

Original Article

The relationship between coastal weather and foraging behaviour of chinstrap penguins, *Pygoscelis antarctica*

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There is increasing interest in using higher-trophic level predators as ecosystem indicators because their performance is presumed to be linked to the overall function of the ecosystem that supports them. In the southwest Atlantic sector of the Southern Ocean, Antarctic krill (*Euphausia superba*) supports huge predator populations as well as a growing commercial fishery. To utilize information from the ecosystem in an adaptive framework for sustainably managing krill catch levels, performance indices of krill predators have been proposed as a proxy for krill abundance. However, there are several potentially confounding sources of variability that might impact predator performance such as the effects of environmental variability and fishing pressure on krill availability at scales relevant to predators. In this context, our study capitalises on the occurrence of an unexpected *El Niño* event to characterise how environmental variability can drive changes in predator foraging behaviour. We demonstrate a clear link between coastal downwelling and changes in the at-sea habitat usage of chinstrap penguins (*Pygoscelis antarctica*) foraging in a local krill fishing area. Penguins tracked from their breeding colonies on Powell Island, Antarctic Peninsula, undertook fewer, longer foraging trips during the downwelling-affected season compared with the season where no such downwelling was detected, suggesting that changes in climate-driven oceanography may have reduced krill availability along the northern shelf of the island. Our study demonstrates that penguin foraging behaviour is modified by scale-dependent processes, which if not accounted for may result in erroneous conclusions being drawn when using penguins as bioindicators of krill abundance.

Keywords: Antarctic krill, bio-indicator, central place forager, chinstrap penguin, oceanographic processes, prey availability

Introduction

The operationalization of ecosystem-based management (EBM) has proved to be challenging (de Groot *et al.*, 2010) not least because of the difficulty in distilling complex ecosystem processes into a set of realistically measurable variables from which management-oriented information can be extracted (Yoccoz *et al.*, 2001). EBM is underpinned by the need to understand the full suite of interactions within ecosystems in the face of potentially confounding factors such as intra- and inter-specific competition and climate change (Pauly *et al.*, 1998).

The commercial exploitation of Antarctic krill (*Euphausia superba*, henceforth krill), represents one fishery that does not yet appear overexploited, with catch levels under 0.5% of the estimated stock size in the area fished (Nicol and Foster, 2016).

However, from a relatively stable catch of 120 000 tonnes per year until 2009 (Nicol *et al.*, 2012), the fishery has increased to ~300 000 tonnes in the last 9 years (Hinke *et al.*, 2017). Krill is a keystone species in the ecosystem of the southwest Atlantic sector of the SO, supporting huge populations of marine predators as well the fishery (Constable *et al.*, 2000). Many of the marine predator species reliant on krill are central place foragers (CPF) during their breeding seasons, alternating between feeding at sea and attending their land-based dependent offspring. Food in the marine environment is patchily distributed, thus CPF are often considered to optimize the time spent foraging versus travelling in order to maximize their net energy gain (Watanabe *et al.*, 2014). Given the difficulties of directly observing predator–prey relationships at sea, the predicted

responses of CPF to changes in food availability and distribution coupled with the need for them to return to land provides an opportunity to collect measurements of performance, which in turn may be useful as bio-indicators of ecosystem function (Boyd *et al.*, 2001).

There are three broad requirements that must be satisfied for bio-indicators to be useful and appropriate: (i) the metrics recorded should not be confounded by other variables and thus reflect key attributes of the ecosystem; (ii) the indicators should respond quickly to (and subsequently recover from) perturbations in the ecosystem; and (iii) the indicator should reflect conditions over relevant spatial scales (Hilty and Merenlender, 2000; Holt, 2010). Commensurate with satisfying these requirements is a large body of literature that suggests how useful marine CPF, such as seabirds, are as indicators of prey abundance (Cairns, 1987; Piatt *et al.*, 2007; Durant *et al.*, 2009). Central to this theme is defining the functional responses of predators to changing prey availability at relevant temporal and spatial scales, under the confounding effects of climate variability and fishing pressure (Piatt *et al.*, 2007). For example, as the breeding season progresses and dependent chicks become more energetically demanding, adult penguins become increasingly restricted as they supply the growing demands of their offspring whilst minimizing deterioration of their own body condition (e.g. Kokubun *et al.* 2010). Thus, performance indices of CPF foraging behaviour during the breeding season integrates information on krill availability over scales dictated by an animal's life history and reproductive strategy. However, the drivers of changing prey availability at fine scales are difficult to determine, as fisheries information and stock assessments are usually carried out at much larger scales (Cury *et al.*, 2011), and the effects of environmental perturbation on krill swarm dynamics is poorly resolved (Tarling and Fielding, 2016).

