference of African penguins. The mean, maximum, and minimum SST and chl *a* recorded along each penguin's foraging track was calculated to assess variation within trips. On some days, cloud cover prevented satellite recordings by the MODIS platform in our region of interest, and on a few occasions 'no data' were available from the database; penguin tracks on these days were thus excluded from analyses. Plots of SST and chl *a* were viewed in QGIS (QGIS Development Team 2015) to identify thermal fronts and other physical processes such as upwelling (Fig. 2).

In order to determine whether penguins demonstrated habitat preference for cooler patches of surface water or waters with higher values of surface chl *a*, we used binomial generalized linear mixed-effects models implementing the lme4 package in R (Bates et al. 2014, R Core Team 2015) to compare the SST and chl *a* in locations where penguins foraged or were absent (Aarts et al. 2008, Wakefield et al. 2011). A set of 10000 pseudo-absence locations (long, lat) within the home range of the birds was generated. Pseudo-absences came from a normal distribution of possible locations within 1.1 times the potential home range of African penguins from Bird Island (110 km radius buffer) (Figs. 1 & 2) with the mean centered at the colony. A normal distribution was selected as penguins are likely to travel as far from the island as is required to locate prey, or until a point where breeding constraints limit further dispersal, e.g. time con-

straints imposed by the necessity to relieve a partner incubating eggs or brooding chicks. We then randomly selected 3 locations from the pseudo-absence dataset for each bird GPS location and assigned these locations habitat information to infer foraging penguin habitat preferences. To each pseudo-absence GPS location and penguin dive location, we assigned the nearest remotely sensed (<1 km) SST and chl *a* values, the depth of the water column (bathymetry inferred from bathymetric charts), sea floor slope, distance from the colony, and distance to the nearest adjacent colony (St Croix Island) to account for possible competition between colonies (Wakefield et al. 2011). Relationships that were clearly not linear during initial data exploration were fitted as quadratic terms, namely bathymetry, distance to the nearest colony, and SST. We used R package MuMIn to conduct multi-model comparison in order to identify the model with the lowest AICc (Barto 2015, R Core Team 2015). Candidate models that were within 4 ΔAIC_c were model averaged. The model with the lowest AICc score was tested using receiver operator curves (ROC) in R package ROCR (Sing 2005). The area under curve (AUC) was used to determine model performance; values over 0.9 are typically associated with an accurate model and AUCs of 0.7–0.9 categorize models with moderate application (Swets 1988).

Habitat use in relation to vertical thermal structure

For each dive, the maximum depth, the duration of the dive, the bottom duration (Kato et al. 2006), ascent rates, and descent rates (m s^{-1}) were calculated. Dives were categorized into foraging and search dives. Foraging dives were characterized by undulations in the bottom phase of the dive, as these undulations are thought to occur during prey pursuit; the number of undulations in the bottom phase of the dive is correlated with beak opening or prey ingestion in other penguin species (Simeone & Wilson 2003, Bost et al. 2007, Hanuise et al. 2010). An undulation in the bottom phase was defined as 3 consecutive points where the vertical displacement was >1 m (Halsey et al. 2007).

The thermal structure of the water column along a penguin track was determined from dives that sampled at least 80% of the water column depth (representative dives) and this structure was then assigned to all other dives that occurred within 750 m and 30 min of the representative dive. African penguins dive and ascend at speeds averaging $\sim 1 \text{ m s}^{-1}$, thus the time lag in the detection of temperature change

by the datalogger ($\sim 2 \text{ s}$) is likely to cause a 2 m error in temperature measurements on both the ascent and descent. Therefore, thermal profiles of these representative dives were averaged into 1 m bins using data from both the ascent and descent of a penguin's dive. This reduces the error in over-estimating temperature on descents and under-estimating temperature on ascents. SST was taken as the 1–2 m bin because the response time of the logger's temperature probe stabilizes in the first 1 m of the water column when the logger moves from air to water. A thermocline was recognized if the temperature difference (ΔT) between the near-bottom waters and the SST differed by $>2^\circ\text{C}$ and ΔT with depth was $>0.25^\circ\text{C m}^{-1}$ (Takahashi et al. 2008, Kuhn 2011). The start and end depths of the thermocline (which indicate thermocline thickness) were measured as the depths at which the rate of ΔT with depth first and last exceeded $0.25^\circ\text{C m}^{-1}$. From these measurements, we calculated the midpoint depth of the thermocline, thermocline intensity (TI) as the ΔT from the top to the bottom of the thermocline (Takahashi et al. 2008, Kokubun et al. 2010), and the thermocline gradient (TG) as the TI divided by the thickness of the thermocline. Thermocline intensity and gradient determine the extent to which the thermocline blocks the vertical diffusion of nutrients. Thermoclines that are more intense have a greater difference in temperature across the thermocline, while the gradient characterizes the extent of vertical compression. A thermocline with a high intensity and a steep gradient forms a well-defined front between different water masses.

