

ARTICLE

Coastal and Marine Ecology

Using seabird and whale distribution models to estimate spatial consumption of krill to inform fishery management

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Funding information

Darwin Plus, Grant/Award Number: 072; Pew Charitable Trusts, Grant/Award Number: PA00034295; World Wildlife Fund; Australian Antarctic Division; Southern Ocean Research Partnership; Hogwarts Running Club; National Science Foundation Office of Polar Programs, Grant/Award Numbers: 1347911, 0337648, 9983751; CNPq, Grant/Award Numbers: PQ 309548/2019-5, PQ 310597/2018-8; National Council for Scientific and Technological Development, Grant/Award Numbers: 407889/2013-2, 408096/2013-6

Handling Editor: Jenifer Dugan

Abstract

Ecosystem dynamics at the northwest Antarctic Peninsula are driven by interactions between physical and biological processes. For example, baleen whale populations are recovering from commercial harvesting against the backdrop of rapid climate change, including reduced sea ice extent and changing ecosystem composition. Concurrently, the commercial harvesting of Antarctic krill is increasing, with the potential to increase the likelihood for competition with and between krill predators and the fishery. However, understanding the ecology, abundance, and spatial distribution of krill predators is often limited, outdated, or at spatial scales that do not match those desired for effective fisheries management. We update current knowledge of predator dependence on krill by integrating telemetry-based data, at-sea observational surveys, estimates of predator abundance, and physiological data to estimate the spatial distribution of krill consumption during the austral summer by three species of *Pygoscelis* penguin, 11 species of flying seabirds, one species of pinniped, and two species of baleen whale. Our models show that the majority of important areas for krill predator foraging are close to penguin breeding

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colonies in nearshore areas where humpback whales also regularly feed, and along the shelf-break, though we caution that not all known krill predators are included in these analyses. We show that krill consumption is highly variable across the region, and often concentrated at fine spatial scales, emphasizing the need for the management of the local krill fishery at relevant temporal and spatial scales. We also note that krill consumption by recovering populations of krill predators provides further evidence in support of the krill surplus hypothesis, and highlight that despite less than comprehensive data, cetaceans are likely to consume a significant proportion of the krill consumed by natural predators but are not currently considered directly in the management of the krill fishery. If management of the krill fishery is to be precautionary and operate in a way that minimizes the risks to krill predator populations, it will be necessary in future analyses, to include up-to-date and precise abundance and consumption estimates for pack-ice seals, finfish, squid, and other baleen whale species not currently considered.

KEYWORDS

Antarctic ecosystem, ecosystem approach, fisheries management, habitat modeling, humpback whales, penguins, seabirds, spatial ecology

INTRODUCTION

The ecosystem approach for fisheries management necessitates consideration of the natural ecosystem (CCAMLR, 2020; Trochta et al., 2018), including use of data from marine predators (Boyd & Murray, 2001; Hill et al., 2020; Hunt Jr et al., 2000; Reid et al., 2005; Warzybok et al., 2018). For fisheries that target forage species (e.g., krill and small finfish), it is increasingly clear that the spatial and temporal scales of management must be aligned with the spatial and temporal scales of the fishery–predator–prey interaction (e.g., Seyboth et al., 2016, 2021; Watters et al., 2020). Fine-scale maps of prey consumption by predators provide one mechanism to inform a risk assessment and identify areas and times of interaction that can be used to inform management decisions about catch allocations. Such risk assessments can be updated as new data become available, particularly in cases where data on a full suite of predators may be incomplete or out of date.

The Antarctic Peninsula (Figure 1) provides a valuable case study for such a risk assessment of fishery–predator–prey interactions because there is an existing ecosystem approach to fishery management framework in place (see www.ccamlr.org/en/organisation/camlr-convention-text; accessed 7 June 2021) and it is an important fishing area for Antarctic krill (*Euphausia superba*). Additionally, the Antarctic Peninsula provides critical breeding and foraging habitats for numerous marine

predators that consume krill and rely on krill as their main prey source during summer (hereafter termed krill

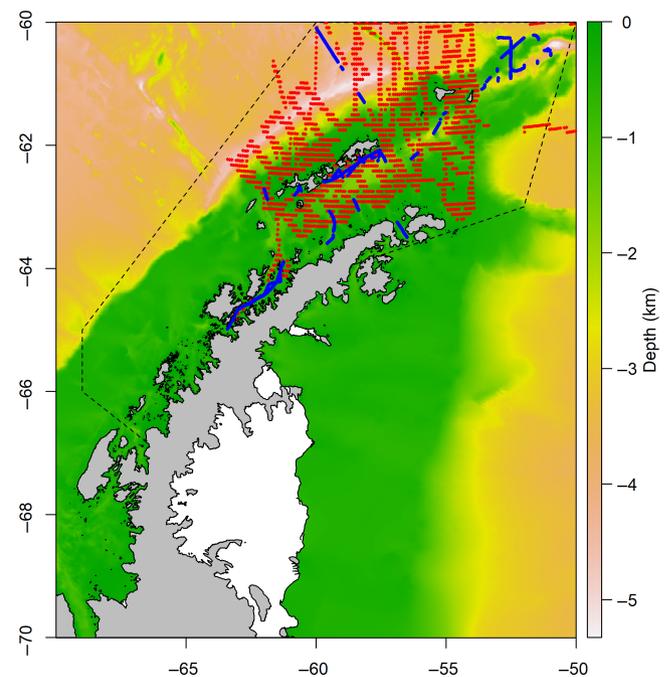


FIGURE 1 FAO Subarea 48.1 (continuous line) with the operational footprint of the krill fishery over the past 5 years (dotted line; from Trathan et al., 2018) and the area surveyed for seabirds and fur seals from US AMLR data (red tracks; Santora & Veit, 2013) and whales from Brazilian PROANTAR data (blue tracks)

predators; Trathan & Hill, 2016). The most recent estimates of abundance for these predators in the Antarctic Peninsula and South Shetlands Islands region (Figure 1) include 1.3 million pairs of Adélie (*Pygoscelis adeliae*), 2.1 million pairs of chinstrap (*Pygoscelis antarctica*), and 120,000 pairs of gentoo (*Pygoscelis papua*) penguins (Humphries et al., 2017). However, estimates for many of these populations date back many decades (Humphries et al., 2017; Trathan et al., 2019) and Strycker et al. (2020) show that chinstrap penguins have declined considerably in this area since some of these estimates were made. Additionally, 6,991 humpback (*Megaptera novaeangliae*, CV: 32.41%), 7,395 minke (*Balaenoptera bonaerensis*, CV: 35.98%), 43 southern right (*Eubalaena australis*, CV: 185.34%), and 1,492 fin whales (*Balaenoptera physalus*, CV: 57.08%) were estimated to forage in approximately the same area during the austral summer of 2000 (Reilly et al., 2004). However, many populations of cetaceans are still increasing as they recover from historical whaling (Branch, 2011; Jackson et al., 2015; Pallin et al., 2018; Tulloch et al., 2018). Indeed, humpback whales in the nearby Western South Atlantic population are believed to have recovered to at least 93% of pre-whaling sizes (Zerbini et al., 2019), whereas the recovery of other cetacean species in the study area is likely less advanced. Consequently, abundance estimates from decades past almost certainly underrepresent the current size of cetacean populations. Furthermore, Antarctic fur seals (*Arctocephalus gazella*, ~13,000 individuals), crabeater seals (*Lobodon carcinophaga*, ~300,000 individuals, CV: 18.6%), finfish (~13,000 million individuals), and flying seabirds are also important consumers of krill in this region at certain times of year (Forcada et al., 2012; Hill et al., 2007; Kock, 1985; Santora & Veit, 2013). Although these studies go some way to increase our understanding about the abundance of some krill predators, many of these estimates are outdated, or contain no measure of interannual variability. Further, population estimates for flying seabirds and finfish remain challenging (Trathan & Hill, 2016). Our understanding of how some of these species distribute themselves at finer scales within this wider region is limited. Shortcomings in our understanding of the abundance, distribution, consumption rates, and foraging ranges of krill predators are of concern because ecosystem dynamics are subject to extensive and ongoing environmental change, while krill are also the target of the largest fishery in the Southern Ocean (Hofman, 2019; Nicol et al., 2012; Seyboth et al., 2016).

As a result of commercial whaling, an estimated 1.8 million whales were removed from the Southern Ocean (Ballance et al., 2006), with at least 16,497 blue, 34,823 fin, and 1,221 humpback whales taken from feeding

grounds in Subarea 48.1 (Allison, 2016). Similarly, demersal finfish and fur seals were harvested to very low levels in this area (Ainley & Pauly, 2014; Bengtson et al., 1990). Such population declines potentially provided a surplus of krill to other krill predators and enabled rapid population growth (Laws, 1985), although others have suggested krill and krill predator dynamics in the whaling and post-whaling period are far from understood (Ballance et al., 2006; Surma et al., 2014; Tulloch et al., 2018). Subsequently, as baleen whale (Branch, 2011), finfish (Barrera-Oro et al., 2017), and fur seal (Boyd, 1993; Hucke-Gaete et al., 2004) populations began to recover, competition between krill predators is likely to have occurred, possibly resulting in a change to ecosystem dynamics. Simultaneously, mean annual air temperature has been increasing at the Antarctic Peninsula since the 1950s (Turner et al., 2016; Vaughan et al., 2003). Long-term increases in air temperature coincide with a gradual decrease in the frequency of cold years with extensive sea ice (Smith & Stammerjohn, 2001). Reduced sea ice may impact predators by changing habitat availability (e.g., Fraser et al., 1992; Trivelpiece et al., 2011), or krill availability, partly as a result of reduced krill recruitment (Loeb et al., 1997; Veytia et al., 2020) leading to changes in the abundance and distribution of krill (Atkinson et al., 2004). Additionally, winter sea ice extent may impact the structure of lower trophic-level communities. For example, reduced sea ice favors the growth of salps (*Salpa thompsoni*), another species of zooplankton, which is only occasionally consumed by krill predators such as penguins, due to its low energetic value and high water content (Thiebot et al., 2017). Such conditions may result in reduced spawning of krill and higher mortality rates of larval krill (Loeb et al., 1997, but see Walsh et al., 2020). Reduced sea ice may also allow cryptophytes, which are too small for krill to graze on, to dominate phytoplankton communities, as opposed to diatoms, which thrive in years of increased sea ice and provide a food source for krill (Mendes, Tavano, Dotto, et al., 2018; Mendes, Tavano, Kerr, et al., 2018). In addition to these long-term trends, the ecosystem is modulated by climatic oscillations including the El Niño Southern Oscillation and the Southern Annular Mode. These mechanisms are thought to drive the interannual variability in the marine ecosystem productivity and dynamics (e.g., Loeb et al., 2009; Loeb & Santora, 2013; Saba et al., 2014; Trathan & Murphy, 2002). It is possible that top-down pressures including increased competition for krill from recovering whale and finfish populations, recovered fur seal populations and commercial fisheries, combined with bottom-up, climate-driven environmental changes could result in reduced krill availability for

penguins and other krill predators (Ballance et al., 2006; Hofman, 2017; Trathan et al., 2012; Trivelpiece et al., 2011).