Yet in the context of using signals from CPF to inform on krill abundance, correctly interpreting what modifies foraging behaviour is crucial to making meaningful management decisions. With this in mind, and capitalizing upon the occurrence of an *El Niño* event, we quantified how extreme weather events influenced the foraging behaviour of a CPF in the absence of fishing pressure. To achieve this, we considered two interdependent questions using chinstrap penguins as our model CPF species: (i) do the prevailing climatic conditions impact how far and for how long penguins remained at sea in search of food? (ii) If so could a detectable, biologically plausible mechanistic link be found with attributes of the physical environment. Given the spatiotemporal constraints chinstrap penguins face during breeding, we hypothesized that extreme weather events such as those that can occur during an *El Niño* could modify local oceanographic conditions and, in turn, alter the distribution of their prey field. Specifically, increased wind speeds for prolonged periods could produce sufficient downwelling of coastal waters, leading to the advection of krill off the shelf into the open ocean.

Material and methods

Our study was conducted on Powell Island in the South Orkney Islands Archipelago (Figure 1) from 28 December to 8 February during the austral breeding seasons of 2013–2014 and 2015–2016, henceforth referred to as the 2014 and 2016 seasons, respectively. The 2016 season was characterized by the second-largest *El Niño*

event on record (Jacox *et al.*, 2016). The prevailing current along the northern shelf is from east to west (Heywood *et al.*, 2004), and all fishing activity during the study was conducted downstream of the area in which penguins foraged; hence the fishery did not impact the birds in our study.

Geospatial data were collected for breeding chinstrap penguins that were observed to be actively provisioning at least one chick at the time of instrumentation. Individual birds (2014: $n = 36$; 2016: $n = 38$) were fitted with highly accurate global positioning system (GPS) loggers (Fastloc F2G or Fastloc F3G, Sirtrack Ltd, Havelock, New Zealand) for at least 5 d (including at least one foraging trip), attached using a combination of Tesa tape© and Loctite© glue. Instruments were programmed to attempt a location fix every 4 min or as soon as possible after surfacing from a dive (wet), and to record one location every 2 h once onboard saltwater switches registered the instrument as being onshore (dry) for longer than 2 h. Colonies were inspected daily for the presence of instrumented birds, and after an individual had been absent for at least 5 d its instrument was recovered.

Data analysis

Chinstrap penguin location data processing

Geospatial data were downloaded using proprietary software (Sirtrack and Pathtrack Archival GPS Version 1.11). Individual location data were then partitioned into discrete foraging trips using the first and last saltwater switch-derived at-sea locations and then linearly interpolated along its length at 4-min intervals.

Upwelling index from locally recorded meteorological data

Meteorological data from the Argentinian Base Orcadas on nearby Laurie Island (Figure 1) were used to derive an upwelling index (UI) over the northern shelf during each study period. Data were downloaded from the Citizens Weather Observer Program (www.wxqa.com), providing wind speed (m s^{-1}) and direction ($^{\circ}$), air temperature ($^{\circ}\text{C}$), barometric pressure (mbar) and dewpoint ($^{\circ}\text{C}$) measurements every 3–12 h. Optimal autoregressive integrated moving average models were then fitted to each irregular time series through minimization of model AICc in the R package “forecast” (Hyndman and Khandakar, 2008). The resulting models were then used to generate a regularized (3 h) time series for each variable. The zonal (v , east-west) and meridional (u , north-south) components of Ekman transport, Q , can be estimated in terms of wind speed (W_u and W_v), seawater density (ρ_w , 1025 kg m^{-3}), a unitless drag coefficient (C_d , 1.4×10^{-3}) and air density (ρ_a), derived iteratively through the meteorological dataset by decomposing the dewpoint into air partial pressure and subsequently calculating its density using the equation of state of a hypothetical gas (González-Nuevo *et al.*, 2014):