In dives where the vertical ΔT of the water was too gradual to be recognized as a thermocline (i.e. $<0.25^\circ\text{C m}^{-1}$), hereafter termed mixed waters, a stratification index was calculated as the ΔT (max. to min. temperature) from the surface to the bottom of dives that covered >80% of the water column. In addition to temperature records provided by GPS-TD loggers, hourly measurements of temperatures were obtained from a string of HOBO Pro v.2 water temperature loggers (Onset), hereafter underwater temperature recorders (UTRs). Recorders were spaced vertically 10 m apart (depth range = 10–70 m) and the string stationed 7.4 km south of Bird Island (Fig. 1). The UTRs provided time series that were used to contextualize our results and were plotted in Ocean Data View v.4 (Schlitzer 2015).

Linear mixed-effect models carried out using the lme4 package implemented in R (Bates et al. 2014, R Core Team 2015) were used to assess the relationships between penguin response parameters and the water structure in which birds dived. In waters pre-

senting a thermocline we modeled the distance within the water column that a bird dived from the midpoint of the thermocline, maximum dive depths, and ascent and descent rates as dependent variables. These were each modeled as a function of the thermocline midpoint depth, TI and TG, as well as SST (family = Gaussian). We ran additional generalized linear mixed-effects models implementing the lme4 package in R (Bates et al. 2014, R Core Team 2015) to determine whether a dive was more likely to be above or below the thermocline midpoint (family = binomial) in response to the same fixed effects (i.e. thermocline midpoint depth, TI, TG and SST) as above.

In mixed waters (where thermoclines were absent), maximum dive depths, bottom times, and ascent and descent rates were modeled as a function of average water column temperature, stratification index, and SST. In addition, bathymetry, time of day, time of day as a quadratic term, and types of dives (foraging or searching) were included as co-variables in all models, as these variables are likely to influence the response variables. Bathymetry constraints on maximum dive depths and daylight (time of day) is likely to explain some variation in the response variables because African penguins are visual hunters (Wilson et al. 1993) and make shallower dives towards dusk and dawn (Ryan et al. 2007). Bird ID was included as a random effect in all models to account for the effect of repeated dives by the same individual. Furthermore, because at the time of the study there was no robust method for sexing birds in the field, individual ID will also account for possible differences between sexes (Pichegru et al. 2013). No co-linearity was observed between fixed effects and this was tested by assessing correlations between fixed effects (correlation coefficients between effects >0.3 were considered to be co-linear). Residuals and random effects were normally distributed. Again, we implemented multi-model comparison in R package MuMIn to compare models ranked by ΔAIC_c values (Barto 2015, R Core Team 2015). Models with ΔAIC_c of <4 were model averaged. Fixed variance structures were fitted to variables that indicated heteroscedacity. Means and SD are reported, unless stated otherwise.

RESULTS

Environmental conditions in Algoa Bay

Of the 88 penguins on which loggers were deployed, 54 yielded more or less ($>75\%$ complete) complete foraging tracks. During deployments, for-

mation of thermoclines was largely a result of cold bottom waters advancing up into the well-mixed surface waters, forming a thermal discontinuity (Fig. 3). During deployments in March 2011, the thermocline maintained a stable position in the water column (thermocline depth = 21.3 ± 5.0 m) for 11 days. During that period we obtained 9 complete GPS tracks and 1411 dives. The thermocline during this period had, on average, a steep TG ($0.58 \pm 0.56^\circ\text{C m}^{-1}$) and a high TI ($5.3 \pm 1.8^\circ\text{C}$). Warm water intrusions from the Agulhas Current were observed during deployments from 12 to 14 May 2010 and 22 April to 2 May 2011, resulting in a mixed water column (column temperature = $17.0 \pm 1.6^\circ\text{C}$). We obtained 11 complete GPS tracks and 2515 dives during these mixed water events. However, renewed upwelling re-established a thermocline, quickly advancing the thermocline towards the surface as upwelling intensified from 15 to 26 May 2010 (Fig. 3). We obtained 15 GPS tracks and 2626 dives during the period when the thermocline was advancing towards the surface. Before upwelling commenced, the thermocline was deep (48.8 ± 4.3 m) and highly stratified (TI = $4.2 \pm 1.7^\circ\text{C}$, TG = $0.5 \pm 0.3^\circ\text{C m}^{-1}$). When upwelling approached the surface, a cool mixed water column was observed. Wind mixing of the water column occurred during a storm event on 28 May 2010, which resulted in the thermocline deepening and dissipating as bottom waters were mixed into surface waters, resulting in a moderately warm ($16.6 \pm 0.2^\circ\text{C}$), mixed water column (Fig. 3). From 28 to 31 May 2010, 5 penguins made trips with complete tracks and 781 dives were recorded.

