

## Managing fishery development in sensitive ecosystems: identifying penguin habitat use to direct management in Antarctica

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**Abstract.** In the Southern Ocean, the at-sea distributions of most predators of Antarctic krill are poorly known, primarily because tracking studies have only been undertaken on a restricted set of species, and then only at a limited number of sites. For chinstrap penguins, one of the most abundant krill predators breeding across the Antarctic Peninsula, we show that habitat models developed utilizing the distance from the colony and the bearing to the shelf-edge, adjusting for the at-sea density of *Pygoscelis* penguins from other colonies, can be used to predict, with a high level of confidence, the at-sea distribution of chinstrap penguins from untracked colonies during the breeding season. Comparison of predicted penguin distributions with outputs from a high-resolution oceanographic model shows that chinstrap penguins prefer nearshore habitats, over shallow bathymetry, with slow-flowing waters, but that they sometimes also travel to areas beyond the edge of the continental shelf where the faster-flowing waters of the Coastal Current or the fronts of the Antarctic Circumpolar Current occur. In the slow-moving shelf waters, large penguin colonies may lead to krill depletion during incubation and chick-rearing periods when penguins are acting as central place foragers. The habitats used by chinstrap penguins are also locations preferentially used by the commercial krill fishery, one of the last under-developed marine capture fisheries anywhere on the planet. As it develops, this fishery has the potential to compete with chinstrap penguins and other natural krill predators. Scaling our habitat models by chinstrap penguin population data demonstrates where overlap with the fishery is likely to be most important. Our results suggest that a better understanding of krill retention and krill depletion in areas used by natural predators and by the krill fishery are needed, and that risk management strategies for the fishery should include assessment of how krill movement can satisfy the demands of both natural predators and the fishery across a range of spatial and temporal scales. Such information will help regional management authorities better understand how plausible ecosystem-based management frameworks could be developed to ensure sustainable co-existence of the fishery and competing natural predators.

**Key words:** Antarctic krill; chinstrap penguins; ecosystem management; habitat models; krill fishery; krill flux; krill surplus hypothesis; ocean currents.

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## INTRODUCTION

The realization that both top-down and bottom-up factors can affect trends in the abundance of many species (Nicol et al. 2007, Estes et al. 2011, Atkinson et al. 2014) highlights the need for an improved understanding about basic ecology and life history processes. This understanding is urgent in some marine systems, in part because our ability to ascribe causality for observed changes in species abundance may decrease, given a rapidly changing system (Smetscek 2008, Trathan and Reid 2009). In addition, the potential for expanding commercial fisheries, such as the fishery for Antarctic krill (*Euphausia superba*; Schiermeier 2010, Jacquet et al. 2010), may also add further complexity to attempts to understand altered food webs, ecosystem dynamics, and species abundance. For key indicator species in the Antarctic, such as chinstrap penguins (*Pygoscelis antarctica*), it is vitally important that we better understand their basic ecology and food web connections, especially as such indicator species are being used as part of the monitoring programme established to assess the regional impacts of environmental change and the krill fishery (Agnew 1997).

Chinstrap penguins are one of the most abundant krill predators breeding across the Antarctic Peninsula and the islands within the Scotia Sea (Humphries et al. 2017). They are the most abundant penguin species in the northern part of the west Antarctic Peninsula, the South Orkney Islands, and the South Sandwich Islands. Consequently, identifying the characteristics of their preferred habitats, particularly during their breeding period, should help identify patterns of spatial and temporal overlap with other ecosystem components and with krill fishery operations. New insights into penguin-krill-ecosystem dynamics are pressing, because of changed fishery operations and increasing krill catches (CCAMLR 2016). Krill fishing in habitats used by marine predators could result in a variety of altered ecosystem properties if it leads to changes in krill availability, with the potential for

inducing changes in penguin distribution and abundance (Trathan and Hill 2016).

The krill fishery is managed by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR; Fig. 1a) using a precautionary approach, with low catch limits relative to the stock size, coupled with agreements to spread the catch spatially in order to minimize effects on predators (Hill et al. 2016). Catches are currently low and evidence to suggest that krill fishing is having any impacts upon krill predators is generally inconclusive (Nicol and Foster 2016). Moreover, predator consumption of krill is very much greater than the current fishery catch (Hewitt et al. 2004). However, CCAMLR is planning to revise the spatial and temporal distribution of catches to accommodate potential future expansion of the fishery. Yet, without a better understanding of how predators might be impacted by altered fishing distributions, particularly at greater catch levels, agreements about how the fishery should develop will be difficult to reach. Therefore, here we identify the preferred habitats used by chinstrap penguins in an attempt to characterize where they are most vulnerable in relation to krill fishery operations. We use and adapt habitat models (Warwick-Evans et al. 2018) that are based on high-resolution global positioning system (GPS) telemetry data from the South Orkney Islands, to project where the preferred habitats occur for chinstrap penguins breeding across the northern part of the west Antarctic Peninsula, validating the models with additional telemetry data from the South Shetland Islands.

A key facet of our models is the incorporation of both inter- and intra-specific competition for resources by other *Pygoscelis* species, Adélie (*Pygoscelis adeliae*) and gentoo (*Pygoscelis papua*) penguins. Such competition will impact both prey availability and the suitability of preferred foraging areas for predators (Wakefield et al. 2013). Habitat preferences are known to vary over temporal and spatial scales, with variable foraging ranges between incubation and chick-rearing periods. Krill availability is presumed to