$$Q_v = \frac{\rho_a C_d}{\rho_w f} \sqrt{(W_u^2 + W_v^2)} W_u,$$

$$Q_u = \frac{\rho_a C_d}{\rho_w f} \sqrt{(W_u^2 + W_v^2)} W_v.$$

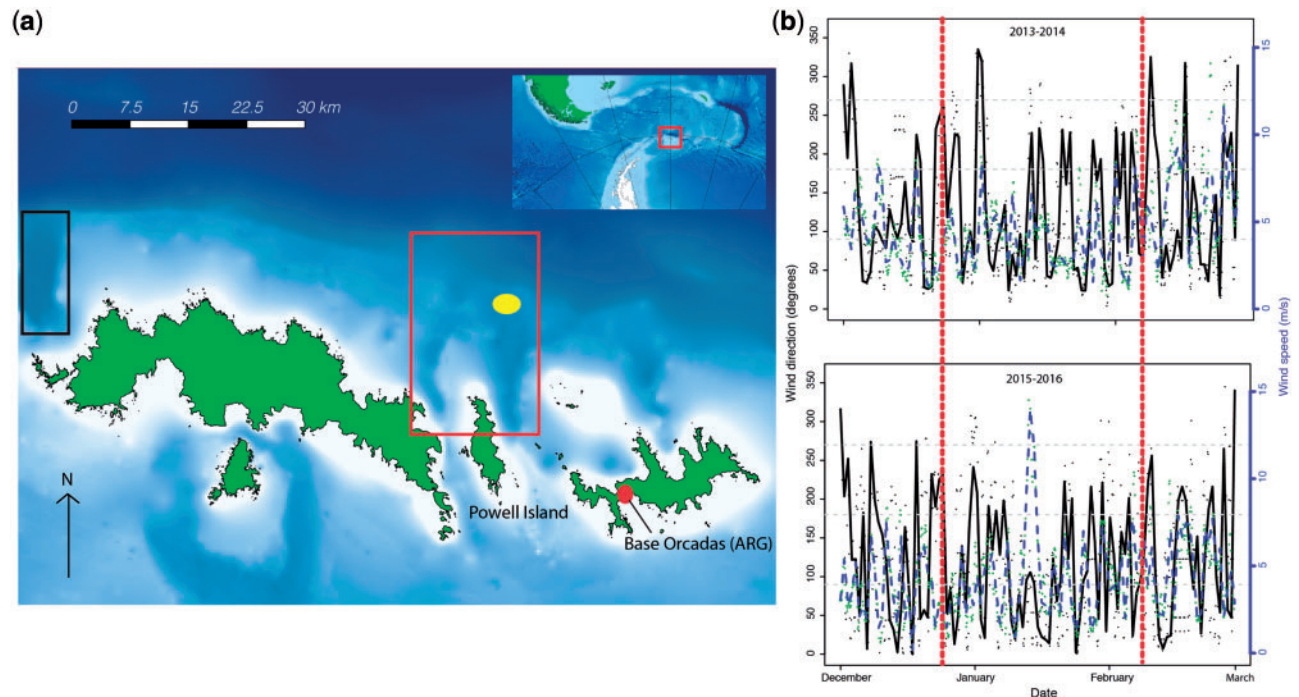


Figure 1. (a) The South Orkney Islands lie at the southern edge of the Scotia sea, east of the west Antarctic Peninsula (inset). The archipelago is characterized by a north facing shelf punctuated along its length by a series of submarine canyons rising from the southern Scotia Sea. Powell Island lies between Coronation Island to the west, and to the east is Laurie Island, and the Argentinian Base Orcadas from which meteorological data were available. (b) Three-hourly predictions of wind speed (dark grey (blue, in color version available online)) and direction (black) modelled from raw data (black and white dots, respectively) during 2014 (top panel) and 2016 (bottom panel). Horizontal dashed grey lines depict west, south, and east (top to bottom, respectively). Satellite derived-comparative measurements of wind speed and direction were acquired at the mouth of the canyon to the north of Powell Island (approximate position highlighted by the grey (yellow in color version available online) dot). Vertical (red vertical in color version available online) dashed lines highlight the period over which the study was conducted in each season. During the study period in 2016, winds were from a more southerly and easterly direction than in 2014, with a pronounced easterly wind during the latter half of January.

The Coriolis frequency f is defined as the product of twice the rotational rate of the earth (Ω , radians s^{-1}) with the sine of the latitude at which it is calculated (ϕ ; González-Nuevo *et al.*, 2014):

$$f = 2\Omega\sin(-\phi).$$

The coastal UI, in the context of a north-facing shelf in the southern hemisphere, is defined as the meridional component of Ekman transport per 100 m of coastline (Bakun, 1975; Jacox *et al.*, 2014) with positive (negative) values representing upwelling (downwelling). A rolling 1-d average UI was calculated to characterize the oceanographic processes throughout each season. We also used Levene's Test to determine whether the variability in predicted UI was comparable between years, reporting significantly different variability at $p < 0.05$.

UI from remotely sensed meteorological data

Given that data exploration suggested an interplay between the weather and penguin foraging behaviour at fine spatial scales, we explored whether remotely sensed data from satellites could be used to detect similar anomalies. Satellite-derived climate data recovered from scatterometer instrumentation (MetOp-A ASCAT Level 2 platform) covering the two seasons at a 12.5- and 25-km sampling and effective resolution, respectively, were downloaded at a position closest to the southern-most point of the small submarine canyons to the north of Powell Island (Figure 1) from the Physical

Oceanography Distributed Active Archive Center of the National Aeronautics and Space Administration Jet Propulsion Laboratory (<http://podaac.jpl.nasa.gov/dataset/ASCATA-L2-Coastal>). Like the Orcadas Base meteorological measurements, these data are collected as an irregular time series (at ~ 1.5 h time intervals) and were thus analysed in the same manner. We add the caveat that the two sources of weather data were not spatially congruent—the *in situ* data were collected several kilometres from the marine foraging grounds whereas the remotely sensed data were extracted from a location on the northern shelf. We thus caution readers that our results are interpreted in this context.