Habitat preference in relation to surface and bottom features

SST and chl *a* data were available for 15 of the 54 penguins that returned with complete tracks. No SST or chl *a* data were available for 38 of these tracks due to cloud cover and for 1 track no data was available on the data server. These birds experienced average differences (max. to min.) in SST along their tracks of $1.04 \pm 0.86^\circ\text{C}$ (range = 0.05 – 3.83°C). We detected no correlation between fixed effects in models describing habitat preference. African penguins preferred temperatures between 18 and 20°C , with strong avoidance of SST $>22^\circ\text{C}$ (Fig. 4). Temperatures $>22^\circ\text{C}$ were largely associated with intrusions of the Agulhas Current south of Bird Island (Fig. 2B–D). Visual inspection of tracks demonstrated that penguins mainly foraged east and south into cooler upwelled waters and along the Agulhas front (Figs. 1 & 2). In

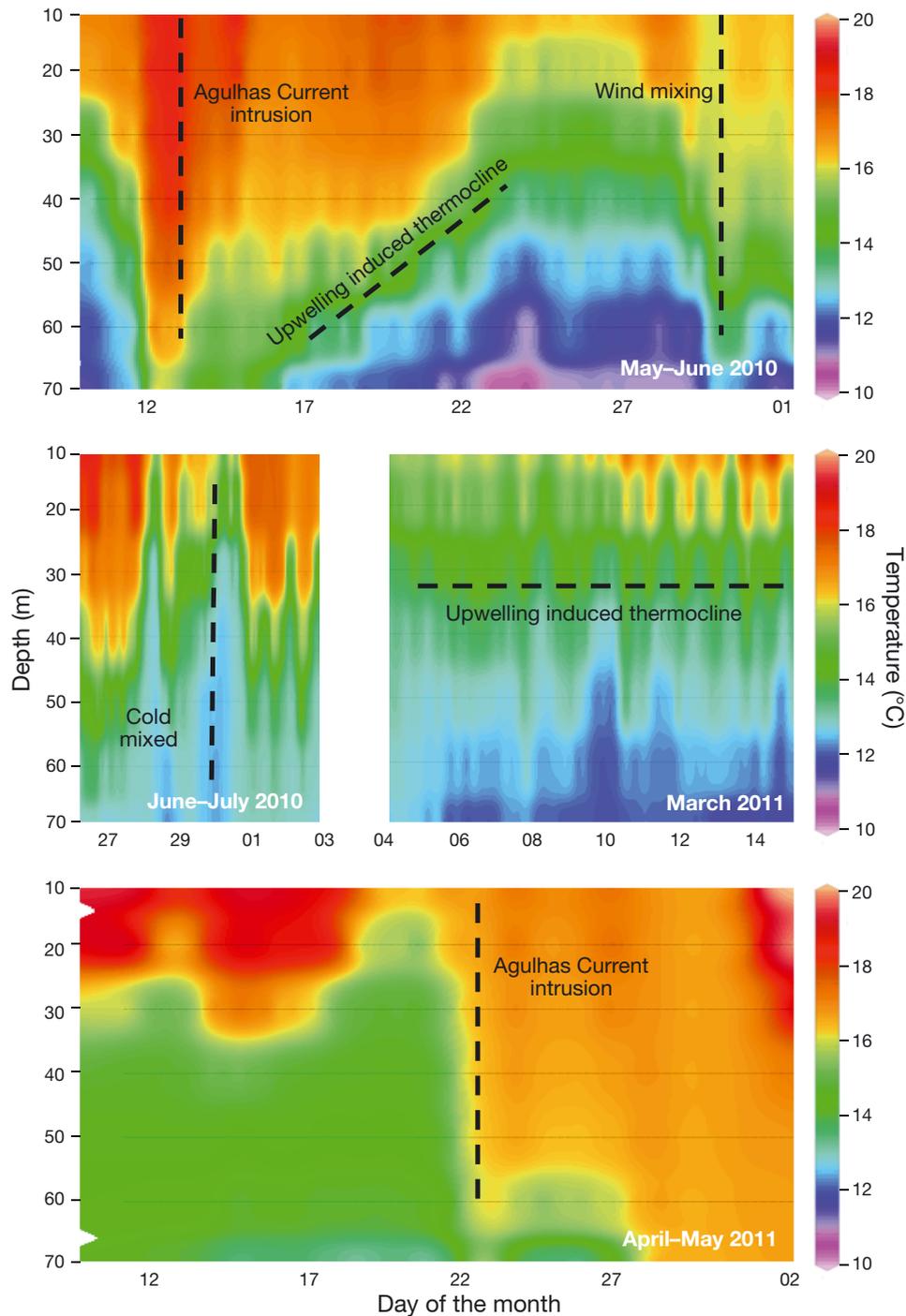


Fig. 3. Temperature-depth plots from a string of underwater temperature recorders (UTRs) situated 7.4 km south of Bird Island, South Africa. UTRs are positioned 10 m apart at depths ranging from 10–70 m. The plots show the variability of the vertical thermal structure of the water column over the chick rearing periods when African penguins were deployed with GPS-TD loggers. Dashed lines denote the occurrence of processes or features (labeled in figure)

some instances however, birds foraged in waters with no distinct front or heterogeneity. During episodes of renewed upwelling, penguins tracked cold-water plumes flowing southwest from Port Alfred (Fig. 2B). In the model with the lowest AIC_c score (see