In the Southern Ocean, krill are abundant over the continental shelves and the open ocean, and high krill density is frequently associated with shelf or shelf-breaks (Nicol, 2006; Trathan et al., 2003). In the Antarctic Peninsula and South Shetland Islands region, larger krill are found mainly in the open ocean and along the shelf-break during spring and summer and juvenile krill occupy the inner shelf waters (Atkinson et al., 2008; Reiss et al., 2008; Siegel et al., 2013). Additionally, adult krill perform seasonal migrations from offshore waters in summer to on-shelf habitats, often under sea ice or in the marginal ice zone, in winter (Lascara et al., 1999; Marschall, 1988; Nicol, 2006; Reiss et al., 2017; Siegel, 1988; Warwick-Evans et al., 2022).

Increasing commercial harvesting of krill, and how the fishery should be managed from an ecosystem perspective in this dynamic environment, is a pressing issue for the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). In 1981, CCAMLR was established with the aim of setting catch limits for the krill fishery in a way that minimizes the risks to populations of krill predators. In the absence of clear ecological understanding about the impacts of fishing, CCAMLR has set regional catch limits (620,000 t) that it believes to be precautionary and which represent approximately 1% of estimated krill regional standing stock (standing stock for the southwest Atlantic is estimated to be 62.6 million tons with mean density of 30 g m^{-2} over 2 million square kilometers and with a sampling coefficient variation of 13%; Figure 1) estimated in 2019 (Hill et al., 2016). However, high levels of local variability observed in availability of krill abundance can equal two or three orders of magnitude (Fielding et al., 2014; Reiss et al., 2008). Furthermore, since the 1990s, the catch has gradually increased (Nicol et al., 2012) and now regularly reaches the local catch limits of 155,000 t at the Antarctic Peninsula (FAO Subarea 48.1). The increase in catch has coincided with a growing concentration of catches in the northwest Antarctic Peninsula (Trathan et al., 2018; Trathan, Fielding, et al., 2021) that may increase the potential for competition for krill with krill predators (Watters et al., 2020). The changes in the operational patterns of the fishery over time highlight the challenges of managing the fishery from an ecosystem perspective. In particular, CCAMLR has no agreed mechanism to respond to information from predators that would allow it to minimize negative impacts from the fishery (Boyd & Murray, 2001; Hill et al., 2020), even though metrics of predator performance are collected at various locations in the region. We argue here that an important step to

strengthening the role of predator monitoring for the management of the krill fishery is to estimate fine-scale, spatially explicit krill consumption needs of krill predators to improve prior risk assessments (e.g., Hewitt et al., 2004; Watters et al., 2013) and identify critical gaps in data availability that reduce our uncertainty about total predator demand. Here, we take the first step to estimate the fine-scale (relative to the scale of management, which is at FAO Subarea scale, or approximately 500–1000 km) distribution of krill consumption using the most up-to-date data on predator abundance and distribution (e.g., Humphries et al., 2017; Santora, Veit, et al., 2017; Secchi et al., 2011). We combine recent telemetry-based behavioral data, at-sea observational surveys, regional estimates of predator abundance, and physiological data to estimate the spatial distribution of krill requirements for 17 species of krill predator. Although this is the largest group of species considered in this context to-date, we recognize that it does not include other important krill predators, notably finfish and baleen whales (other than humpback and fin whales; Figure 2).

METHODS

Study area

Our study area is within FAO Subarea 48.1 (Figure 1), which is becoming increasingly important to the krill fishery, while it also hosts a high abundance and diversity of krill predators. However, the fishery does not operate across the entire Subarea, operating almost exclusively over shelf waters around the South Shetland Islands and northern Antarctic Peninsula. As such, our study area was defined as the operational footprint for the krill fishery between 1980 and 2018 within FAO Subarea 48.1 (Figure 1). This enables us to estimate the consumption of krill in locations relevant to the management of the krill fishery, without extrapolating models beyond the environmental range of surveys; for example, environmental conditions to the northwest of Subarea 48.1 are very different from those within the areas where our data were collected.

Data collection

Penguins

Adélie (*P. adeliae*), gentoo (*P. papua*), and chinstrap (*P. antarctica*) penguins breeding on the South Shetland Islands were tracked during the chick-rearing periods

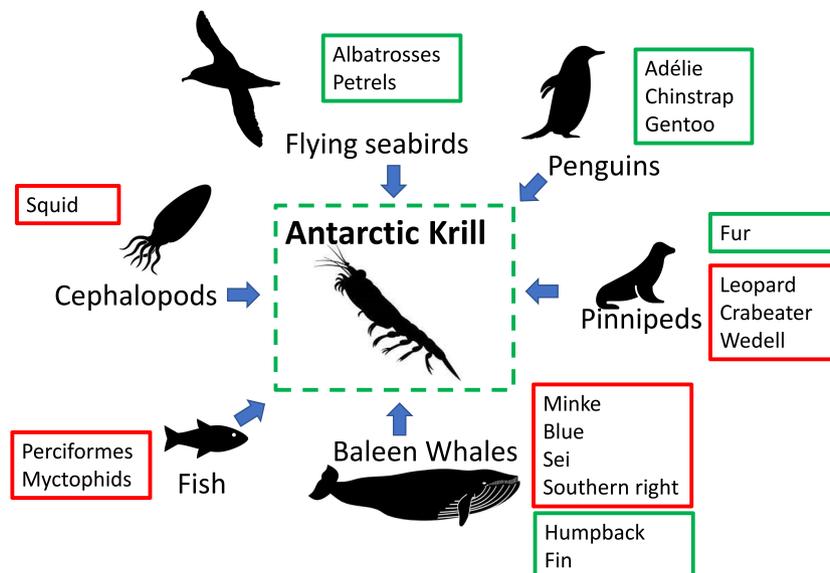


FIGURE 2 The major consumers of postlarval krill in the Antarctic Peninsula region. A green box indicates those modeled in this study. A red box indicates those that have not been included. A green dashed box represents species modeled in Warwick-Evans et al. (2022). Consumption of krill eggs, larvae, and early demographic stages is not considered.

TABLE 1 The location and yearly sample size of penguin colonies and humpback whales that were tracked with GPS/PTT devices and used to estimate the at-sea distribution of each species

Species	Colony name	Colony coordinates	Population size (year estimated)	Year (no. birds tracked)
Adélie	Hope Bay	56.9978 W, 63.3972 S	104,139 (2012)	2013 (5), 2014 (5)
	Admiralty Bay	58.446 W, 62.176 S	3,627 (2013)	2003 (3), 2004 (10), 2005 (10), 2006 (5), 2007 (4), 2010 (4), 2011 (1), 2012 (6), 2013 (7)
Gentoo	Barton Peninsula	58.791 W, 62.224 S	1,684 (2007)	2006 (9), 2007 (5)
	Admiralty Bay	58.446 W, 62.176 S	6,595 (2013)	2003 (2), 2005 (8), 2006 (8), 2007 (8), 2010 (2), 2011 (1), 2012 (3), 2013 (2), 2014 (5)
	Cape Shirreff	60.787 W, 62.452 S	916 (2010)	2003 (5), 2005 (9), 2006 (12), 2007 (13), 2008 (14), 2009 (8), 2010 (8), 2011 (8), 2012 (8), 2013 (3), 2014 (3)
Chinstrap	Admiralty Bay	58.446 W, 62.176 S	2305 (1996)	2005 (3), 2006 (9), 2007 (10), 2010 (3), 2011 (5), 2012 (4), 2013 (5)
	Cape Shirreff	60.787 W, 62.452 S	4127 (2010)	1999 (7), 2001 (3), 2002 (10), 2003 (5), 2004 (4), 2005 (8), 2006 (9), 2007 (8), 2008 (7), 2009 (16), 2010 (9), 2011 (6), 2012 (6), 2013 (5), 2014 (5)
	Barton Peninsula	58.791 W, 62.224 S	3117 (2020)	2006 (5), 2007 (13)
Humpback whale	West Antarctic Peninsula			2012 (5), 2013 (12), 2015 (7), 2016 (9)

Note: Population size is from MAPPPD (Mapping Application for Penguin Populations and Projected Dynamics) data portal (Humphries et al., 2017).