Variation in penguin foraging behaviour relative to hydrographic stochasticity

Exploration of the calculated UI between the 2 years revealed a strong downwelling signal that was detectable over ~ 2 weeks during the 2016 season (Figure 2). The approximate dates bracketing this event (10–28 January) were used to partition the penguin tracking data into two discrete periods (henceforth downwelling and post-downwelling, respectively). Trip distances and durations conducted after the event were compared across years. All adult birds included in the downwelling period group were in the brood-guard phase of breeding. Assessment of the degree of support for mean differences in foraging trip durations and distances were performed using a Bayesian approach (Kruschke, 2012) using a Gibbs resampler (R package “rjags” v.4-6) with 50 000

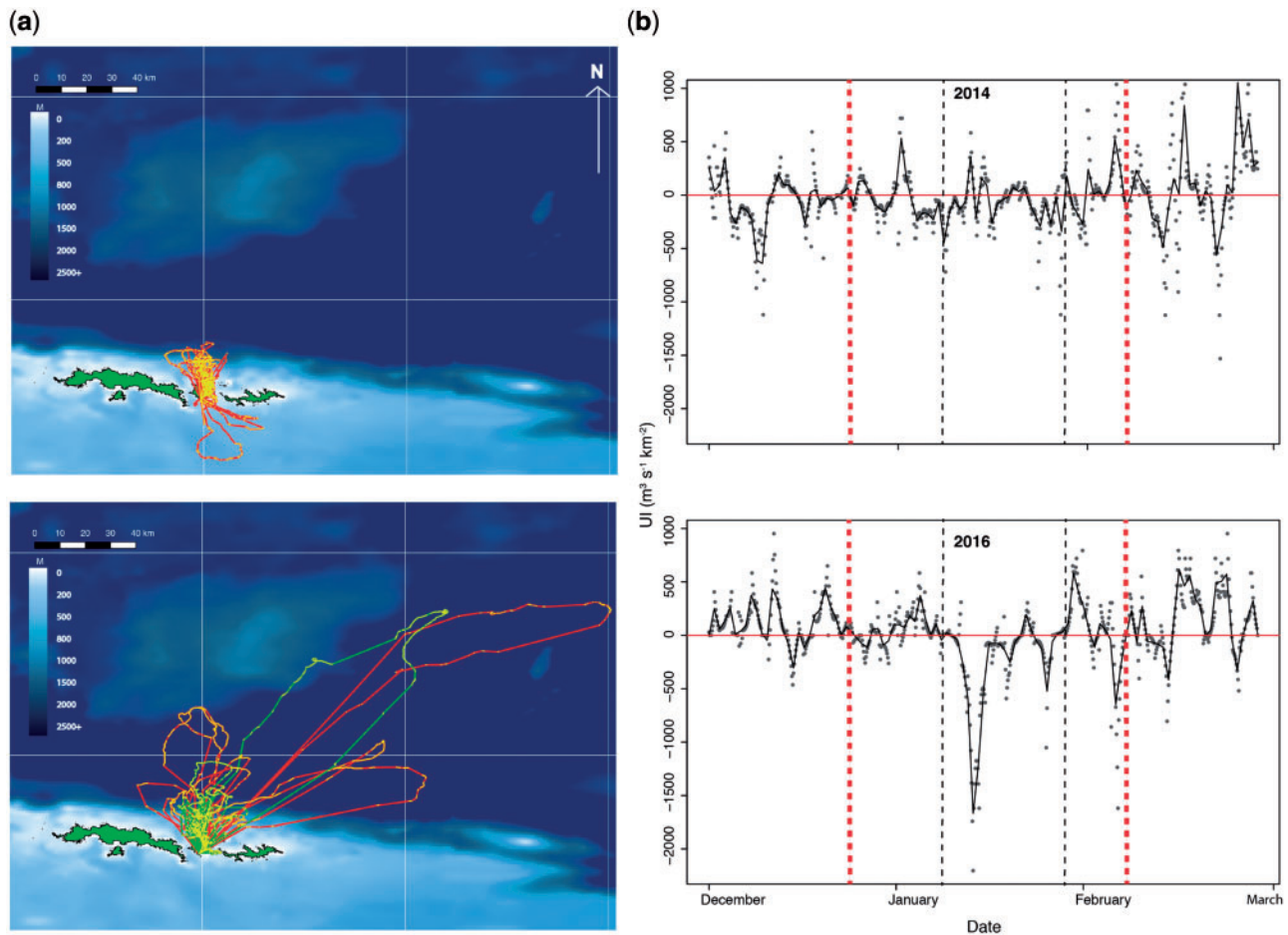


Figure 2. (a) The at-sea GPS location data of adult Chinstrap penguins during 2014 (total $N = 36$, top panel) and 2016 (total $N = 38$, bottom panel) instrumented on Powell Island, colour coded to facilitate comparison of movement during the downwelling period (10–23 January—red) and afterwards (24 January–8 February—green). Yellow dots reflect along-track estimates of ARS. (b) The corresponding UI as a 1-d rolling mean of the meridional component of Ekman transport estimated from Kalman filtered weather station data provided by the Argentinian Base Orcadas situated ~ 14 km to the east on Laurie Island. Grey dots represent the UI derived from the raw, unfiltered weather data. Positive (negative) UI values signify the upwelling (downwelling) of water northwards from the northern shelf of the South Orkneys (red horizontal line to aid visualizing a zero UI value). Red vertical dashed lines bracket the period over which instrumented penguins provided location data. The longer foraging trips conducted by Chinstrap penguins during the latter half of the 2015–16 season coincided with a prolonged and substantial downwelling signal (black vertical dashed lines, 10–23 January each year).