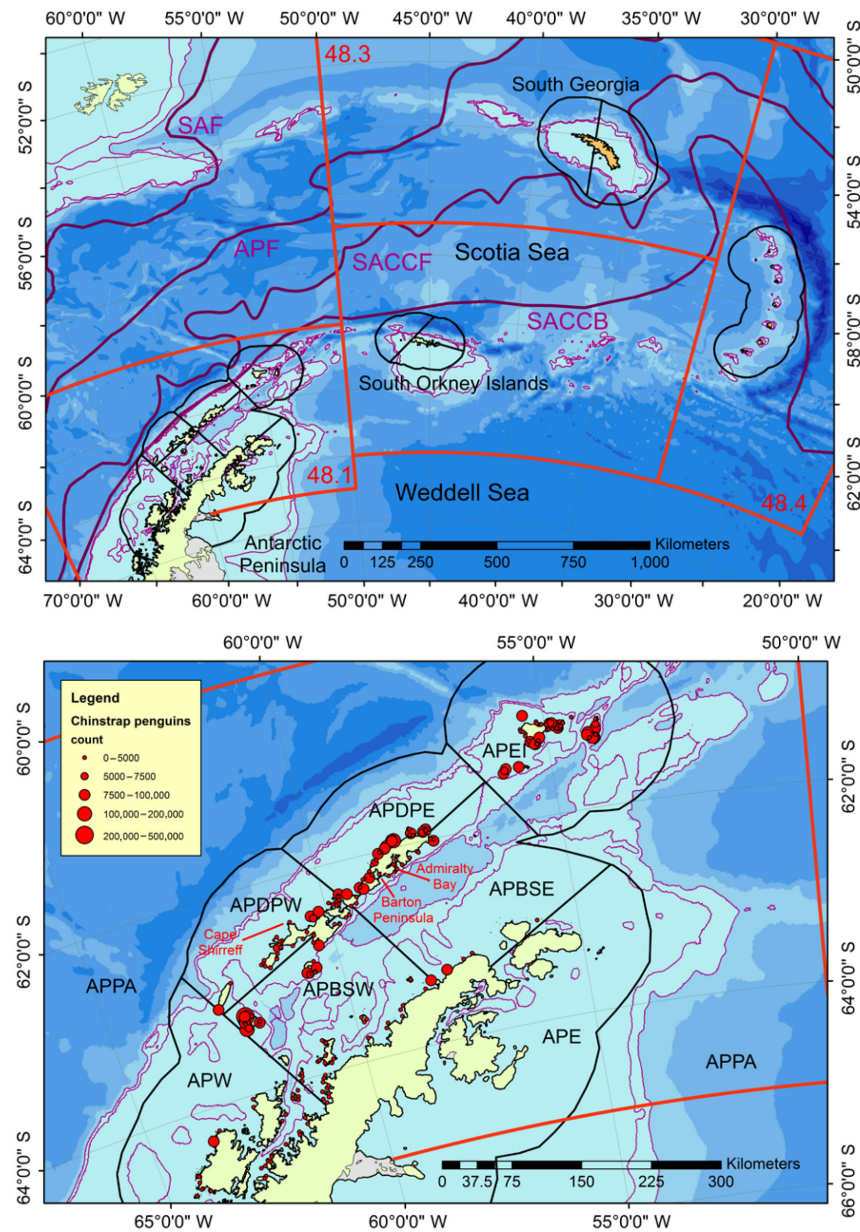


Fig. 1. The Antarctic Peninsula and South Shetland Islands in relation to the Scotia Sea and the Weddell Sea; the 500 m and 1000 m isobaths are shown. (upper panel) The boundaries of FAO Statistical Subareas 48.1, 48.2, 48.3, and 48.4 are shown in red, as are the boundaries of the CCAMLR Small Scale Management Units (SSMU) for the krill fishery in black. The major fronts of the Antarctic Circumpolar Current (ACC) are shown in pink: Southern ACC Boundary (SACCB); Southern ACC Front (SACCF); Antarctic Polar Front (APF); and Sub-Antarctic Front (SAF). (lower panel) The major chinstrap penguin colonies in the study region (red circles scaled to represent relative population size (smallest circle to largest circle <10,000 to >200,000); from Humphries et al. (2017). The boundaries of the CCAMLR Small Scale Management Units (SSMU) for the krill fishery are shown in black, Antarctic Peninsula Pelagic Area (APPA), Bransfield Strait East (APBSE), Bransfield Strait West (APBSW), Drake Passage East (APDPE), Drake Passage West (APDPPW), Antarctic Peninsula East (APE), Elephant Island (APEI), and Antarctic Peninsula West (APW). The positions of the three colonies for which tracking data are available are labeled in red.

be a key driver structuring habitats used by chinstrap penguins. We therefore also consider how their preferred summer habitats can be characterized in relation to the main oceanographic flows that ventilate the west Antarctic Peninsula and the South Shetland Islands. These flows are thought to be important as they facilitate movement of krill from off-shelf to on-shelf habitats (Ward et al. 2007), as well as between different regions of the Antarctic (Murphy et al. 1998, Thorpe et al. 2007).

As such, in this paper we set out to develop a generic model that has the power to predict the foraging locations of chinstrap penguins from untracked colonies, using a relatively restricted tracking dataset, with data from three sites within our study area. Based on identification of the preferred habitats used by chinstrap penguins, we also discuss a number of management issues for CCAMLR.

## MATERIALS AND METHODS

### *The model and the estimation of parameters*

Most of the >200 chinstrap penguin breeding colonies across the Antarctic Peninsula and South Shetland Islands are rarely visited, or studied, and only three have been the focus of published tracking studies, with data readily available ([www.seabirdtracking.org](http://www.seabirdtracking.org)). Therefore, to identify the preferred habitats more broadly used by this species, we first generated models that were developed using high-resolution GPS telemetry and simultaneous dive data collected from chinstrap penguins breeding at the South Orkney Islands (Warwick-Evans et al. 2018), which we then applied to the locally available telemetry data from the South Shetland Islands. Following Warwick-Evans et al. (2018), we used covariate data that comprised both environmental and geometric predictor variables which we considered biologically meaningful with regard to the at-sea distribution of marine top predators; see Appendix S1 for further details and a description of the available data, data processing, and covariate data.

### *Validation of the model*

In our study region (Fig. 1b), a limited amount of GPS tracking data are available, though most tracking data have been collected using

lower-resolution Platform Terminal Transmitter (PTT) devices; there are no simultaneous dive data available. Therefore, to validate the use of PTT data in our models, GPS and PTT data from Signy Island in the South Orkney Islands were used to: (1) validate the use of PTT data in habitat preference models for Signy Island; and, (2) assess whether it is feasible to use individual error-corrected (hereafter raw) PTT data, as opposed to interpolated PTT trip data in such models, given the difficulty in identifying individual foraging trips using lower-resolution PTT data; see Appendix S1 for further details and a description of the use of both raw and interpolated PTT data.

### *Application of the model to consider the foraging habitat*

We created models to predict the distribution of chinstrap penguins throughout our study region using tracking data from: (1) the South Orkney Islands; (2) the South Shetland Islands; and (3) a combination of all data available (from the South Orkney and South Shetland Islands). To achieve this, we (1) identified covariate data for the Signy Island PTT model, considering both environmental variables and geometric variables; before (2) generating habitat projections for the Antarctic Peninsula and South Shetland Islands; and finally (3) determining whether there was a need to vary the predictor variables from those used by Warwick-Evans et al. (2018). See Appendix S1 for further details.

These models were then each weighted by the size of the chinstrap penguin population in order to predict at-sea areas of high penguin density, noting that the most comprehensive dataset of chinstrap penguin population size (Humphries et al. 2017) in this region includes several counts that are approximately three decades old and are often associated with order-of-magnitude level uncertainty.

### *Oceanographic characteristics of penguin habitats*

In order to characterize the oceanographic features of the habitats used by chinstrap penguins, outputs from a high-resolution ocean model of the Antarctic Peninsula and the South Shetland Islands region implemented with the Nucleus for European Modelling of the Ocean (NEMO) modeling framework (Young et al. 2017) were used to

explore hydrographic connections in areas frequented by chinstrap penguins. The model was established with 75 levels in the vertical arranged on a partial-step z-coordinate, and a horizontal resolution of  $1/20^\circ$  longitude by  $1/40^\circ$  latitude. This allowed good representation of the complex shelf bathymetry and steep topography at shelf-edges. The model also included a non-linear free surface that allowed accurate representation of tides. The simulation of sea-ice was included by coupling with the Louvain-la-Neuve sea-ice Model (LIM3). Surface atmospheric forcing was derived from the DFS5.2 reanalysis (Dussin et al. 2016). At the open boundaries, tides were imposed using the Oregon State University global ocean tide model, TPXO7.2 (Egbert and Erofeeva 2002). Three-dimensional temperature and salinity, barotropic flux, and sea surface height at the open boundaries were derived from a global  $1/12^\circ$  implementation of NEMO, provided by the National Oceanography Centre, Southampton, UK. Climatological, spatially varying, terrestrial freshwater inputs were included from a combination of precipitation data from the DFS5.2 reanalysis, and Antarctic Peninsula glacier basin discharge data from the Regional Atmospheric Climate Model (RACMO; Van Wessem et al. 2017). Seasonal mean model outputs were used to characterize the areas used by penguins. We focus on the near-surface (50–150 m) waters as breeding chinstrap penguins mainly forage in the upper 100 m of the water column (Hinke et al. 2017). Additionally, krill occurrence during the summer period is generally within the upper 150 m (Siegel and Watkins 2016).