(January–early February) between 1999 and 2014 (Table 1, Appendix S2: Figure S1). Each individual was instrumented with a GPS or a Platform Terminal Transmitter (PTT) device. Devices were set to record positions when dry (at the surface). The mass of the devices was less than 1% of the birds' body mass. Birds were captured at the nest site and the instrument attached to the center line of the back of each individual using either Tesa tape or plastic cable ties and two-part quick setting epoxy resin following methods adapted from (Wilson et al., 1997). Birds were only selected where both partners were present, with birds taken from both the edge and middle of a colony. Handling time was <10 min per individual on deployment and <5 min on recovery. Birds were recaptured after approximately 5–7 days, at which point the devices were removed and the data downloaded for GPS devices, or recovered from ARGOS CLA for PTT devices. During device recoveries, if the partner was not present, chicks were protected from thermal shock and from predation by predatory seabirds using a blanket and hard shield.

Whales—Tracking data

Humpback whales *M. novaeangliae* feeding in the western Antarctic Peninsula were tracked during January to March between 2012 and 2016 (Table 1, Appendix S2: Figure S2). Individuals were tagged near the dorsal fin, using Wildlife Computers (Redmond, WA, USA) SPOT5 devices, contained in a sterilized housing designed to penetrate the whales skin and blubber up to 290 mm. Tags were deployed using an ARTS Whale Tagging PLT compressed air system and anchored in the tissue using stainless steel barbs, with the transmitting antenna remaining free outside of the animal (Weinstein & Friedlaender, 2017). All whales were presumed to be adults based on their size. Tags deployed in 2012 were duty cycled and only transmitted during 12:00–4:00 AM and 12:00–4:00 PM. All subsequent tags were set without duty cycling and attempted to transmit data on each surfacing.

Whales—At-sea survey data

During February and March between 2013 and 2020, the PROANTAR (Brazilian Antarctic Program) conducted ship surveys for cetaceans in the western Antarctic Peninsula (Figure 1). The surveys were carried out aboard the Polar Vessel Almirante Maximiano, with observation platforms 14.6 m above sea level. Two observers worked simultaneously (one to port and one to starboard) looking

for cetaceans following the line transect protocol (Buckland et al., 2001). Each observer covered one side of the trackline in a 90° quadrant, with a higher searching effort toward the trackline. The observers used Fujinon 7 × 50 reticled binoculars and the naked eye to search for cetaceans. Average ship speed was 10 knots, and surveys were conducted when visibility was >3 nm, and Beaufort Sea state was ≤6. For each sighting, data were collected on species, group size, GPS position of the ship, number of reticles to the sighting, bearing to the sighting, date, time, navigation, and environmental conditions. For a more detailed description of survey protocol, see Secchi et al. (2011).

Flying seabirds and fur seals

Between January and March 2003–2011, the US Antarctic Marine Living Resources (AMLR) program conducted surveys of flying seabirds and fur seals from ship transects in the Bransfield Strait, and South Shetland Islands region (Figure 1). Strip transect methods were used to estimate relative seabird and fur seal abundance and counts were made within a 90° arc out to 300 m on the side of the trackline with the best visibility. The abundance estimates are termed as *relative* to mitigate imperfect detection in the event that not all individuals present within the 300-m strip width were observed. All birds and seals were counted whether flying, porpoising, or resting on the water. For a more detailed description of survey protocol and model development for flying seabirds, see Santora, Veit, et al. (2017) and Warwick-Evans et al. (2021).

Data processing and model fitting

For each species of predator, we used the relevant survey observations, or tracking data locations, to estimate the density of individuals at a scale of 1 × 1 km within the study area using generalized additive models (GAMs). We then combined these habitat distribution models with estimated energy requirements and diet to estimate the spatial distribution of krill consumption by each species.

Tracking data

For penguins, all locations on land and within a 500-m buffer around the nest site were excluded, to retain only positions while on foraging trips; 500 m was selected in order to avoid location errors, while birds were on the nest being classed as trips. For both penguins and whales,

the McConnell speed filter (Sumner, 2012) was applied to remove erroneous positions with speeds $>8 \text{ km h}^{-1}$ (penguins) or $>20 \text{ km h}^{-1}$ (whales). Subsequently, the movement parameters were estimated for each individual (for each trip for penguins) and models were applied in order to interpolate position data to regular intervals; this resulted in location predictions at constant time intervals while taking movement parameters into account. The *crawl* package (Johnson, 2013) interpolates locations between fixes using a correlated random walk model, which is more realistic than assuming linear travel between fixes.

Analyses were conducted separately for each species. For each individual in turn, three control points (pseudo-absences) (Aarts et al., 2008) for each location were randomly selected within a given range, and values of each covariate (as described below) were extracted for all points. For penguins, the range was that of the maximum distance traveled from the colony of tagged individuals of that species. For whales, this range included a subset of the study area (Appendix S2: Figure S2) corresponding with the locations recorded by tracked whales. Pseudo-absences were randomly assigned a date corresponding to the date of the tracking data. The probability of occurrence was modeled as a function of each of the covariates using GAMs with a binomial distribution and a logit link function in the R package *mgcv* (Wood, 2006). The smooth of each covariate was taken, and the number of knots from 3 to 7 was evaluated visually to ensure a good model fit without overfitting. Model overfitting was further reduced by using cubic regression splines with shrinkage, which penalize variables during fitting (Wood, 2006). Semi-variograms produced using the R package *gsta* (Pebesma, 2004) showed some autocorrelation in our data; however, the cross-validation method for model selection, described below, provides a cautious approach to achieve a parsimonious model, and thus, this is unlikely to affect our final models (Aarts et al., 2008). Model selection followed the forwards stepwise approach, using k -fold cross-validation between sites (penguins) or individuals (whales). For each variable, models were constructed using data from all, but one of the sites/individuals for which tracking data were available and evaluated by using the model to predict the distribution for the excluded population. Models were then evaluated using the area under the curve (AUC), which was calculated by generating a receiver operating characteristic curve using R package *pROC* (Robin et al., 2011). Values may range from 0.5 to 1.0, where a value of 0.5 is no better than random, and 1.0 indicates a perfect model. For models based on tracking data, model selection using cross-validation is considered to be the most appropriate method and avoids overfitting models, which may occur if alternative approaches, such as Akaike information

criterion (AIC), are used (Aarts et al., 2008). Each of the models was ranked according to AUC value, and the covariate from the highest-ranking model was selected. The remaining covariates were added to this model in turn, and the best model containing two covariates was identified. This process continued until there was no increase in AUC if another covariate was added. For two models with the same AUC, the model with fewer variables was identified as the final model. For whales, the final models were used to predict the probability of occurrence across the study area. The value for each cell was divided by the total of all cells to create a raster of the relative importance of each cell (i.e., summing to 1).

For penguins, the location and size of all known colonies in Subarea 48.1 were downloaded from the Mapping Application for Penguin Populations and Projected Dynamics (MAPPPD) data portal (Appendix S2: Figure S3; Humphries et al., 2017), and for each colony within the study area (both tracked and untracked colonies), the probability of occurrence of each species in each 1-km^2 cell throughout the study area was predicted using the final GAMs. For each colony, a raster of the relative importance of each cell to that colony was calculated as described above.

At-sea survey data

Whales

The distributions of humpback and fin whales were modeled independently. Traditional methods to calculate the along-bearing distance to each sighting, using the horizon as a reference point (Buckland et al., 2001), were used in most instances. However, during some periods of these surveys, the view of the horizon was obstructed by land. Thus, methods described by Lerczak and Hobbs (1998), which use land as a reference point instead of the horizon, were utilized in these instances (Appendix S1). R package *Distance* (Miller, 2017) was used to identify the most appropriate detection function. The half-normal and hazard-rate key functions were tested, combined with each of the covariates: Beaufort Sea state, sightability, visibility, and swell in turn. Subsequently, combinations of these covariates were tested. Sightability is a combination of other covariates and consequently was not included in models with other covariates. The best model was chosen for each species according to AIC and goodness of fit. The effort data (i.e., trackline) were segmented to 5-km segments to approximately capture the variability in spatial distribution of animals and any influential environmental characteristics. R package *dsm* (Miller et al., 2019) was used to fit a density surface

model (Hedley & Buckland, 2004; Miller et al., 2013), where the relationship between animal density and environmental covariates (as described below) was a GAM and where *dsm* is a wrapper for *mgcv* functionality (Wood, 2006). Along-track density was characterized as a Tweedie distribution in order to capture the overdispersion; the Tweedie parameter was estimated during the GAM fit. Models were applied to each covariate in turn and forward model selection was based on AIC and deviance explained (Miller et al., 2013) as this is the most commonly used approach using this type of modeling framework. We used the functions *rqgam.check()* to investigate model residuals. The final model for each species was used to predict the distribution and density (individuals per square kilometer) of humpback and fin whales at 1 by 1-km resolution across the study area.

Fur seals

The survey effort data were segmented to 5-km segments to approximately capture the variability in spatial distribution of animals and any influential environmental characteristics. All remaining segments, which were <5 km, were removed from the dataset. The position of the midpoint of each segment and the corresponding time that the ship reached this location were recorded. The number of sightings and the number of individuals observed along each segment were summed. Hurdle models were used to model the relationship between seabird sightings and environmental covariates. Hurdle models comprise two component models; first, the probability of occurrence is modeled using a presence-absence general linear model (GLM) with a binomial error structure, and second, the relative density of individuals, conditional on their presence, is modeled using a GLM with a zero truncated negative binomial error structure (Zuur et al., 2009). The hurdle approach helps to overcome the statistical challenges associated with zero-inflation and overdispersion of data (e.g., Goetz et al., 2012; Sveegaard et al., 2012; Waggitt et al., 2020). To account for nonlinear relationships between the environmental predictors and the response variables, the second-order polynomial of the values of environmental covariates was evaluated in addition to the linear value.

Model selection followed the forward stepwise approach: Initially, a null model was run with no covariates in either the count or binomial section. Subsequently, each covariate was input into the binomial model and all covariates which resulted in a model significantly different to the null model were noted. Likelihood ratio tests and AIC values were used to compare models. The procedure was repeated for each covariate in the count model.