Markov Chain Monte Carlo iterations after a burn-in of 1000 iterations. Utilization distributions of at-sea habitat were estimated using the Brownian Bridge approach, which accounts for temporally auto correlated data (Horne *et al.*, 2007) using the R package “adehabitatHR” (Calenge, 2006). We also explored whether variability in the physical environment predictably modified penguin foraging behaviour in line with the expectations of optimal foraging theory. Area restricted searching (ARS) behaviour, assumed to represent foraging along the track of each foraging trip, was estimated from a two-state (ARS or transit) hidden Markov model using the R package “moveHMM” (Michélot *et al.*, 2016), and the proportion of each foraging trip spent in ARS was then estimated for each individual. Additionally, we determined whether the downwelling event in 2016 led to increased ARS over deeper, more oceanic waters in response to a hypothesized decreased availability of krill in coastal waters. Ocean depth under ARS and transit locations were extracted from a 500-m resolution bathymetry dataset (Arndt *et al.*, 2013). Generalized

additive mixed models were used to characterise how the binomially distributed movement behaviour of individuals (ARS or transit) changed with respect to bathymetry between the study periods, using bathymetry and year as fixed effects, a first-order autocorrelation structure to account for serially correlated movement data, and separate foraging trips nested within individual ID as a random effect (R package “mgcv”). All values are reported as mean \pm credible interval (CI) and the degree of support for differences in mean values are reported as Bayesian posterior probabilities (B_{pp}) unless otherwise stated. All analyses were conducted using the statistical language R 3.3.1 (R Core Team, 2016).

Results

During the period 10–23 January 2016, a protracted period of east to south-easterly winds prevailed, ranging from 6 to 15 m s^{-1} (Beaufort Scale 3–7; Figure 1) generating a strong, negative UI signal, which is interpreted as downwelling of surface water off the shelf northwards into the Scotia Sea (Figure 2). This was in marked contrast to the

Table 1. Summary statistics of individual mean number ($\pm SD$, N), durations (h), distances (km), utilization distribution (UD, km²), and the proportion of time spent in ARS of breeding Chinstrap penguin foraging trips conducted between 10 January and 8 February 2014 and 2016, respectively.

	10–23 January \bar{x} ($\pm SD$, n)	24 January onwards \bar{x} ($\pm SD$, n)	10–23 January (downwelling) \bar{x} ($\pm SD$, n)	24 January onwards \bar{x} ($\pm SD$, n)	Degree of support B_{pp} , \bar{x} (CI)
Trips (n)	2.7 (1.98, 38)	3, 3 (15.7, 75)	1.8 (0.6, 20)	1.9 (0.69, 24)	<0.001, 1.4 (0.58, 2.2)
Duration (h)	18.7 (9.69)	16.6 (11.96)	38.2 (31.11)	26.2 (25.91)	<0.001, 16 (2.7, 30) 0.06, 5.2 (1.7, 13)
Distance (km)	52.1 (33.72)	30.6 (35.6)	139 (118.91)	64 (84.96)	< 0.001, 88 (33, 147) < 0.01, 33 (8.5, 59)
UD (km²)	13.9 (10.32)	10.6 (10.3)	45.3 (39.1)	26.4 (35.4)	0.001, 28 (11, 46) 0.002, 11 (3.9, 18)
ARS (%)	39.7 (18.8)	33.9 (21.6)	43.9 (16.1)	42 (22.1)	No support

The dates characterizing a strong downwelling event in 2016 are used to partition summary data from foraging trips conducted during (10–23 January) and after the downwelling event (24 January to 8 February). Adult birds were observed to be guarding chicks at the time of instrumentation with high resolution GPS tags, and each individual was tracked for at least one complete foraging trip. Average UD was constructed using Brownian Bridge movement models. Where there was strong supporting evidence (Bayesian posterior probability $B_{pp} < 0.90$), mean differences in matched values (identified by common superscript symbols) and their corresponding credible intervals (CI) are presented. Adult birds from both years conducted the same number of foraging trips during the downwelling event; however, there was strong support for birds in 2016 conducting longer trips of greater duration, and utilizing a greater area of at-sea habitat than conspecifics in 2014. These trends continued into the post-downwelling period, with the exception of strong evidence that birds in 2016 conducted fewer trips than those in 2014. Interestingly, birds on average spent the same proportion of each foraging trip engaged in ARS between and within the two years.

conditions recorded during the same period in 2014 (Figures 1 and 2). Additionally, the UI in 2016 was much more variable than in 2014 ($F_{19,37} = 0.07$, $p < 0.001$, 95% CI = 0.03–0.15). The downwelling event was undetectable using satellite-derived climate data over the same period (Supplementary Figure S1).

