Habitat selection of southern giant petrels: potential environmental monitors of the Antarctic Peninsula

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Abstract: The southern giant petrel (*Macronectes giganteus*) is a widely distributed top predator of the Southern Ocean. To define the fine-scale foraging areas and habitat use of Antarctic breeding populations, 47 southern giant petrels from Nelson Island were GPS-tracked during the summers of 2019–2020 and 2021–2022. Step-selection analysis was applied to test the effects of environmental variables on habitat selection. Visual overlap with seal haul-out sites and fishing areas was also analysed. Birds primarily used waters to the south of the colony in the Weddell and Bellingshausen seas. Females showed a broader distribution, reaching up to -70°S to the west of Nelson Island, while males were mainly concentrated in waters off the northern Antarctic Peninsula. Habitat selection of both sexes was associated with water depth and proximity to penguin colonies. Both overlapped their foraging areas with fishing sites and females in particular overlapped with toothfish fishery blocks in Antarctica and with fishing areas in the Patagonian Shelf. Due to their habitat associations and overlap with fisheries, when harnessed with tracking devices and animal-borne cameras, giant petrels can act as platforms for monitoring the condition and occurrence of penguin colonies, haul-out sites and unregulated fisheries on various temporal and spatial scales in Antarctica.

Introduction

The Antarctic Peninsula is the region of the Antarctic experiencing the fastest environmental changes (Convey & Peck 2019) and greatest local human impact (Tin *et al.* 2014). Loss of sea ice and the reduction in the length of the sea-ice season (Schofield *et al.* 2018, Vorrath *et al.* 2020), rapid glacier contraction (Silva *et al.* 2020), increased ice-free land (Lee *et al.* 2017), shifts in plankton communities (Schofield *et al.* 2018, Kim & Kim 2021, Schultz *et al.* 2021), probable biomass reduction and contraction in the southward distribution of krill (Atkinson *et al.* 2019, Trathan *et al.* 2022) are some of the observed environmental changes caused by warming. Increased fishing concentration (Nicol *et al.* 2012, Trathan *et al.* 2022, Santa Cruz *et al.* 2022) and increased human presence due to the intensification of tourism and scientific activities (Chown *et al.* 2012, Bender *et al.* 2016) have led to the contamination of several areas through the release of synthetic debris (Tirelli *et al.* 2020, Finger *et al.* 2021) and wastewater effluents, burning of fossil fuels, waste incineration and accidental spillage (Bargagli 2008).

While it is important to continuously track these changes, it is challenging for researchers to simultaneously cover a substantial number of vulnerable areas.

Marine top predators have been considered as tools for monitoring ecosystem changes due to their large-scale distribution and because they amplify trophic information across multiple spatiotemporal scales (Sergio *et al.* 2008, Hazen *et al.* 2019). Seabirds, given their habitat associations (Tam *et al.* 2017, Velarde *et al.* 2019, Krüger 2022) and easier access in comparison to other groups of marine top predators, have been proposed as optimal ocean sentinels (Lascelles *et al.* 2012, Krüger 2022).

For instance, the strong associations of emperor penguins (*Aptenodytes forsteri*) with sea ice make them sentinels of climate change in Antarctica (Jenouvrier *et al.* 2021), while krill-specialist *Pygoscelis* spp. penguins can indicate the state of krill populations (Lynnes *et al.* 2004). On the other hand, population-level generalist seabird species are usually associated with a wide range of environmental conditions and/or habitats and can act as monitors of

human impacts across large spatial scales. Albatrosses, for example, have been suggested as useful sentinels of illegal, unreported and unregulated (IUU) fishing in the mid-latitudes of the Southern Ocean due to their wide oceanic distribution and propensity to interact with fishing vessels (Weimerskirch *et al.* 2020).