Table S1 in the Supplement at www.int-res.com/articles/suppl/m543p257_supp.pdf), penguins were more likely to occur in environments with lower surface chl *a* concentrations (Fig. 4), and closer to their breeding colony than expected, while they demon-

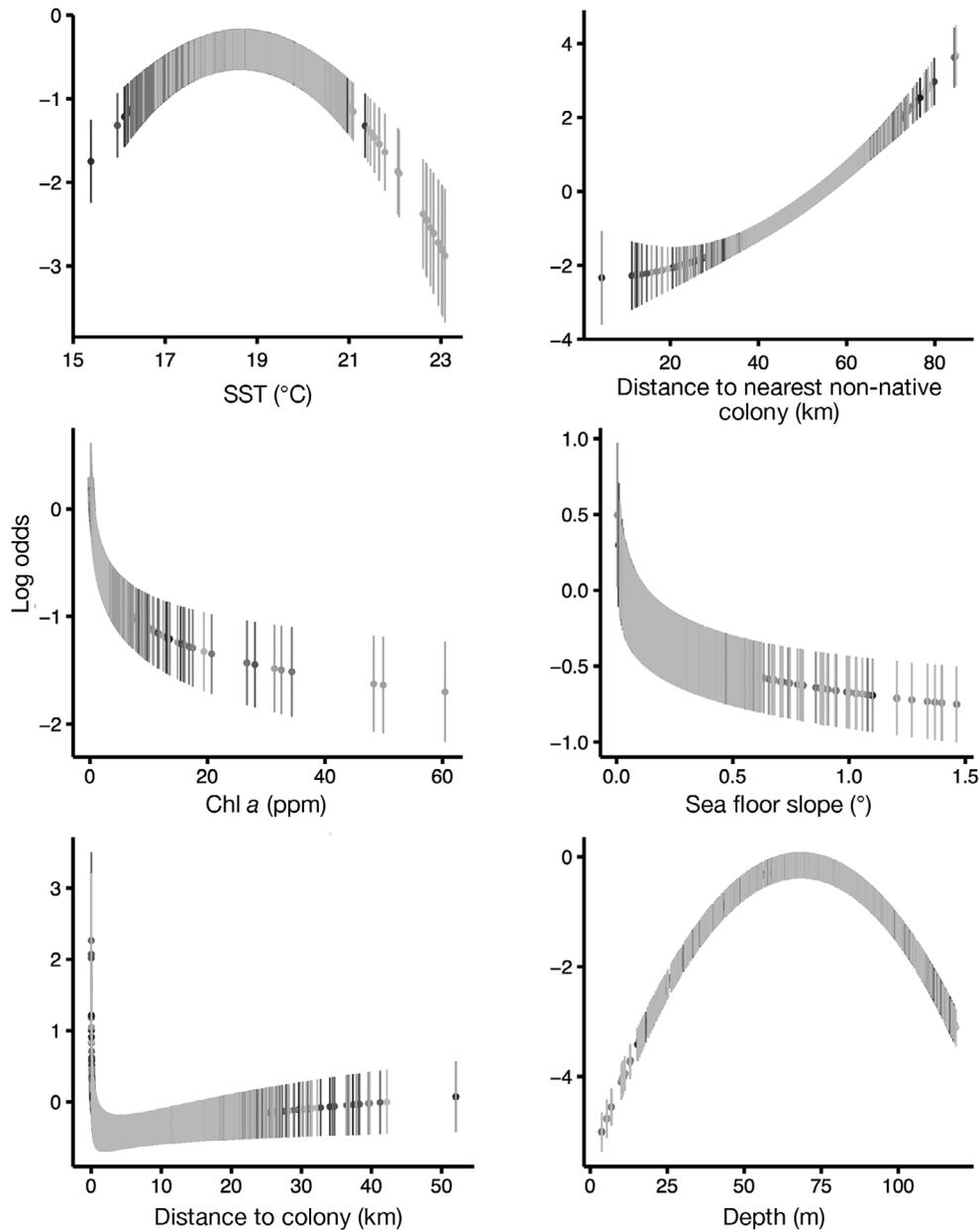


Fig. 4. Generalized linear mixed-effect model (GLMM) predicting the habitat preference of African penguins in relation to sea surface temperature (SST), chl *a* concentrations, distance to the breeding colony, distance from the nearest non-native colony, sea floor slope, and water column depth. Each point represents 1 penguin dive, and each penguin was included as a random effect, with the different shades of grey representing different individuals. Vertical lines represent variance

strated strong avoidance of the neighbouring, larger colony on St Croix Island (Fig. 4). Penguins preferred waters with more gradual sea floor slopes (Fig. 4) and were more likely to forage in waters 60 to 80 m deep. AUC for habitat preference models, from the model with the lowest AIC_c score, was 0.82 and can thus be considered a robust model for predicting African penguin foraging locations in relation to environmental conditions in a state of flux.