Comparative summary statistics for the mean number, distance and duration of foraging trips conducted by breeding chinstrap penguins and the proportion of time spent in ARS between the 2 years are presented in Table 1. During the downwelling period in 2016, the penguins conducted approximately the same number of trips as their 2014 conspecifics, but they travelled further and stayed at sea longer on each trip (Table 1; Figure 2). In both years the penguins spent approximately the same proportions of at-sea time engaged in ARS behaviour (Table 1), but during the downwelling period in 2016 the birds covered almost 30 km² more at-sea habitat on each trip (Table 1; Figure 1). Additionally, the birds tracked during the post-downwelling period in 2016 conducted fewer trips compared with their 2014 conspecifics (Table 1).

During the 2016 downwelling event, individuals displayed a bimodal preference in the depths at which they conducted ARS [GAMM $F_{(\text{smooth bathymetry})} = 372.6$, $p < 0.001$; Figure 3]. In contrast, during the same period in 2014 chinstrap penguins foraged predominantly within the two canyons along the shelf north of Powell Island (Figures 1 and 2), though they appeared to prefer water depths in the upper regions of the canyons (Figure 1; GAMM $F_{(\text{smooth bathymetry})} = 202.8$, $p < 0.001$; Figure 3). Over 50% of all estimated ARS locations were in water deeper than 4000 m during 2016, compared with <6% during 2014 (Table 1; Figure 3).

Discussion

We present clear evidence supporting scale-dependent impacts of environmental stochasticity on the movement behaviour of a centrally foraging marine predator. We echo the sentiment of others (Ropert-Coudert et al., 2009; Dehnhard et al., 2013) that neglecting to account for the effects of local-scale climatology may hinder our capacity to understand how and why predators vary their foraging behaviour. Importantly, the environmental perturbation

we describe using meteorological measurements from an *in situ* weather station could not be reproduced using satellite-sensed climatological data. While the wind directions generally matched those recorded *in situ* this was not the case with wind speed as higher speeds were underrepresented in the ASCAT data. This is not surprising, given that scatterometer measurements become confounded with proximity to the coast (Bentamy et al., 2008), as well as by the presence of precipitation (Portabella et al., 2012). Consequently, at least in the current study, it appears that satellite-derived meteorological data are unable to resolve environmental variability at a scale relevant to breeding penguins. The implications for this are twofold: (i) unless scale-relevant *in situ* environmental data are collected concurrently with predator data, it will remain difficult to determine the drivers of response by predators; and (ii) relying exclusively on remotely sensed environmental data that are of an inappropriate scale or resolution is likely to lead to Type II errors in identifying response drivers.

Our data suggest that wind-driven downwelling occurred on the northern shelf of Powell Island during a critical period within the chinstrap penguin breeding season in 2016. Krill are not passive in their three-dimensional movement (Richerson et al., 2015), and can actively pursue primary food sources, diatoms, which do move passively. Thus, krill likely optimises between conditions suitable for feeding and growth and avoiding predation (Atkinson et al., 2008). Coastal areas and seabed topography near subantarctic islands represent static features against, which prevailing oceanography can provide conditions for increased productivity via upwelling of nutrients. This can lead to conditions during which diatoms can bloom (Anderson et al., 2009) and in turn can attract krill (Santora et al., 2016). Predators probably use cues to locate predictable oceanographic features, timing their arrival and departure with seasonal upwelling (Croll et al., 2005). Conversely, changes in wind-driven coastal oceanography that depresses productivity strongly impact euphausiid growth rates and abundance (Ambriz-Arreola et al., 2012). Consequently, the downwelling we describe here presumably resulted in poor feeding conditions for krill in and around the submarine canyons