Subsequently, a full model was run with all significant covariates in each part of the model. Each covariate was dropped in turn (starting with the least significant according to the summary table), and likelihood ratio tests were used to measure the difference between the models. This procedure continued until no more covariates could be dropped.

Model residuals were checked for spatial and temporal autocorrelation using Moran's *I* tests and autocorrelation function plots. Uncertainty in model predictions was calculated for the final models using a nonparametric bootstrapping approach (Davison & Hinkley, 1997; Fieberg et al., 2020). For each species in turn, the data were resampled with replacement and were input into the final hurdle model. The model was then used to predict the relative density of individuals across the study area, and the predicted density in each grid cell was stored. This was repeated 1000 times and the difference between the 5% and 95% quantiles of predicted density in each grid cell was calculated, providing an estimate of absolute uncertainty. This was standardized by dividing by the maximum value. The final models were then applied to predict the distribution across the survey area at a scale of 1 km².

Flying seabirds

For flying seabirds, we limited our study area by latitude (64° S, the highest latitude of the survey) as it is likely that some of the species observed do not travel toward the southwest of our study area. This was not necessary for penguins and whales as we know the breeding locations of penguins, and we know from the tracking data that humpback whales occur throughout the study area.

Hurdle models developed by Warwick-Evans et al. (2021) and similar to those described for fur seals above were used to predict the density of seabirds (individuals per square kilometer) across the area at a scale of 1 km². The estimates were summed across all cells to estimate the abundance of each species within this area. Confidence intervals were estimated using a parametric bootstrapping approach.

Covariate data

Both static and dynamic biologically meaningful covariate data were used in the analyses (Appendix S2: Table S1 and Figure S4). Chlorophyll *a* provides a proxy for primary productivity, which is frequently used to indicate areas of increased krill prey biomass (Suryan et al., 2012). Although krill may not consume all types of phytoplankton (Haberman et al., 2003), chlorophyll is

frequently used as a proxy for prey in many studies of this type. Sea surface temperature may limit the broad-scale distribution of predators (Hinke et al., 2019), possibly as a result of the underlying distribution of prey (e.g., Nicol et al., 2000). Depth and slope may indicate on-shelf, off-shelf, or shelf-break habitats, or other areas of variation in seabed topography and may result in variation in prey availability (Paiva et al., 2010) or create environments, which retain or aggregate prey (Benjamins et al., 2015; Hunt, 1999). Current speed and sea-level anomaly were included to identify areas of increased eddies or flows, which may concentrate nutrients or prey (Waggitt et al., 2016). The majority of covariates were used for all taxonomic groups with the exception of: bearing and density (penguins only, described below), distance to colony (penguins and fur seals), distance to coast (whales and fur seals only), sea ice concentration (whales, at-sea survey data), and distance to sea ice (whales and fur seals). Whales observed during at-sea surveys were observed in areas of low sea ice, whereas no locations of tracked whales or fur seals were within the sea ice, hence the different covariates.

The distance to the closest of the known fur seal breeding colonies was calculated for each data point using colony locations described in Bengtson et al. (1990), though this variable was not selected in the final model for fur seals. The distance to the breeding colony of tracked penguins was used in model development for penguins. To make predictions across the study area, the distance to each colony in turn was calculated, and predicted distributions were made independently for each colony. The covariate *bearing*, which is a measure of how directly a penguin travels toward the 750-m shelf-break, relates to the hypothesis that penguins may travel toward the shelf-break, as this may provide increased prey availability (Trathan et al., 2018). This is calculated for each interpolated GPS/PTT location point for tagged individuals, and for all pseudo-absences as the difference between the bearing from the colony to the nearest point of shelf-break, and the bearing of each point (location or pseudo-absence) from the colony. When predicting from models that include *bearing*, a 1×1 -km grid of points was created within 100 km from each colony; the *bearing* covariate was calculated for each point.

The dynamic covariates were based on daily values of remotely sensed oceanographic data. Data were downloaded in the L4 format, where space-time interpolation had already been used to fill any gaps in the data due to cloud cover. We considered two values for each of these covariates in our analyses of the data for all groups. First, values corresponding directly to the day of the survey/tracking location were extracted (we subscript these

variables as *real-time*, e.g., $MSLA_{real-time}$). Second, values were averaged across January and February (corresponding with penguin tracking data), or January–March (corresponding with whale survey/tracking data) and averaged across years to obtain a climatology for the region (we subscript these variables as *clim*, e.g., $MSLA_{clim}$). Real-time and climatological values for the same covariate were never included in the same model. No variables where the Pearson correlation coefficient exceeded 0.7 were included in the same model, and as such, for whale tracking models depth and current speed (both real-time and climatological), and distance to ice and temperature (both real-time and climatological) were not included in the same models.

Estimating consumption

Penguins

The daily energy requirements of individuals averaged across the breeding period (egg laying to fledging, approximately December–February; Appendix S2: Table S2) were multiplied by the population size (from MAPPPD), and the proportion of krill in the diet (Hinke et al., 2007; Appendix S2: Table S2), and divided by an estimate of the mean energy density of krill (4.645 kJ g^{-1} ; Clarke, 1980), to estimate the daily krill requirements of each population. Subsequently, the raster describing the relative importance of cells for each population was multiplied by the krill requirements of the population to create spatially explicit estimates for the daily consumption of krill for each population. The rasters for each population were summed to provide daily krill consumption estimates for each species of penguin across the study area. Finally, the daily krill consumption rasters for chinstraps, gentoos, and Adélies were multiplied by the number of days from egg laying to fledging (85, 95, and 95 for chinstraps, gentoos, and Adélies, respectively) to reflect the total consumption of krill by penguins throughout the breeding period (Croll & Tershy, 1998).

Whales—Tracking

Reilly et al. (2004) estimated the abundance of humpback whales in Subarea 48.1 in 2000 as 6991 individuals and Branch (2011) estimated this to be increasing at a rate of 4.6% per annum (95% confidence interval [CI]: 3.4%–12.9%; for Breeding Stock G), corresponding to approximately 17,185 individuals in 2020. We have estimated the abundance for 2020 to provide an estimate of consumption that is directly comparable to the estimates from our at-sea survey data, assuming that habitat preference from

whales tracked from 2012 to 2016 will remain similar into 2020. Reilly et al. (2004) estimate krill consumption by individual humpback whales as 497 kg day^{-1} (averaged over the entire feeding season), and this was multiplied by 17,185 to estimate the total krill consumption by humpback whales in the study area. Subsequently, the raster of relative importance of each cell was multiplied by the krill consumption estimate to provide a spatially explicit estimate of daily krill consumption for all humpback whales in the study area. Finally, this was multiplied by 120 (days) to estimate the total consumption of krill by humpback whales throughout their foraging season (approximately December–April) in Antarctic waters (Lockyer, 1981). Although aggregations of humpback whales have been observed in the region later in the season (e.g., Nowacek et al., 2011; Weinstein et al., 2017), regional abundance estimates at this time are not known.

Whales–At-sea surveys

The predicted density raster (individuals per square kilometer, at a scale of 1 km^2) for humpback whales was multiplied by 497 (as described above) and for fin whales by 693 (Reilly et al., 2004) to estimate daily krill consumption. These were multiplied by 120 to estimate the total consumption of krill by humpback and fin whales throughout their foraging season across the study area.

Fur seals

Boyd (2002) estimates krill consumption by individual fur seals to be 1.7 t per year, although this varies across age, sex, and breeding status. As it is not possible to determine these demographic traits for individuals observed in at-sea surveys, the estimate of 1.7 t was divided by 365 to estimate a daily consumption of 4.45 kg of krill individuals per day. The predicted density raster (in individuals per square kilometer, at a scale of 1 km^2) was multiplied by 4.45 to estimate the daily consumption of krill by fur seals, and then by 90 to estimate the total consumption of krill by fur seals throughout the summer survey period (January–March).

Flying seabirds

The field metabolic rate (FMR) for each species of flying seabird was extracted from Shaffer (2011) who also provided equations to calculate the FMR for species where FMR was not available. The proportion of krill in the diet of each species was extracted from Croxall

et al. (1985), and Equation (1) was used to calculate the individual daily krill consumption (in grams), where P is the proportion of krill in the diet, 0.8 is assimilation efficiency, and E_{krill} is the energy density of krill (4.645 kJ g^{-1} ; Clarke, 1980).

$$K_{\text{ind}} = (\text{FMR} \times P / 0.8) / E_{\text{krill}}. \quad (1)$$

The seabird distribution rasters (Warwick-Evans et al., 2021) were multiplied by individual daily krill consumption estimates for each species to create spatially explicit krill consumption estimates for 11 species of flying seabird. Finally, these were multiplied by 90 to reflect the total krill consumption during the survey period (January–March) in the peak of the austral summer.

Final predictions of the distribution of krill consumption for all groups (penguins, whales, and flying seabirds) were summed. The amount of krill consumed from waters of different depths was extracted from the maps of total krill consumption.

RESULTS

Krill consumption by predators occurs throughout the study area with increased consumption in nearshore areas around the Antarctic Peninsula and South Shetland Islands (Figure 3, Appendix S2: Figure S5). Krill consumption is particularly high in locations proximate to large penguin breeding colonies across the South Shetland Islands and at the tip of the Peninsula. Areas of increased consumption tend to occur in shallower waters with approximately half of all consumption occurring in depths $<500 \text{ m}$ and 70% occurring in depths $<1000 \text{ m}$ (Appendix S2: Figure S6). The lowest levels of consumption for our study species tend to occur in off-shelf waters further from shore.