#### Assessment of fishery-foraging overlap

To examine krill fishing distribution in habitats occupied by chinstrap penguins, we used (1) the CCAMLR C1 krill catch and effort dataset which provides spatially resolved data for the period between the 1979/1980 and 2015/2016 CCAMLR fishing seasons; the spatial resolution of early data is less accurate than that of more recent data which is at the resolution of the individual haul; (2) the CCAMLR Statistical Bulletin V29, which provides catch data at an intermediate level of resolution for the period between the 1985/1986 and 2015/2016 CCAMLR fishing seasons. Throughout, we refer to each CCAMLR fishing season by the start date, such that 1985 = 1985/1986.

We used the kernel density tool in ArcGIS (ESRI Version 10.4.1, Redlands, California, USA) with a raster resolution of 1 km and a search radius of 5 km to calculate the fishing kernels for 30% to 100% of total mass, using the CCAMLR C1 krill catch and effort data; we used data from all commercial hauls carried out during the *Pygoscelis* penguin breeding season (October–March; chinstrap penguin settlement is in October/November, whilst fledging occurs in February/March), using both historical (1979–2015) and recent (2009–2015) time periods. We used the CCAMLR Statistical Bulletin V29, to calculate summed catch between 1985 and 2015 for each of the Small Scale Management Unit; Antarctic Peninsula Pelagic Area, Bransfield Strait East, Bransfield Strait West, Drake Passage East, Drake Passage West, Antarctic Peninsula West, Antarctic Peninsula East, and Elephant Island.

Finally, we quantified the overlap between the foraging habitat of chinstrap penguins and the areas used by the krill fishery. We compared the intensively used areas (top 50%) for penguin or the fishery and the home range areas (top 95%) for penguin or the fishery; we considered both the historic and the recent periods of fishery operation.

## RESULTS

### Habitat models for the South Shetland Islands

Our habitat models based on the distance from the colony and bearing to the shelf-edge, adjusting for the at-sea density of *Pygoscelis* penguins from other colonies, can, with a high level of confidence, be used to predict the at-sea distribution of chinstrap penguins breeding on the South Shetland Islands (see Appendix S1 for details). Based on the area under the curve (AUC) statistic, specificity (correctly predicted absences), and sensitivity (correctly predicted presences), the model using only data from the South Shetland Islands predicted the at-sea distributions of chinstrap penguins from the South Shetland Islands better than the model using data from the South Orkney Islands. Nevertheless, the model based on data from the South Orkney Islands still had high predictive power with AUC values of 0.9 and high values of specificity and sensitivity. Thus, our results, including those using cross-archipelago data, suggest a high level of predictive performance for all the models developed.

Extrapolating the models to predict the distribution of chinstrap penguins for colonies with no tracking data resulted in a smaller predicted area of occurrence when models were based on data from the South Shetland Islands (Fig. 2b) than when created with data from the South Orkney Islands (Fig. 2a), or a combination of data from the South Shetland Islands and South Orkney Islands (Fig. 2c).

We found that regardless of whether models were created with tracking data from the South Shetlands, South Orkneys, or South Orkneys and South Shetlands combined (Fig. 3), as the

difference between the bearing of a point from the colony and the bearing of the nearest available shelf-edge increased, the probability of occurrence decreased. This suggests that individuals move directionally toward the shelf-edge, whilst avoiding high densities of *Pygoscelis* penguin species from other colonies. Additionally, as the distance from the colony increased, the probability of occurrence decreased (Fig. 3). However, when the distance from the colony exceeded ~120 km, the probability of occurrence increased again, especially for the South Orkney Islands (Fig. 3a, c). This suggests that penguins