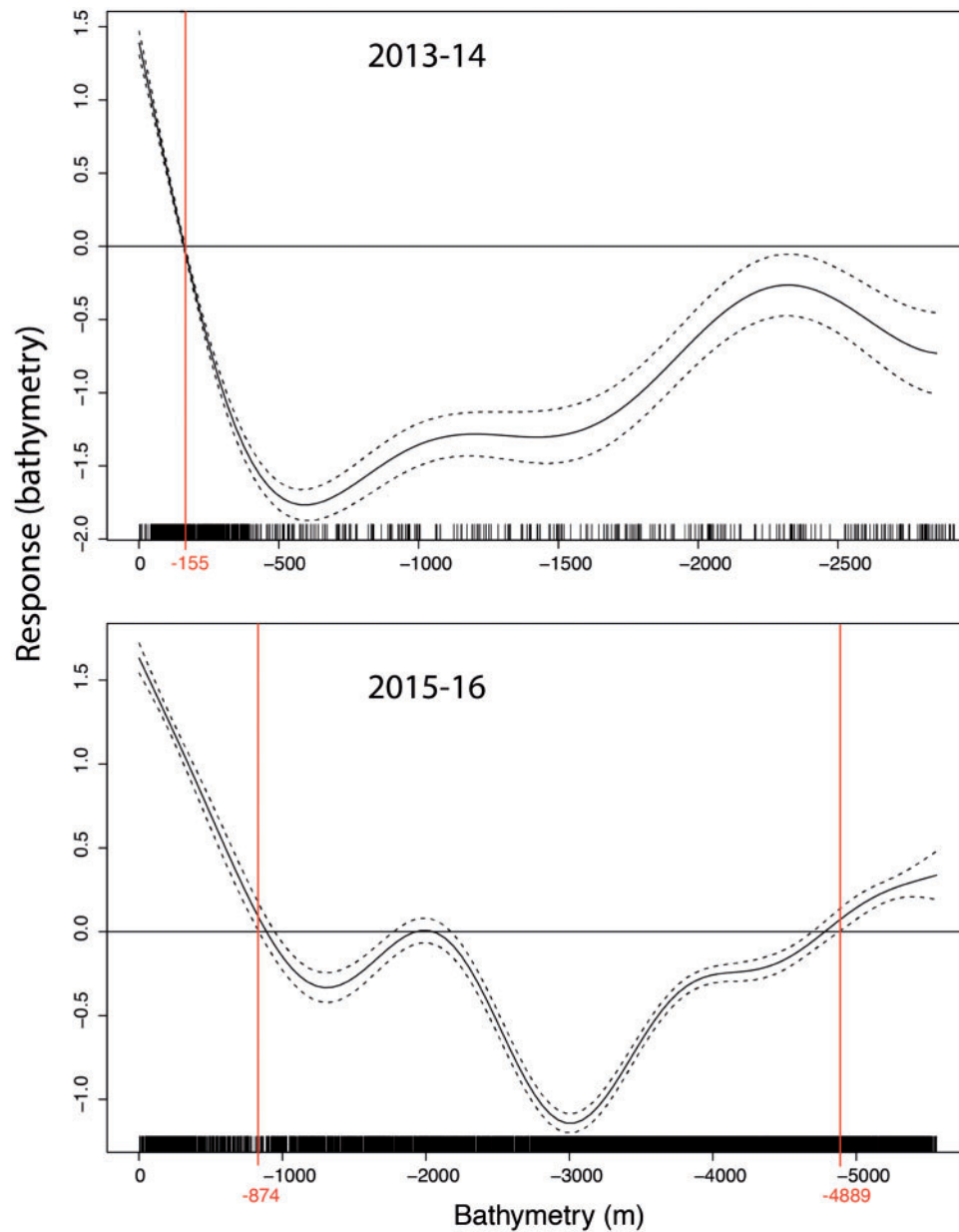


Figure 3. Modelled at-sea ARS response of adult chinstrap penguins to bathymetric depth during the 2014 (top) and 2016 (bottom) instrumentation periods. Red vertical lines and attending values highlight the inflection point of ARS preference relative to depth. During the 2014 season, adults preferentially conducted ARS over shallow water at the mouth of the northern submarine canyons. In contrast, a bimodal trend was observed in 2016, with birds foraging in depths consistent with the outer shelf break or over the ocean abyss (>4500 m).

at the northern shelf of Powell Island, forcing the penguins to travel further and for longer in search of food. Interestingly, the 2016 cohort of tracked penguins continued to prolong their foraging trips after the downwelling signal dissipated, instead of returning to levels comparable with animals instrumented in 2014. Whether this was owing to a continued poor abundance of krill from the coastal areas or an attempt to recover from the poor conditions experienced during the downwelling event is unknown, though our data show a prolonged response to this environmental perturbation.

Although small krill swarms can aggregate around coastal and shelf areas; the large swarms have an oceanic existence, living over water depths >2000 m (Atkinson *et al.*, 2008). However,

away from neritic areas, there is a much lower overall density of krill and a more patchy distribution (Atkinson *et al.*, 2008). Under one of the key optimal foraging models, marginal value theorem (MVT), time spent in ARS presumably searching for and acquiring food should vary in response to the quality of the krill patch encountered, to balance net energy gain with travel time (Charnov, 1976; Watanabe *et al.*, 2014). Thus, over the short-term animals remain in high quality patches until the patch is depleted and the rate of food intake equals the average longer-term intake rate across several patches. In coastal environments under favourable environmental conditions, krill swarms are abundant and predictable, a fact exploited by CPF and commercial fishers alike in their selection of fishing grounds (Santora *et al.*, 2010;

Santora and Veit, 2013; Krafft *et al.*, 2015). Consequently, MVT would predict that predators reduce their patch residency (ARS) time in favour of exploiting other patches. Conversely, when conditions are unfavourable and krill is sparse or absent from predictable features, such as the shelf or shelf break, predators should increase short-term residency time in a patch as the pay-offs are greater than travelling longer between patches. In our study across both seasons, penguins spent the same proportion of time during each foraging trip in ARS, though in 2016 individuals performed longer trips spending more time looking for food. There were also distinct preferences for foraging in shallower, coastal waters in 2014 that were not apparent in 2016 and birds in the latter period showed a bimodal preference for foraging in deeper waters. Consequently, our data are in line with the predictions of MVT that penguins may have been foraging in a patchier oceanic environment in 2016 and needed to increase their time spent in ARS therefore to maximize krill intake. Whether this adjustment was sufficient to balance energy budgets is unknown.