Dive behaviour in relation to thermoclines

Dives that sampled more than 80% of the water column accounted for 34% of the dives recorded. The average temperature at the bottom of foraging dives in stratified water columns (i.e. when a thermocline was present) was $14.1 \pm 2.2^\circ\text{C}$. Thermocline characteristics influenced penguin diving behaviour (Table 1). We detected no correlation between fixed effects in

Table 1. Results of the linear mixed-effect models (LMMs) testing how response variables—dive depth in relation to the thermocline (TC) depth (dive depth – TC depth), maximum dive depth, bottom time, and descent and ascent rates—are influenced by the thermocline mid-point depth, intensity, and gradient, as well as bathymetry, time of day and its polynomial (Time and Time²), whether the dive was a foraging (Foraging: True) or search dive, and sea surface temperature (SST) in stratified waters. All response variables, except descent rate, are model averaged estimates. *z*-values are reported for models that were model averaged, and *t*-values for models that were not model averaged and thus Pr(>|*z*|) values are not reported

Response	Fixed effect	Estimate	SE	<i>z</i> -value	Pr (> <i>z</i>)	
Dive depth – TC depth	Intercept	–28.600	5.282	5.4141	<0.001	
	Bathymetry	0.210	0.015	13.853	<0.001	
	Time	0.686	0.181	3.794	<0.001	
	Time ²	5.719	0.020	12.006	<0.001	
	Foraging: True	1.524	0.368	4.143	<0.001	
	SST	–0.037	0.250	0.149	0.881	
	Thermocline gradient	0.859	0.952	0.902	0.367	
	Thermocline intensity	0.686	0.181	3.794	<0.001	
Max. dive depth	Intercept	–68.863	10.753	6.403	<0.001	
	Bathymetry	0.330	0.020	16.257	<0.001	
	Time	4.871	0.621	7.843	<0.001	
	Time ²	–0.195	0.027	7.310	<0.001	
	Foraging: True	16.277	0.493	32.998	<0.001	
	SST	2.612	0.564	4.629	<0.001	
	Thermocline depth	0.013	0.032	0.394	0.694	
	Thermocline gradient	–2.546	1.185	2.148	0.032	
Bottom time	Intercept	–18.779	7.987	2.351	0.019	
	Bathymetry	0.069	0.015	4.568	<0.001	
	Time	2.657	0.461	5.765	<0.001	
	Time ²	–0.132	0.020	6.680	<0.001	
	Foraging: True	12.592	0.367	34.320	<0.001	
	SST	2.186	0.413	5.293	<0.001	
	Descent rate	Intercept	0.279	0.066	8.823	
		Bathymetry	0.003	0.0003	6.239	
Time		0.064	0.011	4.742		
Time ²		–0.002	0.0004	–3.286		
Foraging: True		0.324	0.008	38.276		
Thermocline depth		–0.003	0.0006	–5.439		
Thermocline gradient		–0.141	0.020	–7.327		
Thermocline intensity		–0.001	0.005	–0.300		
Ascent rate	Intercept	–0.332	0.131	2.537	<0.001	
	Bathymetry	–0.005	0.0004	11.449	<0.001	
	Time	–0.047	0.025	1.874	0.061	
	Time ²	0.001	0.001	1.178	0.239	
	Foraging: True	–0.419	0.009	44.191	<0.001	
	Thermocline gradient	0.152	0.023	6.653	<0.001	

models describing dive behaviour in waters where a thermocline was present. In models predicting foraging parameters in relation to thermocline characteristics (see Table S2 in the Supplement), penguins increased their dive depths with the depth of the thermocline, and decreased their dive depth when TG was steeper. Maximum dive depths were further from the thermocline mid-point depth when the thermocline increased in intensity or in depth. Penguins decreased their descent rates when the thermocline was shallow and when the TG was steep. Similarly, their ascent rates decreased when TG was steep, although TI did not seem to influence diving behaviour.

Although there was no significant difference between search and foraging dives in their distance to the thermocline depth, foraging dives had a higher probability of occurring below the thermocline mid-point than above it (Tables 2 & S3, Fig. 5). Search dives showed greater central tendency around the thermocline, with more dives occurring above the thermocline compared to foraging dives (Fig. 5). In 2010, 51 % of dives were foraging dives, whereas this decreased to 35 % in 2011, possibly indicating that prey was scarcer in 2011. Penguins were more likely to dive below the thermocline mid-point when the thermocline mid-point decreased in depth. They also

Table 2. Generalized linear mixed-effect model (GLMM) results showing the model averaged response of African penguin dives occurring below the thermocline mid-point depth as a function of thermocline mid-point depth, intensity and gradient, as well as bathymetry, time of day and its polynomial (Time and Time²), whether the dive was a foraging (Foraging: True) or search dive, and sea surface temperature (SST)