Southern giant petrels (SGPs; *Macronectes giganteus*) are large (3.0–5.5 kg), avian generalist top predators and the main scavenger species of the Southern Ocean (Hunter 1985). In the Antarctic, they breed mainly on offshore islands of the Antarctic Peninsula, with an estimated population of 5409 breeding pairs on the South Shetland Islands (Patterson *et al.* 2008). During the breeding season, the species uses pelagic, coastal and terrestrial environments of the Antarctic as foraging zones (Granroth-Wilding & Phillips 2019, Corá *et al.* 2020). During the non-breeding season, they use a much wider range of areas as their foraging grounds, including the high seas and the continental shelf of the south-west Atlantic and south-east Pacific (Krüger *et al.* 2018). In terrestrial zones, giant petrels usually concentrate in areas with penguin colonies (Copello *et al.* 2011) and breeding and haul-out sites of seals, where they feed on carrion or faeces (Corá *et al.* 2020). Sexes commonly have spatially segregated foraging areas to decrease intersexual competition, especially during the breeding season (González-Solís *et al.* 2008, Granroth-Wilding & Phillips 2019). Females are mainly pelagic and feed primarily on marine prey, such as squid, fish and crustaceans, while males have a more coastal distribution and feed primarily on seabird and mammal carrion (Hunter 1983, Forero *et al.* 2005, González-Solís *et al.* 2008, Copello *et al.* 2011). Both sexes have been found to be attracted to fishing vessels for the consumption of discards on the south Atlantic Ocean and Indian Ocean (Otley *et al.* 2007, González-Solís *et al.* 2008, Thiers *et al.* 2014, Krüger *et al.* 2017). Due to their diverse habitat associations and top predator/scavenger position in the Antarctic trophic web, SGPs are a potential platform for monitoring the state of Antarctic populations and environments.

In this study, we show that, by continuously tracking movements of a single SGP population using GPS tracking devices, it is possible to assess a large array of areas and habitats along the Antarctic Peninsula. First, we describe foraging trip metrics and define foraging areas and important sites for the SGP population during reproduction using fine-scale GPS data and then run step-selection functions (SSFs) to identify which variables are responsible for sexes selecting a specific habitat, considering interindividual variability. Considering the known spatial and dietary segregation of the species, we expect males to make shorter trips, forage closer to the colony and be associated with penguin colonies and seal haul-out sites, and we expect females to make farther and longer trips, forage on productive, pelagic areas and, to a larger extent than males, to use areas with fishing activities.

Materials and methods

Tracking breeding southern giant petrels

Tracking data were obtained from SGPs breeding at Harmony Point, Nelson Island, Maritime Antarctica (62°18'S, 59°11'W). During the 2019–2020 and 2021–2022 seasons, 67 birds (33 females and 34 males) were tagged with GPS tracking devices: 18 were tracked with solar-powered GPS-UHF KITE-L devices (Ecotone Telemetry, $58 \times 27 \times 18$ mm; 17 g), 4 with Axy-Trek Marine GPS loggers (TechnoSmArt, $40 \times 20 \times 8$ mm; 14g), 8 with CatLog ThermoSeal GPS devices (Mr. Lee, $53 \times 26 \times 7$ mm; 20 g), 16 with CatLog GPS devices with an epoxy-filled enclosure (Mr. Lee, $53 \times 45 \times 20$ mm; 50 g) and 20 with BirdCam, a GPS device coupled to a small video camera (Mr. Lee, $70 \times 26 \times 17$ mm; 24 g). KITE-L devices were attached using a backpack harness of tubular Teflon tape and the other devices were attached to dorsal feathers with 3M #2800 series duct tape and Loctite super glue. KITE-L and CatLog ThermoSeal devices were set to collect a fix every 5 min and Axy-Trek, BirdCam and CatLog epoxy devices were set to collect a fix every 10 min due to their lower battery capacity. KITE-L tracking data were downloaded to a local base station each time a bird returned to the colony following a foraging trip. Data from the other devices were downloaded following recapture at the end of the tracking period. Devices were removed from the birds by cutting supporting feathers with scissors. Birds were tracked for an average of 40.6 ± 8.9 days from 30 November 2019 to 25 January 2020 and for an average of 21.8 ± 6.9 days from 12 December 2021 to 25 January 2022. The tracking periods corresponded to the late egg incubation stage and the chick-rearing stage, the latter starting *ca.* 12 January.

Data processing

GPS data were filtered to remove locations at the nest. Due to data gaps and differences in fix sampling rates between devices, tracks were interpolated using the '*track_resample*' function of the '*amt*' R package (Signer *et al.* 2019) by resampling all locations to an equal 30 min interval, which was the highest median interval. Regular sampling rates are required for SSFs, because selection is not scale-invariant (Barnett & Moorcroft 2007, Signer *et al.* 2017), and thus sampling rates should be similar for different individuals.