Generally, CPF respond to decreases in prey availability by spending longer periods at sea and travelling further in search of food before having to return to land (Boyd, 1999), though this foraging plasticity is limited by the ability of offspring to fast (Boersma and Rebstock, 2009). During the guard and crèche stages of breeding, penguins are tightly constrained in the duration they can be away from offspring. Chinstrap penguins breeding at nearby Signy Island travelled up to 55.6 km during peak breeding (Lynnes *et al.*, 2002), a similar distance to adults in the current study in 2014. Elsewhere across the species range and during the same stage of breeding, adult chinstraps travelled only a mean maximum of 14.97–21.64 km across two seasons at the South Shetland Islands (Kokubun *et al.*, 2010) and only 10 (± 12) km at Bouvetøya in the South Atlantic (Blanchet *et al.*, 2013); this suggests that there is considerable plasticity in foraging behaviour in this species. Importantly in the current study, during 2016, adult birds travelled between 3 and 10 times the maximum distances commonly reported for chinstrap penguins elsewhere. Our study lacked data to test whether the profound differences in movement behaviour ultimately led to a demographic response. However, other penguin species exhibited negative relationships between breeding success, adverse weather events and food availability, typically characterized by increased foraging trip distances and durations, nest desertions and increased chick mortality (Bost *et al.*, 2015).

Our study also highlights the challenges of interpreting and extrapolating behaviour from telemetry studies of wild animals, particularly in the absence of appropriate explanatory data. In the context of marine CPF, prey availability can be considered as a product of absolute abundance, depth, patchiness in the environment and distance from the breeding colony (Boyd *et al.*, 2016). Thus, predator responses to prey availability occur at the spatial and temporal scales over which the predator can operate, given its physiological and life history constraints. Seabirds are often cited as CPF that are suitable bio-indicators of marine food supplies (Piatt *et al.*, 2007), particularly in relation to EBM of fisheries *sensu* CCAMLR. Using multi-species approaches and considering a wide range of indicator metrics, both Reid *et al.* (2005) and Piatt *et al.* (2007) suggested that foraging trip durations may be a useful within-season indicator of prey availability, as its response threshold probably scales with a minimum prey density above which individuals can meet their energy budgets. Penguin foraging trip duration may therefore be an appropriate

indicator for assessing the variability in prey availability over a scale of a few 10s of kilometres (Reid *et al.*, 2005). For example, assuming our data reflects changes in the availability of prey to chinstrap penguins, the location and timing of our study, as well as the availability of fine-scale local meteorological data, allowed us to rule out fishing pressure and to identify wind-driven downwelling as a biologically plausible cause. Environmentally driven functional responses at the scale of individual foraging trips are described in other centrally foraging marine species from areas that are not exposed to fishing pressure and that are relatively rich in remotely sensed environmental data (Carroll *et al.*, 2016). However, in regions such as the SO where krill fishing broadly overlaps with predator foraging habitat (Hinke *et al.*, 2017), and environmental data at a scale and resolution relevant to predators is absent or not considered, disentangling the cause of prey depletion will remain challenging. Our study reinforces the critical need for *in situ* climate data to be collected alongside CPF performance indices to address this challenge. Such data are easy and relatively inexpensive to collect if, for example, archival weather stations were incorporated with the remote camera network currently being deployed to collect information on penguin breeding phenology at monitoring sites in the SO (Southwell and Emmerson, 2015). Ultimately, testing these hypotheses will require actual information on prey abundance and distribution, rather than proxies that may or may not be accurate indicators of prey resources.

Conclusions

The second year of our study was conducted in the middle of a strong yet short-lived *El Niño* event, a climactic event that leads amongst other things to increased wind speeds from variable directions. These events strongly impact the marine environment and are predicted to increase in frequency as the global climate continues to change (Raphael *et al.*, 2016). Predator foraging datasets that can help elucidate the impact of extreme climate events are rare as studies cannot be planned *a priori*, but as climate variability increases marine predators are likely to experience such impacts with increasing regularity. Long-term datasets are now describing demographic responses to environmental variability (e.g. Bost *et al.* 2015) and, encouragingly, new wildlife instrumentation and advanced statistical treatments are making functional responses easier to quantify (e.g. Piatt *et al.* 2007) such that centrally foraging predators may become increasingly useful as indicators of ecosystem status. However, the behavioural plasticity of a species to the magnitude and duration of the environmental perturbation will likely be important in considering its utility as a bioindicator. The results of our study show that hypothesized decreases in prey at scales over which chinstrap penguins operate might be induced by natural variation in oceanographic conditions, independent of any fisheries influences. Clearly, several hurdles remain before such bioindicators can transition into fisheries management tools.

Supplementary data

Supplementary material is available at the ICES/JMS online version of the manuscript.

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