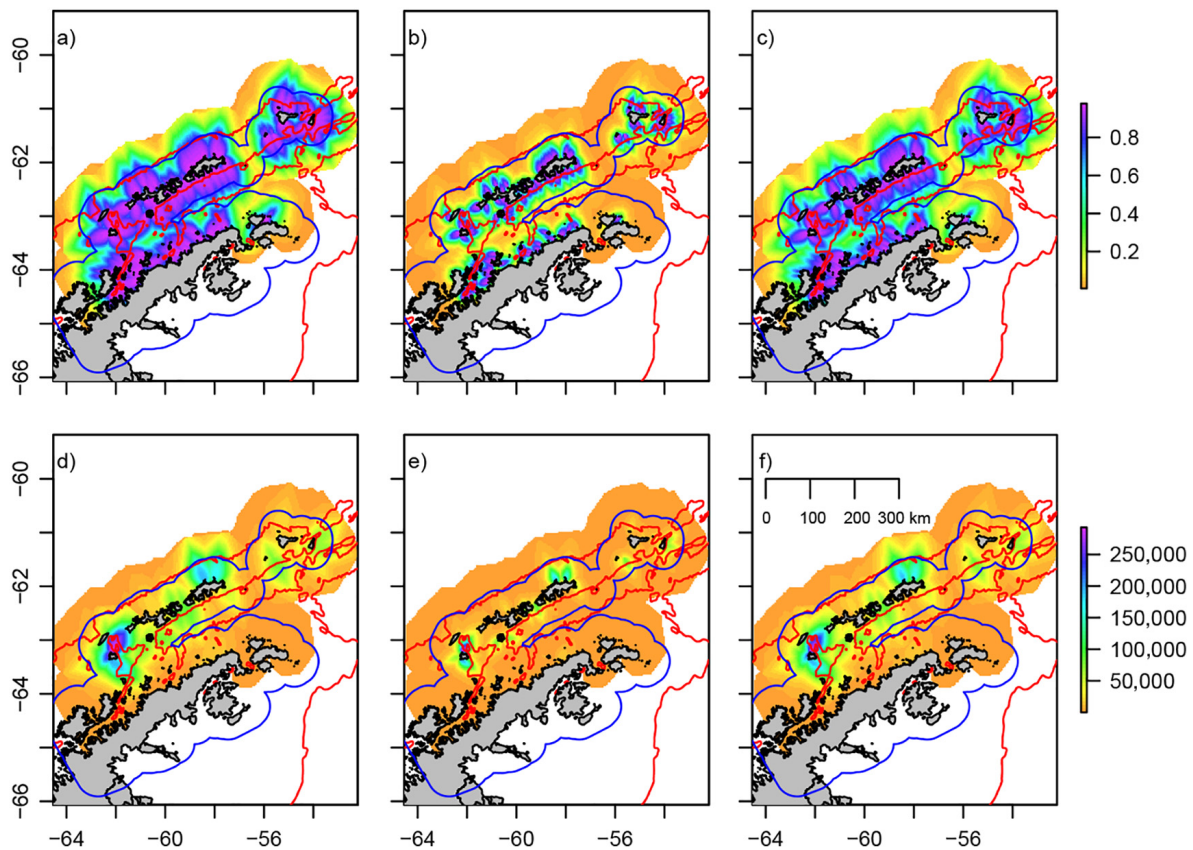


Fig. 2. Spatial predictions of the probability of occurrence of all chinstrap penguins breeding on the Antarctic Peninsula and South Shetland Islands during brood. Models were created using: (a) GPS tracking data from five year/site groups tracked from the South Orkney Islands, (b) GPS ( $n = 1$ ) and Platform Terminal Transmitter ( $n = 2$ ) data from three colonies tracked at the South Shetland Islands, (c) all five year/site groups tracked from the South Orkney Islands and three groups from the South Shetland Islands. Predictions were weighted by population size (see text for uncertainty about population size in some areas), (d–f) for each method, respectively. Predictions are from GAMs where distance and bearing from the colony were used as predictors. The 750 m isobath, representing the shelf-edge, is indicated in red. The 95th percentile of trip distance (Appendix S1) is shown in blue.

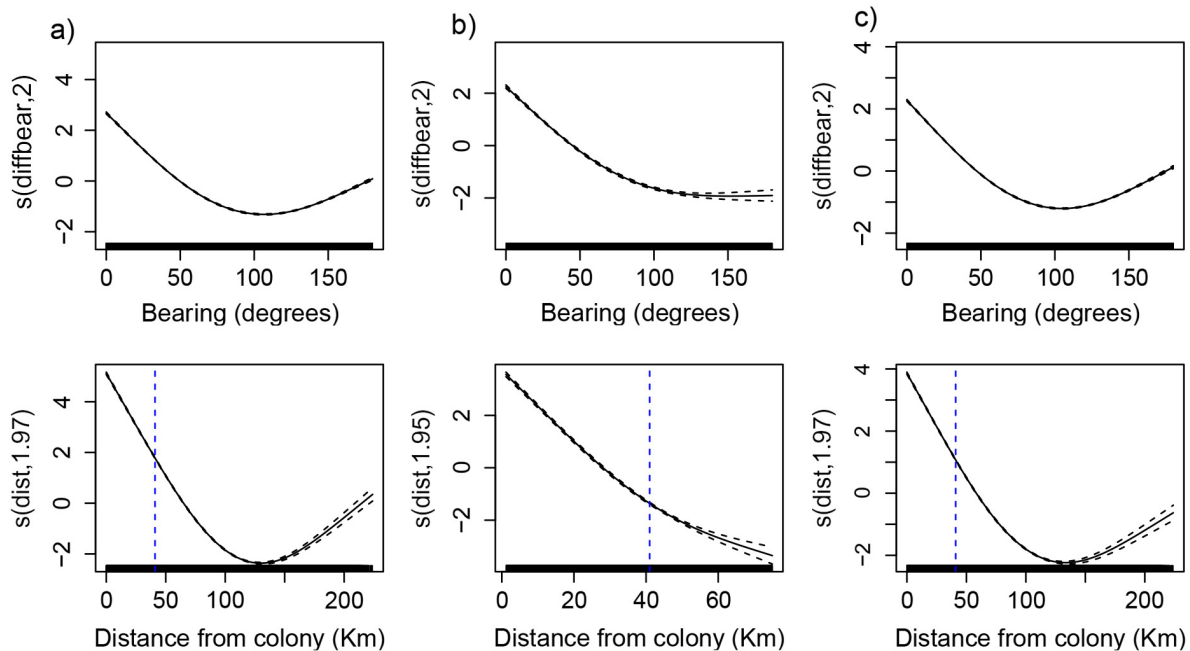


Fig. 3. Model response curves for models using distance and bearing to predict the probability of occurrence of all chinstrap penguins breeding on the Antarctic Peninsula and South Shetland Islands during the brooding period. Models were created using (a) GPS tracking data from five year/site groups tracked from the South Orkney Islands, (b) GPS ( $n = 1$ ) and Platform Terminal Transmitter ( $n = 2$ ) data from three colonies tracked at the South Shetland Islands, (c) all five groups tracked from the South Orkney Islands and three groups at the South Shetland Islands. The 95% percentile of trip distance is shown in blue.

may be dispersing more widely when they are further from the colony (Fig. 3a, c). This pattern was not observed in models that were based only on data from the South Shetland Islands where birds travelled less far (Fig. 3b), indicating that penguins from the South Shetland Islands do not show exactly the same behavioral patterns as those from the South Orkney Islands. This highlights potential discrepancies that may occur when using models based on information from one location to predict the distribution of birds elsewhere.

#### *Oceanographic characteristics of penguin habitats*

Selected outputs from the NEMO modeling framework for the northern Antarctic Peninsula during the latter part of the penguin breeding season (January–March, brood and crèche) are shown in Fig. 4, with a more complete description provided by Young et al. (2017). Nucleus for European Modelling of the Ocean is a hind-cast model, so a single example year, 1998, is shown.

The main flow patterns during this year are representative of the other years within the analysis.

The Bransfield Strait receives important contributions of cold, dense waters from the continental shelf of the western Weddell Sea. These cold water flows enter the study region around the tip of the Antarctic Peninsula (Fig. 4a, b). Circumpolar Deep Water and warm surface waters from the Bellingshausen Sea enter the Bransfield Strait from the southwest, mainly to the west of the South Shetland Islands. The NEMO model recreates well, the Antarctic Circumpolar Current Southern Boundary to the north of the South Shetland Islands, the Antarctic Slope Front, and the Coastal Current (Thompson et al. 2009, Dotto et al. 2016).

The influence of the relatively shallow topography around the edge of the Bransfield Strait limits the mixing of waters with the surrounding oceans, and the circulation is characterized by a cyclonic gyre. The flow fields highlight that the Coastal Current is an important topographically steered feature within the Bransfield Strait; it