Penguins—Tracking data

Models to predict the at-sea distribution of Adélie, chinstrap, and gentoo penguins had high predictive power and deviance explained (Table 2). For all species, *distance from the colony* was the best predictor variable and was negatively associated with probability of occurrence (Appendix S2: Figure S7). Probability of occurrence was greater than 0.5 within 36, 41, and 13 km of the colony for chinstraps, Adélie, and gentoo penguins, respectively. Models for Adélie and gentoo penguins did not improve when additional covariates were included (Appendix S2: Table S3). Models for chinstrap penguins were improved by the addition of the covariate *bearing*,

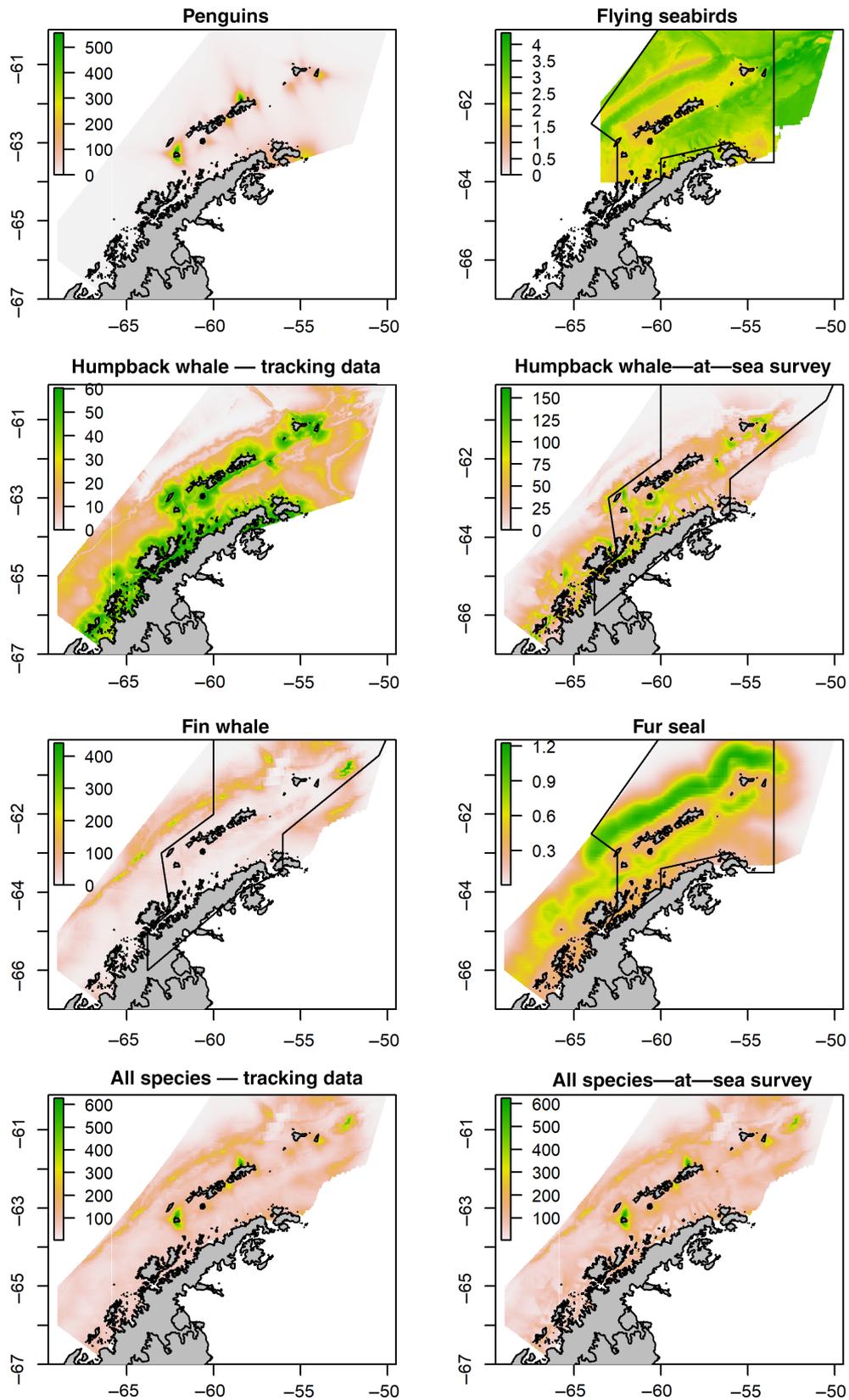


FIGURE 3 Estimates of krill consumption (in kilograms per day) by predators (penguins, flying seabirds fur seals, humpback, and fin whales) using data from at-sea surveys and tracking data in the operational footprint of the krill fishing industry in FAO Subarea 48.1. The rate of humpback population increase for the tracking data was estimated at 4.6% per annum (Branch, 2011) from estimates of 6,991 in 2000 (Reilly et al., 2004). The area surveyed for humpback and fin whales, fur seals, and flying seabirds is indicated by a black line.

TABLE 2 Area under the curve (AUC) values for the final models used to predict the at-sea distribution of penguins, humpback and fin whales, and fur seals from tracking data

Species	Predictor	AUC	Deviance explained	NRMSE
Adélie	Distance to colony	0.92	47	
Gentoo	Distance to colony	0.93	49	
Chinstrap	Distance to colony + bearing	0.93	59	
Humpback (tracking)	Distance to coast + depth	0.87	27	
Humpback (at-sea survey)	Depth + slope + distance to coast		26	
Fin whale	Depth + slope + distance to coast + current speed + SST + chl <i>a</i>		33	
Fur seal	Binomial: distance to coast ² + current ² + sea-level anomaly ² + temperature; count: distance to coast ² + sea-level anomaly ² + temperature			0.037

Note: No AUC value is provided for whales as these models were evaluated using Akaike information criterion. No AUC or deviance explained is presented for fur seals as this is not appropriate for hurdle models. Normalized root mean square values are presented instead.

which increased deviance explained from 40 to 59%, indicating directional movement toward the shelf-break. The location and spatial scale of krill consumption varied among species (Figure 4), and important areas of consumption occurred at very fine spatial scales. In the most highly used areas, Adélie, chinstrap, and gentoo penguins consume up to 280, 560, and 17 kg km⁻² day⁻¹ of krill, respectively (Figure 4).

Whales—Tracking data

The model to predict the distribution of humpback whales using tracking data had moderate predictive power (Table 2) and explained 27% of the deviance. Probability of occurrence was negatively associated with distance to the coast and had a quadratic association with depth, peaking at ~500 m (Appendix S2: Figure S8). Moran's *I* test showed little autocorrelation in model residuals. Estimates from this model suggest that in the most highly used areas, humpback whales may consume up to 60 kg km⁻² day⁻¹ of krill (Figure 3).

Whales—At-sea surveys

In total, 1,369 groups (2,960 individuals) of humpback whales and 326 groups (853 individuals) of fin whales were sighted during 7,053 km of effort (Appendix S2: Figure S9). Appendix S2: Table S4 provides a summary of environmental conditions throughout the survey. For both species, the most parsimonious model to estimate the detection function used the hazard rate key, with no

additional covariates, and revealed a mean probability of detection of 0.69 (CV: 0.12; Appendix S2: Table S5 and Figure S10) out to the truncation distance for humpback whales, and 0.40 (CV: 0.12; Appendix S2: Table S5 and Figure S10) for fin whales. The best model to estimate the abundance and distribution of humpback whales in the area included distance to the coast, depth, and slope (Table 2, Appendix S2: Table S6 and Figure S11). The best model to estimate the abundance and distribution of fin whales in the area included distance to the coast, depth, slope, current speed, chlorophyll *a*, and sea surface temperature (Table 2, Appendix S2: Table S6 and Figure S12). Both models had a good fit, with no residual autocorrelation detected. The estimated abundance of humpback whales in the study area was 12,724 individuals (95% CI = 10,944–14,791, CV = 0.06) and of fin whales was 14,360 individuals (95% CI = 8,645–23,946, CV = 0.23). Consumption estimates suggest that in the most intensively used areas, humpback whales may consume up to 162 kg km⁻² day⁻¹ (Figure 3), and fin whales consume up to 415 kg km⁻² day⁻¹. When alternative consumption estimates described by Reilly et al. (2004) and Savoca et al. (2021) were combined with the high and low confidence bounds, the amount of krill consumed by humpback and fin whales in the study area varied considerably (Appendix S2: Table S7).

Fur seals—At-sea surveys

In total, 1,029 groups (1,393 individuals) of fur seals were sighted during 27,235 km of survey effort (Appendix S2: Figure S13). The best model to estimate the abundance