Response	Fixed effect	Estimate	SE	z-value	Pr (> z)
Presence below the thermocline	Intercept	-0.112	0.143	0.784	0.433
	Bathymetry	0.333	0.043	7.7734	<0.001
	Time	0.181	0.074	0.683	0.495
	Time ²	-0.170	0.003	0.649	0.516
	Foraging: True	1.647	0.066	24.910	<0.001
	SST	0.395	0.080	4.953	<0.001
	Thermocline depth	-0.689	0.066	10.376	<0.001
	Thermocline gradient	-0.275	0.049	5.631	<0.001
	Thermocline intensity	-0.048	0.062	0.784	0.433

concentrated their dives above the thermocline when TG increased in steepness, hence in the presence of a more diffuse thermocline (Table 2). TI had no significant effect on whether a dive was above or below the thermocline but the model averaged results suggest that penguins dived below the thermocline when the TI increased. When penguins foraged in waters with increasing SST, the depth of their dive in relation to the thermocline had a higher probability of being below the thermocline mid-point (Table 2). These models had an AUC of 0.79, thus the models predicting dives to be above or below the thermocline have a high classification power.

Finally, penguin dive depth was influenced by SST in waters with a thermocline, with birds diving deeper and with a longer bottom time in relation to higher SST, as well as diving closer to the thermocline (Table 1). Generally, bathymetry had a strong influence on penguin diving behaviour, with birds diving deeper for a longer time, with higher descent

and ascent rates in deeper waters (Table 1). Similarly, foraging dives, i.e. presenting undulations at the bottom, were generally deeper with a longer bottom time, and associated with rapid descent and slow ascent rates (Table 1).

Dive behaviour in mixed water columns

The average temperature at the bottom of foraging dives when there was no identifiable thermocline was $16.8 \pm 1.4^\circ\text{C}$. In the absence of thermoclines, penguin dive depths were influenced by the average water column temperature, increasing their dive depth when waters were on average warmer, as well as when the stratification index increased (Tables 3 & S4). However, in mixed waters birds performed shallower dives with a slower descent rate when SST was high (Table 3). Neither bottom times of dives nor ascent rates were correlated with any of the thermal properties of the water column (average column temperature, SST, or stratification index), but bathymetry strongly influenced foraging behaviour (Table 3).

DISCUSSION

Ocean physical processes create a heterogeneous landscape that top predators can use to locate profitable foraging grounds such as fronts, eddies, currents or upwelling zones. Species that remain at sea for long periods or travel over vast distances tend to use predictable meso- to large-scale features to locate their

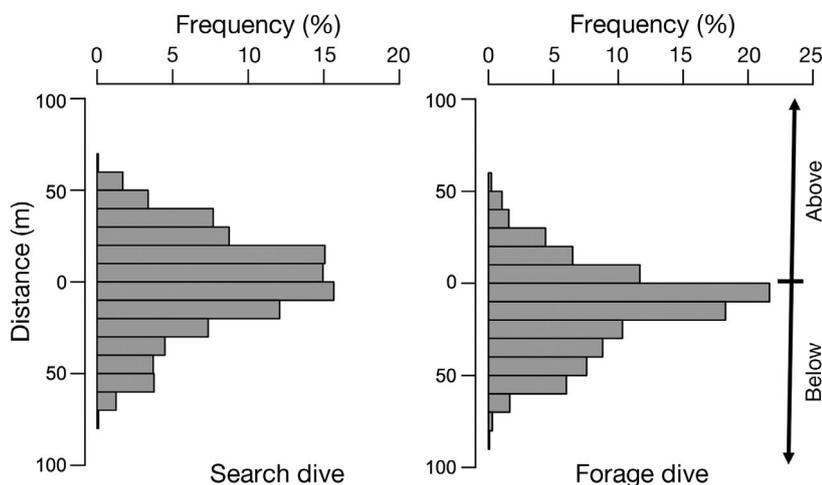


Fig. 5. Distributions of distances of search and foraging dives above and below the thermocline midpoint (0 m)

Table 3. Linear mixed-effects model (LMM) results describing penguin diving behaviour in mixed waters (with no apparent thermocline) as a function of the average water column temperature, water stratification index, bathymetry, time of day and its polynomial (Time and Time²), whether the dive was a foraging (Foraging: True) or search dive, and sea surface temperature (SST). All response variables, except ascent rate, are model averaged estimates. *z*-values are reported only for models that were model averaged, and *t*-values for models that were not model averaged and thus Pr(>|*z*|) values are not reported