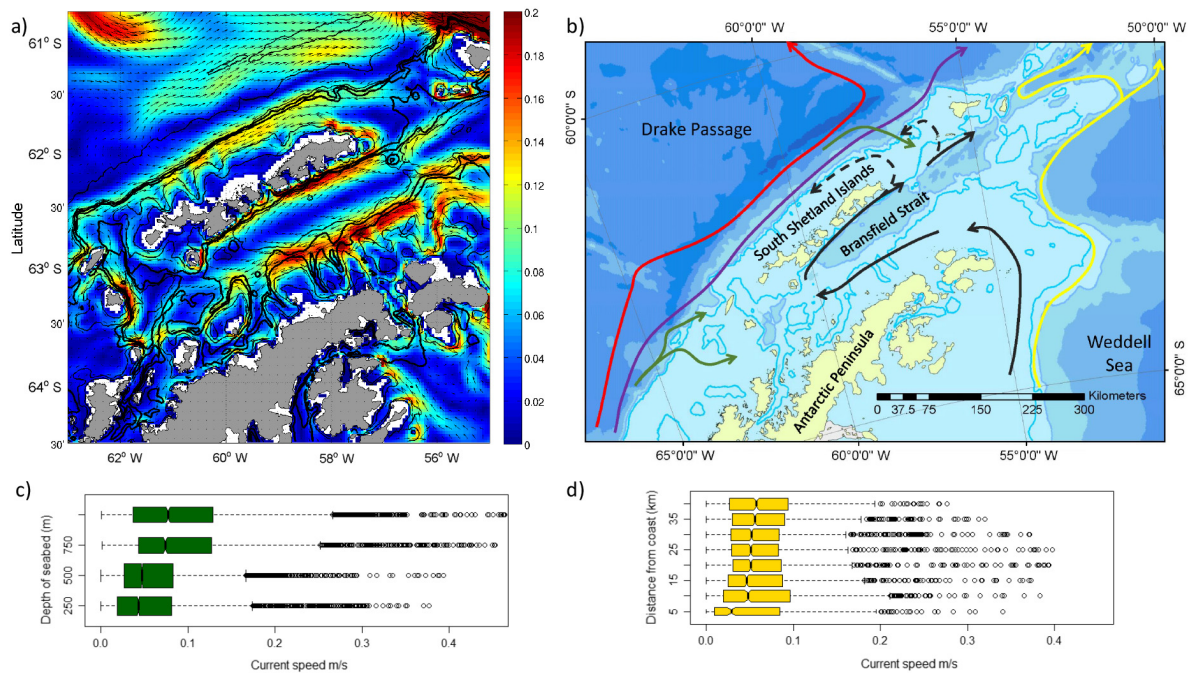


Fig. 4. (a) Simulated mean summer (January–March) near-surface (averaged over 50–150 m) oceanographic flows for the northern Antarctic Peninsula and South Shetland Islands during 1998. The colored shading represents speed (m/s) with arrows indicating current direction (every 3rd flow vector is shown). The 100, 200, 500, 750, 1000, 2000, and 3000 m isobaths are shown, with the 500 and 750 m isobaths shown in bold. (b) Schematic of the surface currents near the Antarctic Peninsula following Thompson et al. (2009) and Dotto et al. (2016). The positions of the South Shetlands shelf-edge current (Black dashed), Coastal Current (Black), the Antarctic Slope Front (Yellow), the Antarctic Circumpolar Current (ACC) Southern Boundary (Purple), and Southern ACC Front (Red) are shown. Weddell Sea shelf water contributes to the Coastal Current from the east whilst the Bellinghshausen Sea surface water and the Circumpolar Deep Water (Green) enter the Bransfield Strait from the west. (c) Current speeds within different distances of the coast, to 40 km. (d) Current speeds over different depths of seabed, within 40 km of the coast. For (c) and (d), the boxes are drawn with widths proportional to the square-roots of the number of observations in the groups; where the notches of boxes do not overlap, there is strong evidence that the medians differ; also, circles represent extreme values. There are significant differences with distance from the coast (ANOVA,  $F = 5.147$ ,  $P < 0.010$ ), but greater significant differences with depth of seabed (ANOVA,  $F = 1672.0$ ,  $P < 0.001$ ).

extends from the surface waters to near full depth and is located in close proximity to steep topography characterized by the 500 and 750 m isobaths. The mean flows within the Coastal Current show speeds  $>0.15$  m/s. Over the shallow topography close to land around the Peninsula and the South Shetland Islands, the flows are much weaker with mean speeds generally around  $\sim 0.05$  m/s. More detailed mean flow characteristics close to land are shown in Fig. 4, in particular, mean absolute flow speed within consecutive 5-km distance zones (as far as 40 km from land; Fig. 4c), and

within consecutive 250-m depth zones (as deep as 1000 m; Fig. 4d). These boxplots indicate that bathymetry influences current speed more than does distance from land.

The areas utilized by chinstrap penguins, based on all the habitat models (Fig. 2), encompass both shelf waters and the faster moving Coastal Current, but the highest probability of at-sea occurrence of penguins is mainly coincident with the more quiescent shelf waters (Fig. 4). At the South Orkney Islands, chinstrap penguins may travel over 150 km during the



brood period (Warwick-Evans et al. 2018); at the South Shetland Islands, birds travel less far and the shelf waters and the faster moving flows at the edge of the shelf are preferred (Fig. 3).

#### *Assessment of fishery-foraging overlap*

Krill catches during the breeding season (1979–2015) occurred across the study region (Fig. 5), with some areas being particularly attractive to the fishery. The spatial distribution of the fishery has varied over time; harvesting in recent years has moved from areas to the north of the South Shetland Islands and Elephant Island to areas within the Bransfield Strait. All of the “hotspots” occur over the shelf in areas with shallow bathymetry (within the 500 m isobaths). The localities used by the fishery coincide with areas predicted to be high-intensity penguin foraging areas (Fig. 6). A number of the hotspots also occur close to the shelf break, close to waters with speeds of approximately  $>0.15$  m/s (Fig. 4). A number of submarine canyons occur to the north of Cape Shirreff and to the north of the Antarctic Peninsula, close to intense fishing locations, suggesting that the penetration of off-shelf waters might lead to predictable concentrations of krill. The level of catch is variable over the past 30 yr, including variation in the amount taken during both summer and winter (Appendix S3). Catches are currently at a historical high in both summer and winter. The catches have reached the CCAMLR local interim catch limit in five out of the past seven years.

The percentage of the chinstrap penguin foraging distribution (based on Fig. 2e) in intensively used areas (50% of area used) that overlaps with intensively used areas used both historically and recently by the fishery is 0% (Fig. 6, Table 1). However, during the same periods, 26% and 15%, respectively, of the chinstrap distribution home range areas (95% of area used) overlap with areas used by the fishery. For comparison, we also include in Table 1, estimates of overlap from the other foraging distribution models (Fig. 2d, f), in order to illustrate sensitivity of the overlap metric to model choice.

## DISCUSSION

### *Habitat model performance and limitations*

Our study set out to create a generic model that had the power to predict foraging locations

using a relatively restricted tracking dataset, with data from three sites within the study area. In this context, our models performed well, achieving high AUC values and high levels of both specificity and sensitivity. Our models were similar to those of Warwick-Evans et al. (2018) that used high-resolution tracking data for colonies outside our study region. Cross-validation between regions (South Shetland and South Orkney Islands) and between colonies at the South Shetland Islands showed that our objectives were achieved based on models using relatively simple inputs (Figs. 2, 3; see Appendix S1 for further details). Our models appear robust to both sparse tracking data and sparse covariate data.

Our model is a generic habitat model that explores the main characteristics of habitat selection by chinstrap penguins. It does not, nor is it intended to, account for interannual variation in foraging behavior, interannual changes in the environment, or environmental variation such as responses to climate change. Undoubtedly, such drivers will lead to variation in foraging behavior (Lynnes et al. 2002, Lowther et al. 2018); however, our model was developed in order to predict the foraging locations of chinstrap penguins from untracked colonies so that we could explore the generality of preferred habitats used by chinstrap penguins in relation to the fishery for Antarctic krill.

The models performed better when they were based on data from within the region (Appendix S1), but still performed well with data from outside the region. Of the three models developed (Figs. 2, 3), we suggest that the most appropriate model for management purposes is that based solely on the South Shetland Islands tracking data (Fig. 2b, e) as this model has a slightly higher AUC value. Additionally, it predicts the smallest habitat areas, whilst the response curves from this model show slightly different patterns compared with those based on the South Orkney Islands tracking data (Fig. 3); at the South Shetland Islands, penguins disperse to a lesser degree when further from the colony. Thus, we suggest that models based solely on local data from within the region would provide the most accurate portrayal of spatial use.