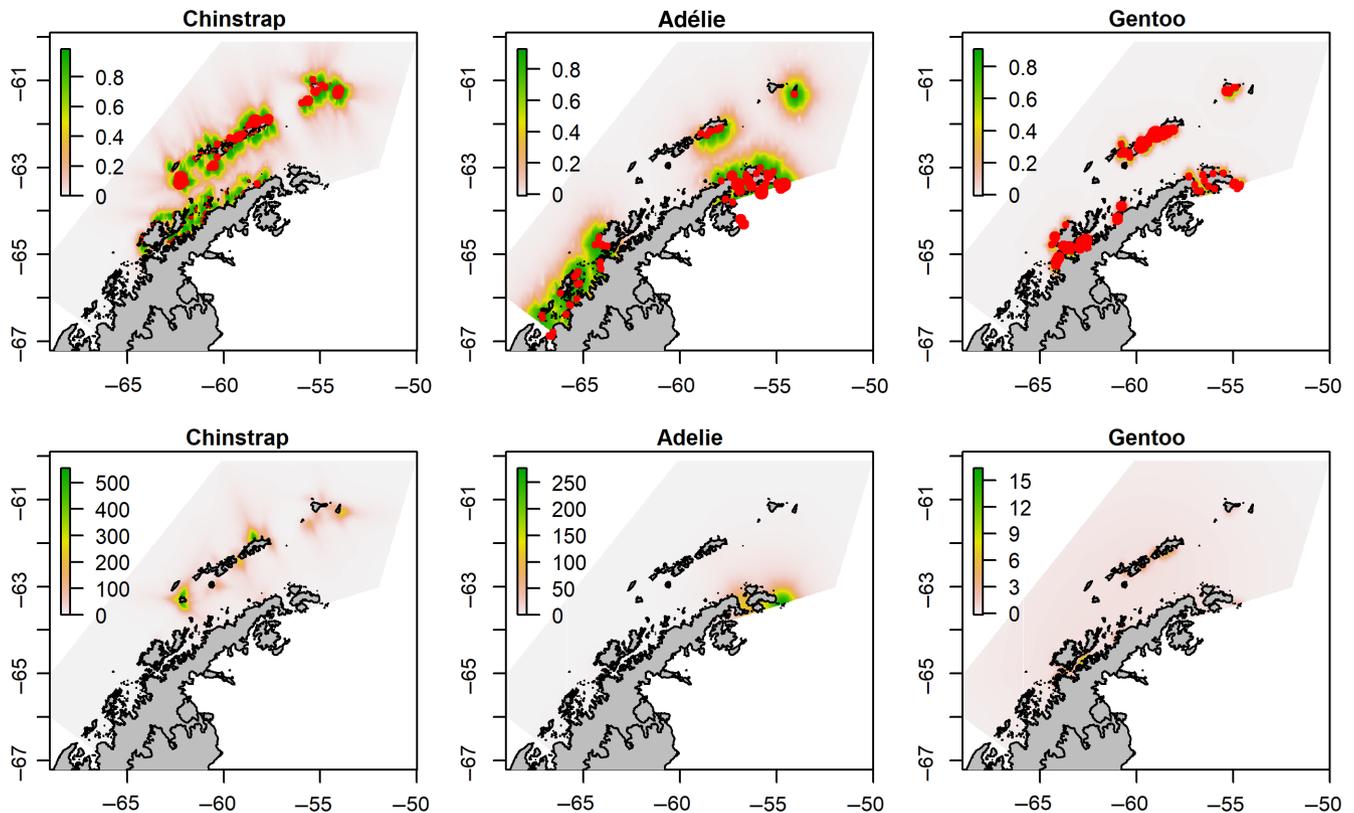


FIGURE 4 Estimated probability of occurrence (top panel) and estimates of krill consumption (in kilograms per day; bottom panel) by penguin species in operational footprint of the krill fishery in CCAMLR Subarea 48.1. The location of penguin colonies is marked in red. Note the different scales between the species.

and distribution of fur seals included distance to coast², current², sea-level anomaly², and temperature in the binomial model and distance to coast², sea-level anomaly², and temperature in the count model (Table 2, Appendix S2: Table S8 and Figure S14). The model had good fit with little residual autocorrelation. The estimated abundance of fur seals in the study area was 25,193 individuals (95% CI = 22,365–33,195). Consumption estimates from this model suggest that in the most intensively used areas fur seals may consume up to 1.2 kg km⁻² day⁻¹ (Figure 3).

Flying seabirds—At-sea surveys

The models for flying seabirds performed moderately to well in their ability to predict the probability of occurrence and density of seabirds in the region (Warwick-Evans et al., 2021). Confidence intervals for abundance estimates were large, particularly in species where large flock sizes were observed (Table 3). Krill consumption was highly variable among species (Table 3, Figure 5), with southern fulmars (*Fulmarus glacialis*) and cape petrels (*Daption capense*), both medium-sized local breeders, being the principal krill consumers. Small species and nonlocal breeders

consumed the least krill. The scale of krill consumption by flying seabirds was lower relative to estimated consumption by penguins and humpback whales (Figure 3, Table 3).

DISCUSSION

We present spatially explicit estimates of krill consumption by penguins, flying seabirds, fin whales, humpback whales, and fur seals during austral summer in the northern Antarctic Peninsula and South Shetland Islands region. Our models were robust with moderate to high predictive power and explained model deviance. Our predicted distributions are similar to those from previous studies (e.g., Dias et al., 2018; Santora, Sydeman, et al., 2017). We show that krill consumption is highly variable across the region, and often concentrated at very small spatial scales, highlighting the need for the management of the krill fishery at spatial scales similar to the scales at which predators operate (Watters et al., 2020). We believe that these estimates may be useful to krill fisheries management and ecosystem modelers, and discuss limitations and gaps in the current understanding of the distribution and abundance of krill predators in the region.

TABLE 3 Estimates of abundance and krill consumption with confidence intervals (in parentheses; breeding populations of penguins downloaded from MAPPPD [Mapping Application for Penguin Populations and Projected Dynamics] data portal, estimated abundance of whales, fur seals, and flying seabirds from at-sea surveys)

Species	Percentage of krill in diet	Abundance estimates for the study area (no. individuals)	Energetic requirements per individual (kJ day ⁻¹)	Individual krill requirements (g day ⁻¹)	Krill requirements (mg day ⁻¹)	Summer krill requirements (mg ⁻¹)
Chinstrap penguin	97.5	4.2 million	3918	821	3448	294,072
Gentoo penguin	82	240,000	5767	1005	241	23,162
Adélie penguin	98	2.6 million	4665	949	2467	237,970
Wandering albatross	10	5174 (4300–6178)	5050	109	0.56 (0.47–0.67)	50 (42–61)
Gray-headed albatross	15	9527 (7773–12,357)	3003	97	0.91 (0.75–1.2)	83 (67–107)
Black-browed albatross	38	82,957 (68,265–103,022)	2940	241	20 (16–25)	1799 (1480–2234)
Wilson's storm petrel	45	139,415 (129,313–154,237)	149	14	2 (1.8–2.2)	176 (163–194)
Black-bellied storm petrel	48	80,965 (75,814–86,196)	238	25	2 (1.9–2.2)	182 (171–194)
Prions	58	88,191 (70,036–123,445)	489	61	5.5 (4.3–7.5)	484 (384–677)
Southern giant petrel	80	62,793 (54,041–71,349)	5412	932	58 (50–66)	5267 (4532–5984)
Cape petrel	85	1,039,873 (833,532–1,295,439)	1495	274	285 (228–355)	25,650 (20,520–31,950)
White-chinned petrel	27	33,047 (27,969–40,762)	2905	168	5.5 (4.7–6.8)	500 (423–616)
Southern fulmar	85	661,208 (505,811–872,497)	1805	330	218 (167–287)	19,638 (15,022–25,913)
Blue petrel	83	42,444 (27,957–86,921)	561	100	4.2 (2.8–8.7)	378 (252–783)
Fur seal	90	25,193 (22,365–33,195)	...	4450	112 (99–147)	10,080 (8910–13,230)
Fin whale	100 ^a	14,360 (8645–23,946)	...	693,070	9951 (5991–16,595)	1,194,120 (718,920–1,991,400)
Humpback whale						
At-sea survey	100	12,724 (10,944–14,791)	...	497,230	6327 (5441–7354)	759,240 (652,920–882,480)
Tracking data	100	17,185 (3500–79,144)	...	497,230	8545 (1740–39,352)	1,025,400 (208,843–4,722,334)
Sum of all species						
Using humpback at-sea survey data	23,150 (18,165–31,014)	2,572,851 (1,423,806–2,955,762)
Using humpback tracking data	25,368 (14,578–63,012)	2,839,011 (979,729–6,795,616)
Sum of all species including other baleen whale estimates from 2000 ^b						
Using at-sea survey data	24,838 (19,853–32,702)	2,775,411 (1,626,366–3,158,322)
Using tracking data	27,056 (16,266–64,700)	3,041,571 (1,182,289–6,998,176)

Note: Summer estimates are for the duration of 85, 95, 95, 120, 120, 90, and 90 days for chinstrap, Adélie, and gentoo penguins, humpback whales, fin whales, fur seals, and flying seabirds, respectively. Confidence intervals were obtained using a bootstrapping approach, sampling the data with replacement, and simulated 10,000 times. Estimates of error are unavailable for the population sizes of penguins obtained from MAPPPD.

^aFor calculation purposes, Reilly et al. (2004) assumed 100% of fin whale diet was krill, however acknowledged that it is likely that fin whales have a more varied diet.

^bFrom Reilly et al. (2004).