Response	Fixed effect	Estimate	SE	<i>z</i> -value	Pr (> <i>z</i>)
Max. dive depth	Intercept	-65.943	28.075	2.347	0.019
	Bathymetry	0.666	0.049	13.512	<0.001
	Time	1.574	1.419	1.109	0.267
	Time ²	-0.136	0.087	1.564	0.118
	Foraging: True	16.403	1.068	15.351	<0.001
	SST	-3.430	2.148	1.597	0.175
	Column temperature	5.028	2.363	2.128	0.033
	Stratification index	2.228	1.148	1.941	0.052
Bottom time	Intercept	-10.824	22.536	0.480	0.631
	Bathymetry	0.199	0.042	4.781	<0.001
	Time	0.900	1.453	0.620	0.535
	Time ²	-0.030	0.065	0.458	0.647
	Foraging: True	13.746	0.857	16.024	<0.001
	SST	0.930	1.413	0.658	0.510
	Stratification index	0.240	0.611	0.393	0.694
Descent rate	Intercept	0.563	0.339	1.1660	0.097
	Bathymetry	0.007	0.001	9.271	<0.001
	Foraging: True	0.296	0.018	16.197	<0.001
	SST	-0.007	0.019	0.397	0.692
Ascent rate	Intercept	-0.303	0.061	-4.996	
	Bathymetry	-0.009	0.0008	-10.380	
	Foraging: True	-0.364	0.021	-17.635	

prey (Charrassin & Bost 2001, Nel et al. 2001, Hyrenbach et al. 2006, Cotté et al. 2007, Bost et al. 2009). It is less well understood how top predators locate prey at finer scales, where such physical features are ephemeral. During our study, Algoa Bay showed high variability in both the SST and the vertical temperature profile of the water column. Strong thermoclines were present where there was upwelling, and these features changed in position and strength as upwelling advanced towards the surface. Storm events and warm water intrusions from the Agulhas Current further influenced the thermal structure of Algoa Bay, presenting a highly heterogeneous and ephemeral marine environment for foraging African penguins breeding on Bird Island.

Habitat preference in relation to surface and bottom features

The waters encountered by African penguins along their individual tracks showed little variation in SST on a daily scale, but habitat preference models showed that penguins avoided warm waters associated with Agulhas Current intrusions and structured

their trips to anticipate cool, upwelled water east and south of Bird Island. Top predators such as king penguins travel down thermal slopes towards fronts or eddies, suggesting that these birds may use thermal slopes as cues to locate preferable foraging grounds (Cotté et al. 2007, Trathan et al. 2008). However, king penguins travel hundreds of kilometers and thus are likely to anticipate more predictable meso-scale features. African penguins have limited ability to predict cooler waters associated with their main prey species, sardines *Sardinops sagax* and anchovies *Engraulis encrasicolus* (Petersen et al. 2006, Pichegru et al. 2012), given the small scale at which the penguins forage (generally <50 km) and the temporal heterogeneity in SST observed in their foraging range during our study. The penguins' prey show preference for waters with SST between 15 and 20°C, and are largely absent from waters with SST >20°C (Barange & Hampton 1997), which in part explains the habitat preference of African penguins for SST of 18 to 20°C. This upper temperature threshold is the typical near shore edge temperature of the Agulhas Current (Goschen & Schumann 1994). Cool waters from the Port Alfred upwelling cell enter the bay from the east and flow southwest around Bird Island (Lutjeharms

et al. 2000). Upwelling visible in SST images in the region around Bird Island occurs for ca. 45% of the year, which reinforces the notion that African penguins in Algoa Bay are confronted by a highly stochastic environment where oceanographic conditions can change dramatically within a few days (Lutjeharms et al. 2000). Furthermore, small pelagic fish surveys have revealed that the biomass of anchovies was highest east and south of Bird Island in 2001 (Barange et al. 2005) and together with SST associations, these processes are likely to govern the habitat preference of African penguins.

African penguins showed little preference for high values of chl *a*. It is generally accepted that chl *a* is a poor indicator of small pelagic fish biomass, as mismatch between upwelling and where seabirds forage can be experienced due to time lag effects in productivity and subsequent shifts in prey distributions (Moloney & Field 1991, Simmons & Cordes 2000, Grémillet et al. 2008). Furthermore, anchovies typically avoid newly upwelled waters where chl *a* concentrations are likely to be lowest given the time lag between nutrient injection into the photic zone and peaks in primary production (Agenbag et al. 2003). Given that African penguins are not strongly associated with chl *a* concentrations, and that they are known to adjust their trip length and time spent at sea in relation to prey availability, this finding further supports the match-mismatch hypothesis (Grémillet et al. 2008, Pichegru et al. 2010). However, subsurface chl *a* may be an important characteristic predicting penguin occurrence (Scott et al. 2010). It is also worth noting that, given the scale and temporal variability in the oceanographic conditions of Algoa Bay, this match-mismatch is most likely further enhanced by such a dynamic system.