Given the relatively limited sample size available for input into this model, additional tracking

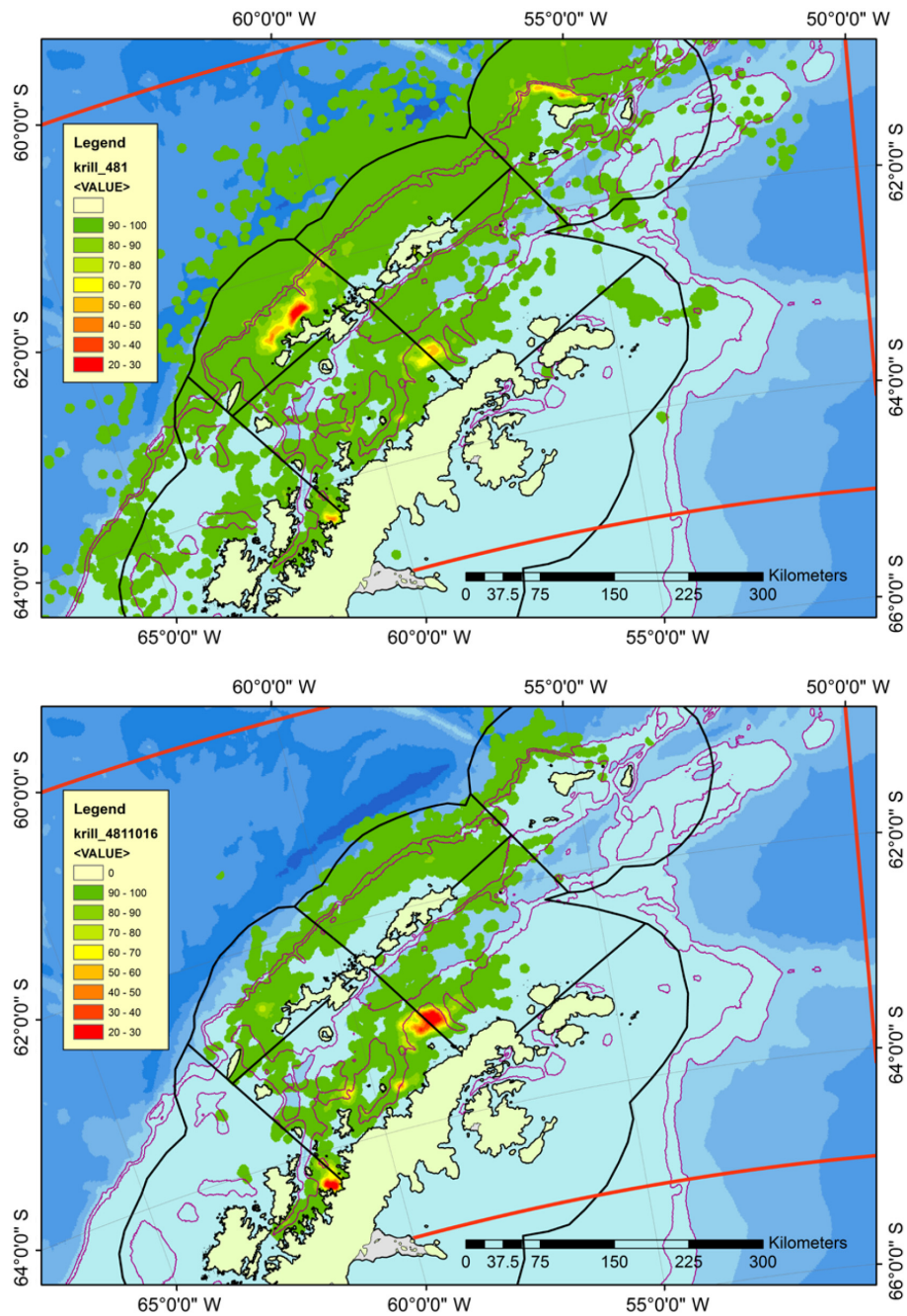


Fig. 5. Antarctic krill kernel density estimation of summed catch within Subarea 48.1 (CCAMLR C1 catch and effort dataset, 2016) during the *Pygoscelis* penguin breeding season (October to March) between the (upper panel) 1979 and 2015 fishing seasons and (lower panel) 2010 and 2015 fishing seasons. CCAMLR Small Scale Management Unit are indicated. The 500 m and 1000 m isobaths are highlighted. Kernels were developed using a 1 km grid with a 5 km search radius.

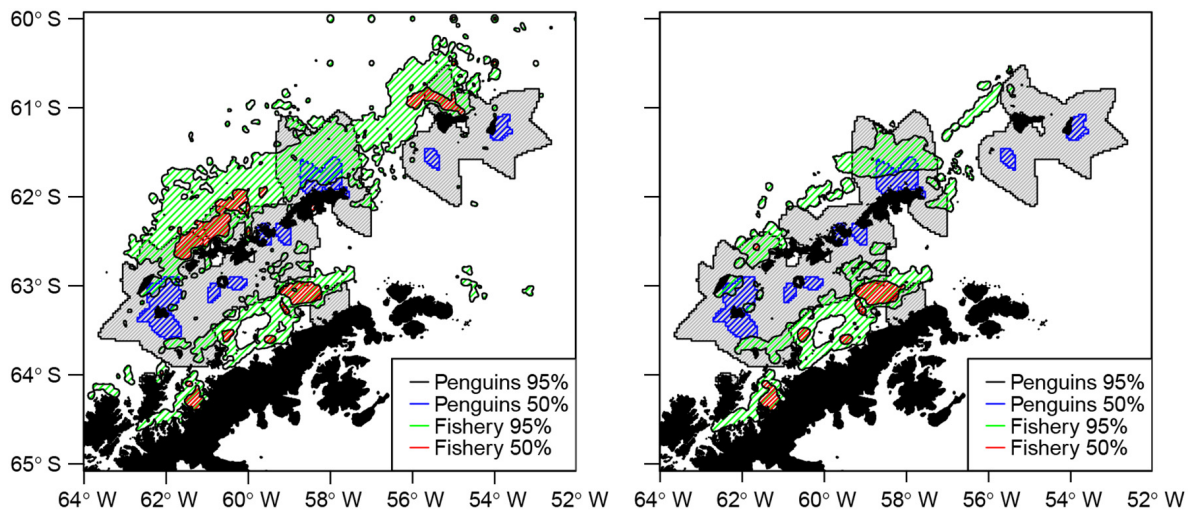


Fig. 6. The overlaps between the predicted at-sea distribution of chinstrap penguins and the krill fishery during the penguin breeding season (fisheries data are for October–March). Shown are the 50% intensively used areas and the 95% home range areas, during (left panel) historic (1979–2015); and (right panel) recent (2010–2015) fishing seasons.

Table 1. The quantified at-sea overlap between the population of chinstrap penguins breeding on the South Shetland Islands and the northern Antarctic Peninsula (Fig. 2e), and the krill fishery (historical fishery 1979–2015 and recent fishery 2010–2015 fishing seasons).