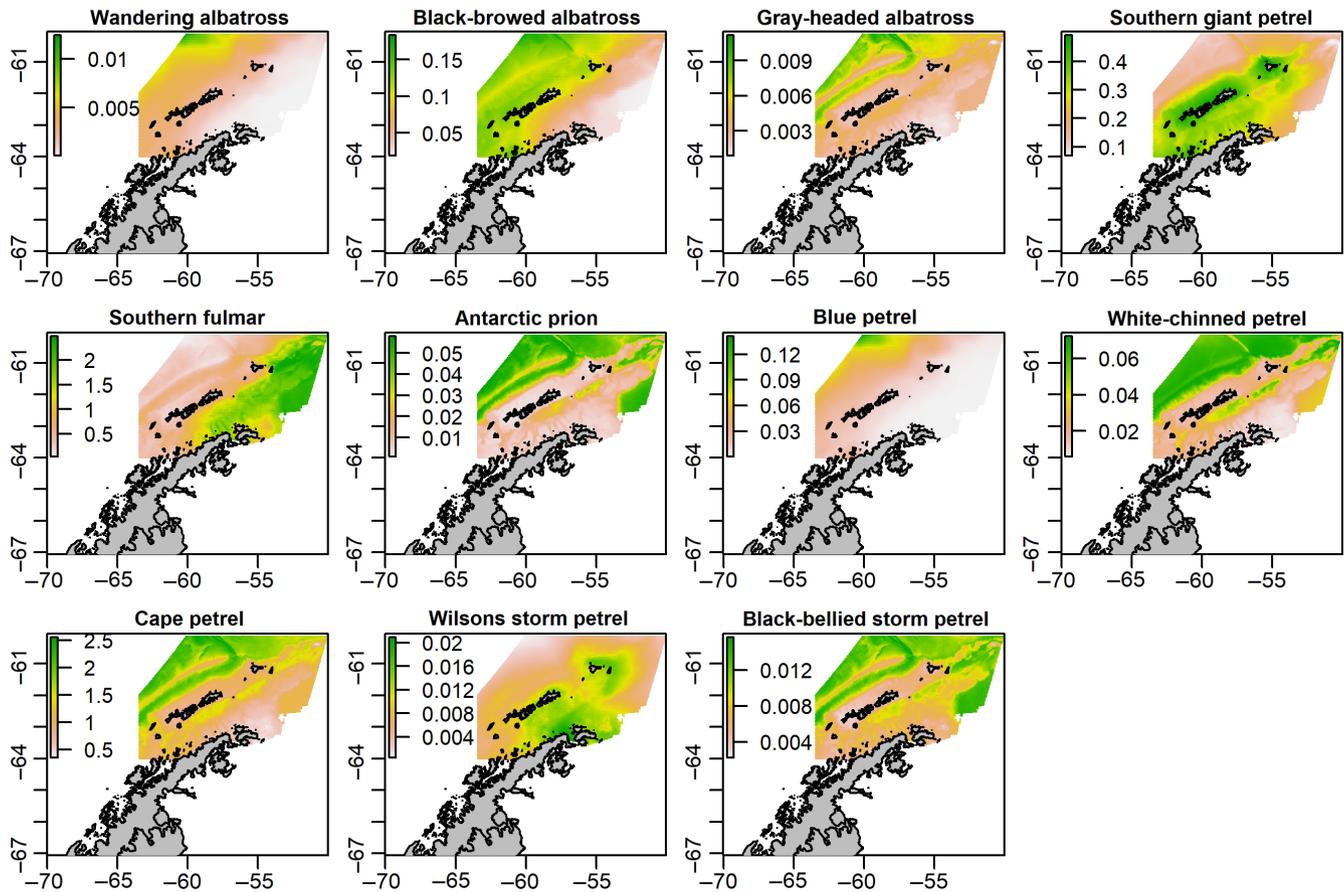


FIGURE 5 Estimates of krill consumption (in kilograms per day) by species of flying seabird in the area used by the krill fishing industry in CCAMLR Subarea 48.1. Note the different scales between the species.

Model performance and limitations

High model performance metrics indicate that our models performed moderately to well for all groups and approaches. As such, we can be confident that our models provide reasonable predictions of the distribution of these predators in the region. However, as with most ecological models, uncertainty remains in some of the parameter estimates used in our calculations (Table 4). These are discussed further in Appendix S2, along with a comparison of tracking and at-sea survey data to model whale consumption, and a comparison of approaches and results among groups.

Characteristics of foraging grounds

Penguins

The probability of occurrence of all species of penguin during the breeding season was negatively associated with the distance from the colony, an association that is frequently observed in seabirds (e.g., Baylis et al., 2019; Soanes et al., 2016; Wakefield et al., 2011; Warwick-

Evans et al., 2018). Breeding penguins behave as central place foragers during the breeding season and must return to the colony frequently to incubate eggs or to provision chicks. As such, they are limited in the distance they may travel on foraging trips, and must trade-off the benefits of traveling to foraging areas further from the colony, and the energy and time required to do so (Burke & Montevecchi, 2009). In addition, chinstrap penguins traveled toward the shelf-break. Increased densities of large krill are often observed over shelf-breaks (Siegel, 1988; Siegel et al., 2013), where ocean currents may influence large scale distribution (Hunt Jr et al., 2016; Murphy et al., 1998). Consequently, chinstraps are likely to travel toward this feature to take advantage of krill aggregations and increased krill replenishment rates. Visual inspection of the tracking data suggests that chinstrap penguins do move directionally away from the colony (i.e., not in a radius in every direction); therefore, it is perhaps not surprising that the model for this species involved the additional covariate (*bearing*). What is perhaps surprising, is that the model for Adélie penguins, which occur in large numbers at the tip of the Peninsula, and also appear to have some directional movement away from the colony, is based on distance to

TABLE 4 Model limitations and data gaps

Limitation	This study	For fisheries management
Outdated population/abundance estimates	Penguins, cetaceans, fur seals	Krill, fur seals, crabeater seals, finfish, penguins, cetaceans
Uncertain energy and krill requirements	Penguins, cetaceans, seabirds, fur seals	Fur seals, crabeater seals, finfish, penguins, cetaceans
Tracking/survey limited both temporally and spatially	Penguins, cetaceans, seabirds	
Breeding individuals only/unknown demographic status	Penguins, seabirds, fur seals	Need estimates for nonbreeders of all species
Population growth rate	Cetaceans (tracking data only)	All species
Vessel attraction/avoidance	Seabirds	

Note: Column 2 relates to discussions in Appendix S2 about how these limitations may impact the results of this study. Column 3 highlights data gaps in our current knowledge, which would be useful to improve in order to advise fisheries management.

colony alone. This could be due to the complexity of the topography, and oceanography, in this region. No environmental variables were important in the models for any of the penguin species. This may be because individuals travel to accessible and historically profitable foraging areas close to the breeding colony (Fraser & Trivelpiece, 1996). Models suggest that krill distribution in the region may be associated with on-shelf areas, areas of increased chlorophyll concentration, and moderate sea-level anomaly (Silk et al., 2016). Although these relationships were not consistent between regions, they do suggest that krill density is related to environmental drivers. It is plausible that we did not detect these relationships in our models for penguins as a result of a mismatch between the scale of the tracking data and the scale of the remotely sensed environmental data, which are generally collected at a much larger spatial resolution than the fine-scale tracking data (Kerr & Ostrovsky, 2003; Wakefield et al., 2011). Including environmental covariates at a scale, which is more closely matched to the tracking data, may aid in our understanding of the true mechanics of predator decision making and of foraging hotspots.

Whales

Our modeling approaches indicated that the density of humpback whales is negatively associated with distance to coast and slope (at-sea survey data only), and quadratically associated with depth, peaking at ~ 500 m. For fin whales, the probability of occurrence is positively associated with slope and depth, and quadratically associated with distance to coast, sea surface temperature, chlorophyll concentration, and current speed (peaking at 100 km, -0.5 to 2°C , 1 g m^{-2} , and 0.15 m s^{-1} , respectively). These covariates are likely act as a proxy for the distribution of krill, which are associated with bathymetric features and environmental characteristics observed in the Antarctic Circumpolar Current (ACC), particularly the Southern ACC Front (SACCF) and the Southern ACC Boundary (SACCB) (Loeb & Santora, 2015; Prézelin et al., 2004). These features flow close to the shelf-break of the Antarctic Peninsula, concentrating primary production, krill, and top predators (Loeb & Santora, 2015; Prézelin et al., 2004), and can be characterized by moderate temperature, current speed, and sea-level anomaly (Santora et al., 2014). During both summer and winter, krill biomass is higher over shelves and shelf-breaks relative to off-shelf areas (Atkinson et al., 2008; Reiss et al., 2017; Trathan et al., 1998) and may form dense aggregations in inshore environments (Lascara et al., 1999; Nowacek et al., 2011). Additionally, increased tidal forcing in coastal areas combined with shallow bathymetry may aggregate prey and increase the availability of prey to predators (Bernard et al., 2017; Cotté & Simard, 2005). Indeed, habitat models using concurrent measurements of krill and humpback whales found krill density to be the strongest predictor (Friedlaender et al., 2006; Santora et al., 2010, 2014). Thus, while other environmental variables that act as proxies for krill have often shown positive correlation with whale distribution, the most robust determinant of baleen whale distribution is area with high krill density.

It is likely that whales have developed a resource partitioning mechanism to reduce interspecific competition for prey (Friedlaender et al., 2009; Herr et al., 2016). This may explain the variation in the predicted distributions of fin and humpback whales from these models and elsewhere (Herr et al., 2016; Santora et al., 2010, 2014). Indeed, humpback whales forage almost exclusively on Antarctic krill while in the Southern Ocean, possibly selecting smaller, juvenile, krill which are elevated on-shelf and in the Bransfield Strait. Conversely, fin whales have a more varied diet (Herr et al., 2016; Reilly et al., 2013) and forage in upwelling areas around shelf-breaks, within eddies and fronts, and show a preference for large swarms of mature Antarctic krill (Herr et al., 2016, Santora et al., 2010, 2014), which aggregate around the shelf-break during summer (Atkinson et al., 2008).

Fur seals

Our models suggest that fur seal abundance is positively associated with sea surface temperature (increases with degrees Celsius), and quadratically associated with sea-level anomaly (peaks at 0-m height), current speed (peaks at 0.2 m s^{-1}), and distance to coast (peaks at 5 km). As described above, the southern part of the ACC potentially concentrates primary production, krill, and top predators (Loeb & Santora, 2015; Santora & Veit, 2013) and provides a profitable foraging ground for fur seals. During both the breeding and nonbreeding season, it is necessary for fur seals to haul out of the water to rest. During winter, fur seals may haul out on floating ice floes, whereas during summer, fur seals must haul out on land. For a more detailed discussion of fur seal distribution around the South Shetland Islands, see (Santora, 2013).