Dive behaviour in relation to the thermocline

African penguins actively track thermoclines; not only did their foraging dives increase in depth concurrently with increased thermocline depth, but they modified their descent and ascent rates with TG, increasing their speed when the gradient was steeper (i.e. high Δ temperature/ Δ depth). Faster descent and ascent rates are associated with foraging dives, compared to commuting or search dives in many air-breathing marine predators. Thermoclines with a steeper gradient probably concentrate prey below the thermocline because these are formed as a result of a more pronounced 2-layer system of warm surface waters fronted by cooler bottom waters where

productivity is higher. Therefore, such a 2-layered system provides a strong cue for foraging as birds dive rapidly to reach more productive waters near the thermocline. Similarly, Cape cormorants *Phalacrocorax capensis* have faster descent rates when targeting the benthos, a predictable foraging area, compared to pelagic foraging (Cook et al. 2012). A thermocline that is more diffuse, which occurs when there is mixing of waters above and below the thermocline, is less likely to concentrate prey. Penguins did not react to the intensity of the thermocline (i.e. the temperature change across the thermocline), but only its gradient, unlike northern fur seals *Callorhinus ursinus* (Kuhn 2011) and thick-billed murrelets (Kokubun et al. 2010), which increase their use of the thermocline as its intensity increases. For example, in the Bering Sea, where these species were studied, the intensity of the thermocline and the temperature of the waters below the thermocline are associated with the availability and vertical distribution of prey, which influences predator behaviour (Stabeno et al. 2001, Hunt et al. 2008, Kuhn 2011). African penguin prey are likely to be associated with the cold upwelling that forms the thermocline. A greater thermocline gradient could also provide a reliable cue of prey occurrence, given a rapid change in temperature associated with a greater gradient, while a high TI is not necessarily indicative of a rapid temperature change but rather a large difference in temperature across the thermocline.

Interestingly, dive bottom times did not differ in relation to thermocline structure or depth, suggesting that feeding time was unaffected (even though foraging effort, e.g. dive depth, was) by the thermal structure of the water column. Birds dived closer to the thermocline when SST was higher, which can be expected as thermoclines are reinforced by positive heat fluxes (Largier & Swart 1987) and birds likely associate with cooler waters below the warmer surface mixed waters.

Dive behaviour in mixed water columns

African penguins responded as expected to water temperature when there was no clear thermocline, diving deeper in warmer than cooler mixed waters. Agulhas Current waters, which bring warm mixed waters within the bay, are nutrient poor (Goschen & Schumann 1988) and likely force prey deeper in search of cooler, more nutrient-rich bottom waters. African penguins increased their dive depth in more stratified ('less well-mixed') waters, similarly to little

penguins *Eudyptula minor* (Pelletier et al. 2012). Measuring flipper beats revealed an increase in little penguin foraging effort in mixed waters with low prey encounter rates, suggesting that prey were distributed over a greater depth range, making foraging more challenging. Even though African penguins dived deeper in more stratified and warmer water columns, neither the stratification nor the mixed temperature of these water columns had an effect on their dive bottom times. If bottom time is considered to be a proxy for foraging time, penguins did not spend more time searching or chasing prey in these contrasting conditions. Bottom time has been shown to have a non-linear decrease with depth, as penguins maximize their bottom times regardless of the depth they dive (Wilson et al. 2005). However, because penguins dived deeper in warmer mixed waters, this further highlights the energetic consequences of having to dive deeper to reach prey. Aerial surveys from the northern Eastern Cape to the Natal Bight have shown that foraging activity by top predators, such as Indo-Pacific bottlenosed dolphins *Tursiops aduncus*, long-beaked common dolphins *Delphinus capensis*, and cape gannets *Morus capensis*, shift inshore as SST offshore increases, presumably because small pelagic fish move inshore in response to these waters remaining cooler (O'Donoghue et al. 2010). However, this effect may not be observed due to the continental shelf extending further south in Algoa Bay, and in the presence of a warm water wedge intruding into the bay, pelagic prey may instead migrate to deeper depths, thus influencing penguin dive behaviour.

Descent rates were higher when foraging, suggesting that birds focused their dive effort (as was also seen with bottom times) when foraging. Descent rates were lower during times of increased SST, thus relatively high SST which is closely linked with Agulhas Current intrusions could reduce the availability of prey to African penguins, resulting in reduced dive speeds towards targeted fish shoals.

CONCLUSIONS

African penguins in Algoa Bay forage in a highly variable marine environment and have adapted to cope with this variability when locating prey by using temperatures specific to those of their main prey species on small temporal and spatial scales. Given the declines in African penguin populations, further variability may, however, limit their ability to locate accessible prey and consequently increase the

energetic costs of finding prey. To further improve our understanding of how African penguins find scarce and patchy food resources, an ecosystems approach is required to construct models of marine food webs and the processes that govern primary production through to pelagic prey assemblages and finally top predator behaviour. Very little is known of how small pelagic prey respond to the oceanography of Algoa Bay, and this limited our study to draw on specific predator–prey interactions; however, penguin behaviour can help us infer the likely habitat preference of their prey. This study also presents an important opportunity to predict how changes in the Algoa Bay oceanography due to climate change may impact the conservation and survival of one of its top predators and most iconic species.

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