Model	Level of use	Historical fishery		Recent fishery	
		Intensively used area (%)	Full area (%)	Intensively used area (%)	Full area (%)
South Shetland Islands model (Fig. 2e)	Intensively used area (%)	0	24	0	13
	Full area (%)	0	26	0	15
South Orkney Islands model (Fig. 2d)	Intensively used area (%)	1	40	0	31
	Full area (%)	2	34	<1	23
South Shetland and South Orkney Islands model (Fig. 2f)	Intensively used area (%)	1	38	0	30
	Full area (%)	2	33	<1	23

Notes: The intensively used area comprises the top 50% of penguin or fishery locations, and the full area encompasses 95% of the penguin or fishery locations. For comparison, models using data from the South Orkney Islands are also shown (Fig. 2d, f).

data from other sites would almost certainly allow us to refine the model, so we encourage the collection of similar data from other sites, especially sites with large colonies and where geography allows birds to forage in multiple alternative directions. Additionally, although our model is valuable for predicting the distribution of penguins from untracked colonies, the most accurate approach to gauge the colony specific overlap between penguins and fisheries would be to use empirical data from tracking individual penguins at all colonies of interest.

#### Interpreting the parameters of the model

The *distance* from the colony and the difference in bearing between foraging locations and the nearest accessible shelf-edge (adjusting for the density of *Pygoscelis* penguins) were strong predictors for our models during the breeding season (see Warwick-Evans et al. 2018 for a detailed discussion of habitat use). The model suggests that it is important to consider the impacts of nearby colonies when attempting to understand the travel direction of birds during foraging. We hypothesize that this is plausibly linked to prey

depletion and/or interference competition from competing predator species, certainly such factors are likely to be important aspects of foraging behavior. If prey depletion proves to be a major driver of foraging behavior, then information on replenishment rates of prey through reproduction, growth, or import via ocean currents (Murphy et al. 1998, Hunt et al. 2016) will be critical for understanding foraging opportunities for different sized penguin colonies. Indeed, breeding sites where prey are naturally predictable, or where prey replenishment rates are sufficient to meet colony demands, are likely to be preferred.

Though such hypotheses are highly plausible, it is essential to test them, if we are to better understand chinstrap penguin foraging behavior, especially in relation to the distribution of krill. Moreover, testing these hypotheses will facilitate understanding about how krill distribution and abundance influences penguins, including also about how krill interact with different oceanographic features (Murphy et al. 1998) and tidal cycles (Bernard and Steinberg 2013). Such consideration should also include issues related to the active movement of krill (Thorpe et al. 2007), and changing primary production (Moline et al. 2004); understanding this in the context of other krill predators will certainly require additional inter-disciplinary field programmes.

#### *Oceanographic characteristics of penguin habitats*

Our models highlight the importance of the shelf-edge for foraging penguins, especially in terms of distance and orientation. This is perhaps not unexpected, as the direction and speed of water movements near the Antarctic Peninsula (Fig. 4) are strongly affected by bathymetry and by frontal features, including the Antarctic Slope Front and the Coastal Current (Heywood et al. 2004, Thompson et al. 2009, Renner et al. 2012). In the surface mixed layer, currents carry material from the northwest of the Weddell Sea around the tip of the Peninsula into the Bransfield Strait where they may be recirculated and transported toward the South Scotia Ridge and into the Scotia Sea, thus connecting populations of Antarctic krill (Thorpe et al. 2007, Renner et al. 2012). The Coastal Current is especially important for bringing krill into the Bransfield Strait, though sea-ice distribution and movement can modify ocean transport pathways (Ichii et al.

1996, Thorpe et al. 2007, Youngs et al. 2015); see also Appendix S4 for comparative purposes.

Results from the model of Young et al. (2017) highlight the presence of relatively slow-moving water in regions of shallow bathymetry, compared with more rapid flows at the shelf-edge and in deeper oceanic regions; these findings accord well with existing hydrographic models and empirical studies (e.g., Dinniman and Klinck 2004, Heywood et al. 2004, Dotto et al. 2016). Transport between off-shelf and on-shelf waters is complex, but is almost certainly a vital process regulating the flow of krill into the foraging range of chinstrap penguins. Elsewhere, Young et al. (2014) have shown that shelf retention shows a high degree of seasonal variability, and similar complex patterns may also occur close to the Peninsula and South Shetland Islands.

The growth and production of krill over the shelf is augmented by krill advected onto the shelf, including via cross-shelf canyons, whilst at the same time being depleted by advection off the shelf and by natural mortality, including by consumption from a range of krill predators. Insight into the key drivers of seasonal variability in krill distribution and abundance (Siegel 1988, Trathan et al. 1993) will be vital for understanding the distribution of all predators, especially in the context of a developing fishery. Given the high levels of spatial and temporal variability in oceanographic flows and in krill consumption, it seems unlikely that “average ecosystem states” ever occur. The modeled preferred habitats of chinstrap penguins occur predominantly over the shelf in relatively slow-moving waters with mean flow speeds of  $\sim 0.05$  m/s, although the direction of foraging trips is toward the faster-flowing currents at the shelf-edge where mean flow speeds are greater. Given the relatively weak flows over the shelf, krill depletion following consumption by predators is likely, but cannot be assumed without a better understanding of krill replenishment rates.

Many of the largest chinstrap penguin colonies in the South Shetland Island region occur in close proximity to fast moving water, either in the Coastal Current or the Antarctic Circumpolar Current. Advection of krill into the vicinity of these colonies is likely to be substantial and predictable, presumably supporting high rates of

krill transport into penguin foraging habitats. In particular, the combination of high rates of krill transport and/or retention and ice-free breeding terrain probably contribute toward colony situation and colony size. Levels of primary production in areas of krill retention are also likely to be important.

#### *Penguin habitat—krill fishery overlap*

Our model highlights that nearshore areas are vital for all colonies and that more than 95% of all trips occur within ~42 km of the colony (Appendix S1). Nearshore habitats can have elevated levels of krill biomass (Warren and Demer 2010), and at the Antarctic Peninsula, krill harvesting is concentrated at a small number of locations, some of which occur close to shore, thus having the potential to impact krill predators. Our results during the breeding season are therefore consistent with observations of concurrent overlap of krill predators and the krill fishery in this region at other times of year (Hinke et al. 2017).

Almost two million tonnes of krill have been harvested from Subarea 48.1 since 1985 with a substantial proportion having been taken during the breeding season of chinstrap penguins (Appendix S3), particularly during brood, crèche, and the post-breeding periods when naïve fledglings are becoming independent and when adults are regaining body condition prior to their energy intensive molt. However, on an annual basis the krill catch in Subarea 48.1 is generally <9% of the standing stock (Hill et al. 2016), based on the biomass estimate from a local krill monitoring programme (Kinzey et al. 2015). Nevertheless, our habitat models demonstrate overlap between chinstrap penguins and the krill fishery, though catches are currently low and do not necessarily always directly overlap with the highest at-sea density of chinstrap penguins. Indeed, the percentage of the foraging distribution in intensively used areas (50% of area used) that overlaps with Intensively used areas occupied both historically and recently by the fishery, is extremely low (Fig. 6, Table 1). Nevertheless, the home range areas (95% of area used) do overlap with areas used by the fishery (Fig. 6, Table 1). Should the fishery expand, and/or should krill decline for other reasons (e.g., cetacean recovery or climate change; Trathan et al. 2012), increased

pressure on resources is likely to be important over small space and time scales. Continued targeted research within penguin habitats is therefore essential in order to help provide a better understanding of krill movement and chinstrap penguin productivity, a key issue given their role in CCAMLR ecosystem monitoring.