Flying seabirds

The distribution of flying seabirds was highly variable among species and tended toward either on-shelf or off-shelf environments, most likely as a consequence of dietary preference, foraging behavior and habitat availability (Santora, Veit, et al., 2017; Wakefield et al., 2011; Weimerskirch et al., 1988). Covariates in models predicting the distribution of flying seabirds generally included SST and/or depth. SST gradients in the study area reflect on-shelf and off-shelf zonation and are frequently associated with the broad-scale foraging distributions of seabirds (e.g., Scales et al., 2016; Wakefield et al., 2011). Many species of seabird show preferences for water of specific depths, including on-shelf, shelf-break, and off-shelf waters (Hunt et al., 1990; Santora, Veit, et al., 2017; Warwick-Evans et al., 2016; Weimerskirch et al., 1997). Upwelling associated with bathymetric features or shelf-breaks may transport nutrients to the surface, promoting phytoplankton growth, and consequently attracting krill and other higher trophic-level species. Additionally, shallow bathymetry and tidal forcing may increase prey availability to seabirds (Lavoie et al., 2000). Alternatively, fronts and eddies, such as those associated with the SACCF, may aggregate prey and become a predictable target for seabirds foraging in off-shelf waters (Scales et al., 2014).

Wider implications

Developing fine-scale, spatially explicit estimates of krill consumption for predators using the northwest Antarctic Peninsula allows us to address some of the gaps that limit

our understanding of this complex ecosystem, as well as our ability to manage krill fishery operations. However, it is clear that this ecosystem is continuing to change as a consequence of biological and physical processes (Ducklow et al., 2013), and management objectives can only be resolved within this context.

Results from the guild of krill predators that we consider suggest that humpback and fin whales may currently account for $\sim 73\%$ of krill consumed by our study species in the northwest Antarctic Peninsula. This is important, as CCAMLR does not explicitly consider cetaceans within its management framework. Humpback whales consume $\sim 760,000$ or $\sim 1,000,000$ t from the study area during the summer period (depending on modeling approach, estimated duration of 120 foraging days), fin whales consume $\sim 1,100,000$ t, while the fishery currently takes $\sim 155,000$ t. The fishery may reach these catch limits within weeks, whereas whales (and other species) forage in the region for many months. Further, when evaluating competition with the fishery, it is important to recognize the spatial scale of the fishery, which is becoming increasingly concentrated within smaller areas, as well as considering how krill may move back into an area after depletion (Trathan, Warwick-Evans, et al., 2021). If we include estimates of consumption by right and minke whales using abundance and consumption estimated by Reilly et al. (2004), based on data from surveys in 2000 (Trathan & Watkins, 2001), estimated overall krill consumption would increase by $\sim 7\%$. These estimates do not consider any population changes for right and minke whales over the past 20 years, or a robust data-driven estimate of daily consumption, and so are very likely to underestimate krill consumption by baleen whales, possibly by a considerable amount. Indeed, the consumption estimates by Reilly et al. (2004) are highly uncertain and vary considerably according to methods used. Using a novel approach combining lunge feeding frequency and prey density, Savoca et al. (2021) estimate that the consumption of krill by cetaceans may be up to three times that previously estimated. As krill predator populations continue to recover, their consumption of krill will increase, and potentially increase competition among other krill predators. Indeed, Strycker et al. (2020) show that many populations of chinstrap penguins in this area have decreased, coinciding with the recovery of baleen whales. Ballance et al. (2006) previously concluded that chinstrap penguins showed the clearest impacts of whale removal. Thus, although it is challenging to attribute cause and effect, this may provide evidence that recovering cetacean populations are already impacting chinstrap penguin populations (Trivelpiece et al., 2011), further emphasizing the need for a precautionary approach when managing the krill fishery. Similarly, during the

1970s–1980s, demersal finfish were harvested to very low levels, and as a result, CCAMLR closed those fisheries in this area (Ainley & Pauly, 2014). Many of these species are now recovering (Barrera-Oro et al., 2017) such that fish are now thought to be one of the main consumers of krill in the region (Hill et al., 2016). As krill-eating fish continue to recover, it is vital that they are considered in management of the krill fishery.

In addition to the recovery of previously depleted krill predators, the northwest Antarctic Peninsula ecosystem is experiencing physical changes as a result of climate change (Cook et al., 2005; Kerr et al., 2018; Stammerjohn et al., 2008; Vaughan & Doake, 1996), potentially impacting krill recruitment (Atkinson et al., 2008) and ecosystem dynamics (Loeb et al., 1997; Mendes, Tavano, Dotto, et al., 2018; Mendes, Tavano, Kerr, et al., 2018; Moline et al., 2004). Models project continued and rapid warming in Antarctica (IPCC, 2019), and potential declines in krill biomass (Atkinson et al., 2019; Klein et al., 2018; but see Cox et al., 2018). Understanding how the Antarctic marine ecosystem will respond is a key issue, and management practices should be more conservative to recognize ongoing uncertainty (Trathan & Agnew, 2010). For CCAMLR, this is vital, as most monitoring data are currently based on observations of penguin populations, yet these are already known to be changing (Lynch et al., 2012).

The krill consumption estimates reported here allow us to underpin evidence-based approaches for management of the krill fishery. However, improved estimates of krill consumption across the food web, particularly from recovering populations of cetaceans, but also for other groups, including flying seabirds, fish, pack-ice seals, and some *Pygoscelis* penguin populations (Trathan & Hill, 2016), are required. Additionally, improved methods for calculating krill consumption by all species of baleen whale will be vital, as humpback, blue, and fin whales continue to recover from historical harvesting. Furthermore, obtaining accurate estimates of krill biomass is vital if we are to understand the predation pressure, and calculate evidence-based krill catch limits for the fishery. Such data gaps need to be addressed at spatial scales that are comparable to that at which the fishery operates in order to remain precautionary against the backdrop of a complex and changing ecosystem.

Conclusions

We show that the location of areas that are important for krill consumption during the peak summer months by krill predators varies widely among species and can be concentrated at very small spatial scales. The majority of such areas are close to penguin breeding colonies and in

nearshore and shelf-break areas where humpback and fin whales concentrate for feeding. However, we recognize that important krill predators including finfish and other species of baleen whales have not been included in these analyses, and their inclusion might highlight alternative important foraging areas. The substantial quantities of krill consumed by krill predators recovering from historical harvesting add further evidence in support of the krill surplus hypothesis (Laws, 1985), and that recovering populations of krill predators may be related to declines observed in chinstrap penguin populations in the region. However, the evidence for the krill surplus hypothesis is at best confusing. The fine-scale distributions of predator krill consumption highlight the importance of management at small spatial scales when considering the potential risks of the krill fishery to krill predators. It is fundamental that management frameworks applied to revise catch limits using an evidence-based approach and are populated with sufficient up-to-date data to accurately identify the areas of importance to predators, as well as important areas for krill. However, we highlight that important data gaps remain. Our models show that even though CCAMLR does not explicitly consider cetaceans, these species consume a very significant proportion of the krill consumed by natural predators. Furthermore, understanding the foraging behavior of juvenile or nonbreeding krill predators, or krill consumption outside of the summer period is essential given both the rapidly changing environmental conditions that allow for extended foraging seasons for non-ice-affiliated krill predators (Nowacek et al., 2011; Weinstein & Friedlaender, 2017) and temporal shifts by the krill fishery to operate later in the summer and into autumn. A robust approach to managing the krill fishery in this area requires that these data gaps are filled.

ACKNOWLEDGMENTS

This paper is a contribution to the BAS Ecosystems program, funded by Darwin Plus 072 and the Pew Charitable Trusts under PA00034295. The ship-based whale surveys were conducted within the activities of research projects Baleias and Interbiota, of the Brazilian Antarctic Program, financed by the National Council for Scientific and Technological Development (CNPq grant numbers 408096/2013-6 and 407889/2013-2), under the Brazilian Ministry of Science, Technology, Innovations and Communications—MCTIC. CNPq provided research fellowships to E. R. Secchi (PQ 310597/2018-8) and L. Dalla Rosa (PQ 309548/2019-5). We thank all crew members of the polar vessel Almirante Maximiano, and the researchers Artur Andriolo, Alexandre Azevedo, Franciele Castro, Jonatas H. F. do Prado, Jorge Acevedo, Juliana Di Tullio, Manuela Bassoi, Marco Aurélio Crespo, Liane Dias, Pedro Fruet, Renan C. de Lima, Rodrigo Genoves, and Thaise Albernaz, who participated

on whale data collection. Humpback whale satellite tracking studies were supported by grants to Dr A. Friedlaender from the National Science Foundation Office of Polar Programs, the Hogwarts Running Club, the Southern Ocean Research Partnership, Australian Antarctic Division, and World Wildlife Fund. This study is a contribution of the Research Group “Ecologia e Conservação da Megafauna Marinha-EcoMega/CNPq” and is within the scope of the Capes PrInt Program (public notice 041/2017) and of the Whales and Climate Research Program. J. A. Santora thanks the NOAA-NMFS U.S. AMLR program researchers and crew on shipboard surveys during for 2003–2011; data collection and synthesis were also supported by National Science Foundation Office of Polar Programs (awards 9983751, 0337648, and 1347911).

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All tracking data are available from the seabird tracking database https://seabirdtracking.org/mapper/?dataset_id=753, id numbers 910, 911, 912, 913, 914, 926, 928, 753). The at-sea sightings data for cetaceans in the Antarctic Peninsula region under the scope of the Brazilian Antarctic Program are available upon request to the Laboratory on Ecology and Conservation of Marine Megafauna at Universidade Federal do Rio Grande-FURG (docadm@furg.br, l.dalla@furg.br and edu.secchi@furg.br). Data for the other species, as well as the raster layers of our model outputs (Figure 3) are available from the dryad data repository (doi:10.5061/dryad.4qrfj6qc5).

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How to cite this article: Warwick-Evans, V., N. Kelly, L. Dalla Rosa, A. Friedlaender, J. T. Hinke, J. H. Kim, N. Kokubun, et al. 2022. “Using Seabird and Whale Distribution Models to Estimate Spatial Consumption of Krill to Inform Fishery Management.” *Ecosphere* 13(6): e4083. <https://doi.org/10.1002/ecs2.4083>