#### *Implications for CCAMLR*

Our study is the first description of predator foraging habitat in relation to a detailed understanding of oceanography and krill fishing operations and is the first study to attempt to identify how waters carrying krill move into the foraging range of an abundant krill consumer. Our study is also the first to statistically calculate the extent of the overlap between a population of an abundant krill consumer and the fishery. This is important because it allows us to determine which hydrographic features are important and where competition amongst predator species or between predators and the krill fishery might be most intense. With respect to the regional context, we recognize that krill transport occurs across a range of spatial and temporal scales (Murphy et al. 1998, Bernard and Steinberg 2013). However, we still know relatively little about krill flux and retention around the South Shetland Islands and inside the Bransfield Strait. We therefore suggest that a better understanding of how krill move into the region is important, including from the Weddell Sea, and from across the western shelf along the Peninsula (Piñones et al. 2013). Improved understanding about local processes of cross-shelf exchange and retention is important. This will require detailed field studies of krill distribution in relation to local oceanography and bathymetry in areas important to both predators and the fishery. This will need to be combined with broader studies that examine larger-scale krill distribution and flux to understand the main routes of transport and supply. This will also need to be underpinned by multi-scale modeling studies aimed at understanding supply, transport pathways, local processes (from 100 m to 10+ km scale), retention, growth, and mortality. Such fine-scale models are not yet available, but are technically feasible. We demonstrate that improving our understanding of local oceanographic processes influencing krill availability in areas where predators forage and

fisheries operate will be crucial for developing management procedures that relate to appropriate ecosystem scales.

We also suggest that similar characterizations of habitat for other krill predators will be important, as this may help illuminate aspects of interspecific competition for krill (Trathan et al. 2012). For example, though most species of baleen whale that occur in the Scotia Sea and Antarctic Peninsula region remain depleted to some extent (Reilly et al. 2004), humpback whales (*Megaptera novaeangliae*) have recovered more rapidly than others (Clapham et al. 1999, Matsuoka et al. 2006, Herr et al. 2016) and could now represent competition to penguins in coastal areas. Humpback distribution appears to be related to the distribution and abundance of krill, particularly in nearshore locations (Friedlaender et al. 2006, Nowacek et al. 2011, Weinstein et al. 2017). It is interesting that one of the most rapidly recovering whale species apparently occupies habitats analogous to those used by chinstrap penguins. This raises the prospect that these species probably do compete for krill in similar habitats and that both species might compete with the krill fishery.

Our results highlight the importance of managing krill fishing activities at temporal and spatial scales relevant to the population processes of predators. Evidence is now accumulating that krill predators preferentially occupy habitats that are also important to the krill fishery (e.g., Hinke et al. 2017, Weinstein et al. 2017), but for which we have no understanding in terms of krill retention, depletion, or replenishment. These processes are key to understanding both the future recovery of baleen whale stocks and the future sustainability of penguin populations and the krill fishery. Our results highlight that there are places, including in fishing areas beyond the 1000 m isobath, where chinstrap penguins and the fishery do not overlap; nevertheless, we need to know the spatial and temporal scales of connectivity between the areas used by the fishery and those used by predators, even if there is no direct overlap. Where the fishery does directly overlap with areas important to predators, we critically need to understand the magnitude of the interaction. Comparisons between predator life history processes and population trends are vital in both fished areas and unfished areas. All this requires

more work to understand the local processes that determine krill availability and predator foraging success and abundance.

Attempts to determine how fisheries deplete forage fish stocks and therefore impact dependent species have been attempted in other ecosystems (e.g., Pichegru et al. 2010, 2012, Bertrand et al. 2012, Sherley et al. 2015, Barbraud et al. 2017). In the Antarctic, following more than 40 yr of krill harvesting, it is also timely to explore the fine-scale spatial distribution of krill in relation to the reproductive success of predators. Such an approach has been advocated by Hilborn et al. (2017), who suggested that it is the only means for understanding the impacts of forage fish fisheries. In this context, we suggest that CCAMLR consider implementing a small number of special krill research zones within which harvesting is closely managed during the penguin breeding season, at least until further information is available on krill depletion and replenishment rates. These research zones should include areas that occur within preferred habitats of penguins, including at sites where krill move onto the shelf. A number of the areas preferentially used by the krill fishery are located over the shelf and in close proximity to cross-shelf canyons (Fig. 5). These locations are also important areas for a variety of other krill predators (Santora and Veit 2013), including marine mammals and seabirds, and also for some species that breed outside our study region (e.g., albatross and petrel species). Harvesting within these zones could be managed in a manner that will help provide an enhanced scientific understanding about the spatial and temporal distribution of krill in relation to oceanography and the reproductive success of predators (both cetaceans and penguins, as well as other krill-eating species). Key objectives should include an improved understanding of krill movement and retention, and how the foraging efficiency of predators is affected by not only the global quantity of krill available, but also the temporal and spatial patterns of krill harvesting (Bertrand et al. 2012). It is vital to determine the threshold of availability, or depletion, required to trigger detectable signals in krill predators. Determining the circumstances under which the fishery is capable of depleting the krill stock would provide vital management information.

## CONCLUSION

We show that in the case of chinstrap penguins during their breeding season, habitat models can, with some confidence, be extrapolated to predict the at-sea locations where animals from untracked colonies probably forage, even in different regions and across different archipelagos. We show that chinstrap penguins prefer near-shore habitats over shallow bathymetry with slow-flowing water, habitats similar to those used by krill-eating humpback whales (Weinstein et al. 2017), offering insights into the plausibility of the krill surplus hypothesis (Sladen 1964, Laws 1977). These habitats can have elevated levels of krill biomass (Warren and Demer 2010), which reinforces the need to better understand bottom-up and top-down forcing in the Antarctic. It also highlights the need for a greater level of fundamental ecological knowledge when developing an ecosystem-based management framework for the krill fishery, as our results suggest that nearshore areas may be higher risk areas for predators. Thus, as the krill fishery develops, CCAMLR needs to better understand how krill movement can satisfy the demands of both natural predators and the krill fishery across a range of spatial and temporal scales. Calibrated acoustic survey data from the fishing fleet combined with oceanographic moorings and detailed predator studies would help support better understanding of krill prey field dynamics.

Given the available tracking data and covariate data with which we parameterized our habitat model, we believe that our model performs well and is statistically robust, achieving high AUC values and high levels of both specificity and sensitivity. Interpretation of model parameters also highlights areas of considerable ecological importance for both predators and the fishery, and therefore for CCAMLR. Based on these results, we suggest that our modeling framework has potentially wider applicability to other sites and for other central place predators. We conclude that in the absence of empirical tracking data from all penguin colonies, this modeling approach allows us to quantify the overlap between chinstrap penguins and the krill fishery with a high level of confidence.

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## SUPPORTING INFORMATION

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