Trip metrics

To determine foraging trip characteristics, we split tracking data into individual foraging trips using the

'*tripSplit*' function in the '*track2KBA*' *R* package (Beal *et al.* 2021). We defined trips as periods of ≥ 1 h spent away from the colony at a distance of 250 m, since some individuals can make short trips and feed on seal faeces at the nearby glacier (Corá *et al.* 2020). We then calculated trip length (days), cumulative distance travelled between all locations (km) and maximum distance from the colony (km; hereafter 'maximum range') using the '*tripSummary*' function. Incomplete trips (unknown beginning or end dates) were removed from the analysis. The normality (Shapiro-Wilk test) and homoscedasticity (Bartlett test) of the data were verified before each statistical test. Generalized linear mixed models (GLMMs) with a penalized quasi-likelihood parameter estimation were used with trip metrics as response variables to assess differences between sexes, breeding stage and years. To incorporate the dependency among observations of the same individual, ID was used as a random intercept. We used a gamma error distribution with an inverse link function for cumulative distance and trip duration data and a Gaussian distribution with a log link function for maximum range data. We first evaluated whether a mixed model was necessary by running a linear model without a random effect (ID) and checking whether there was residual variance by plotting the residuals against the levels of ID. As residual variance was confirmed, we proceeded to select the most adequate mixed model by decreasing model complexity and comparing Akaike information criterion corrected for small sample sizes (AICc) values between models. Those with the highest AICc values were selected.

Estimating foraging areas

To visually identify geographical areas used by female and male SGPs, we computed 25%, 50%, 75% and 95% kernel utilization distributions (KUDs) for individuals of each sex using the '*estSpaceUse*' function from the '*track2KBA*' *R* package (Beal *et al*. 2021). We used the scale of each sex's area-restricted search (ARS) as the kernel smoothing parameter (*h*), which was calculated using the '*findScale*' function. Females had an ARS scale of 9.5 km and males of 9.0 km. As at-sea distribution changes according to the breeding stage and associated breeding duties (González-Solís *et al.* 2008, Granroth-Wilding & Phillips 2019), we therefore estimated KUDs for incubation and chick-rearing stages separately. The 50% KUD is defined as the 'core' foraging area where birds spent 50% of their time (Ford & Krumme 1979, Soanes *et al.* 2013, Lascelles *et al.* 2016). To ensure that data were representative of the foraging distribution of the colony-level population (~480 breeding pairs), we used a bootstrapping approach implemented in the '*track2KBA*' *R* package

(described in Lascelles *et al.* 2016), which analyses the representativeness of the foraging areas as a function of sample size. Finally, we identified and delineated important sites for the population, which are areas used by a substantial portion of the population. We used the '*findSite*' function that first calculates the proportion of individual core areas (i.e. % KUD areas) overlapping per grid cell. This proportion of overlapping tracks is then multiplied by the proportional representativeness of the tracked sample to adjust the sample-derived pattern by the degree of representativeness. The result is a scaled estimate of the proportion of the source population that predictably uses each grid cell in the study region during the season of interest.

Habitat characteristics

To assess characteristics of foraging habitats, we classified track points according to their speed and turning rate using the Expectation-Maximization Binary Clustering ('*EmBC*') *R* package (Garriga & Bartumeus 2016). Foraging locations were defined as those with low speed ($< 1.0\ \mathrm{ms^{-1}}$) and high turns (> 0.48 rad), parameters that characterize an intensive search behaviour. At these points, we extracted values of sea-surface chlorophyll *a* (which is a proxy for primary productivity), sea-surface temperature (SST), gradients of SST (SSTg; which indicate the positions of fronts more clearly), terrestrial and sea-ice concentration (SIC; referring to the proportion of the area that is covered by ice relative to open water, such as leads and polynyas), sea-bed depth and elevation (m; including both marine and terrestrial relief), distance from known penguin colonies (km) and distance from ice-free areas (km; which are potential unknown penguin colony sites or beaches used by seals as haul-out sites). Dynamic variables, except for ice concentration, were downloaded as December and January mean composite '*netCDF*' files from Giovanni Browser (https://giovanni.sci.gsfc.nasa.gov/giovanni/). Chlorophyll *a* concentration ($\mathrm{mg\ m^{-3}}$) and SST at night (°C) were downloaded for a spatial resolution of 0.04° (~4 km). SIC (%) data were obtained as daily composites from the Sea Ice Remote Sensing Data browser - University of Bremen (Spreen *et al.* 2008, https://seaice.uni-bremen.de/databrowser/) as georeferenced .tiff images with a 6.25 km spatial resolution. Bathymetric data were obtained from the ETOPO1 Global Relief Model (www.ngdc.noaa.gov/mgg/global/global.html) with a spatial resolution of 0.01° (~1 km). Penguin colony distribution was obtained from the Mapping Application for Penguin Populations and Projected Dynamics online database (MAPPPD; http://www.penguinmap.com). This dataset includes data on emperor penguin (*Aptenodytes forsteri*), Adélie penguin (*Pygoscelis adeliae*), chinstrap penguin (*Pygoscelis antarcticus*) and gentoo penguin
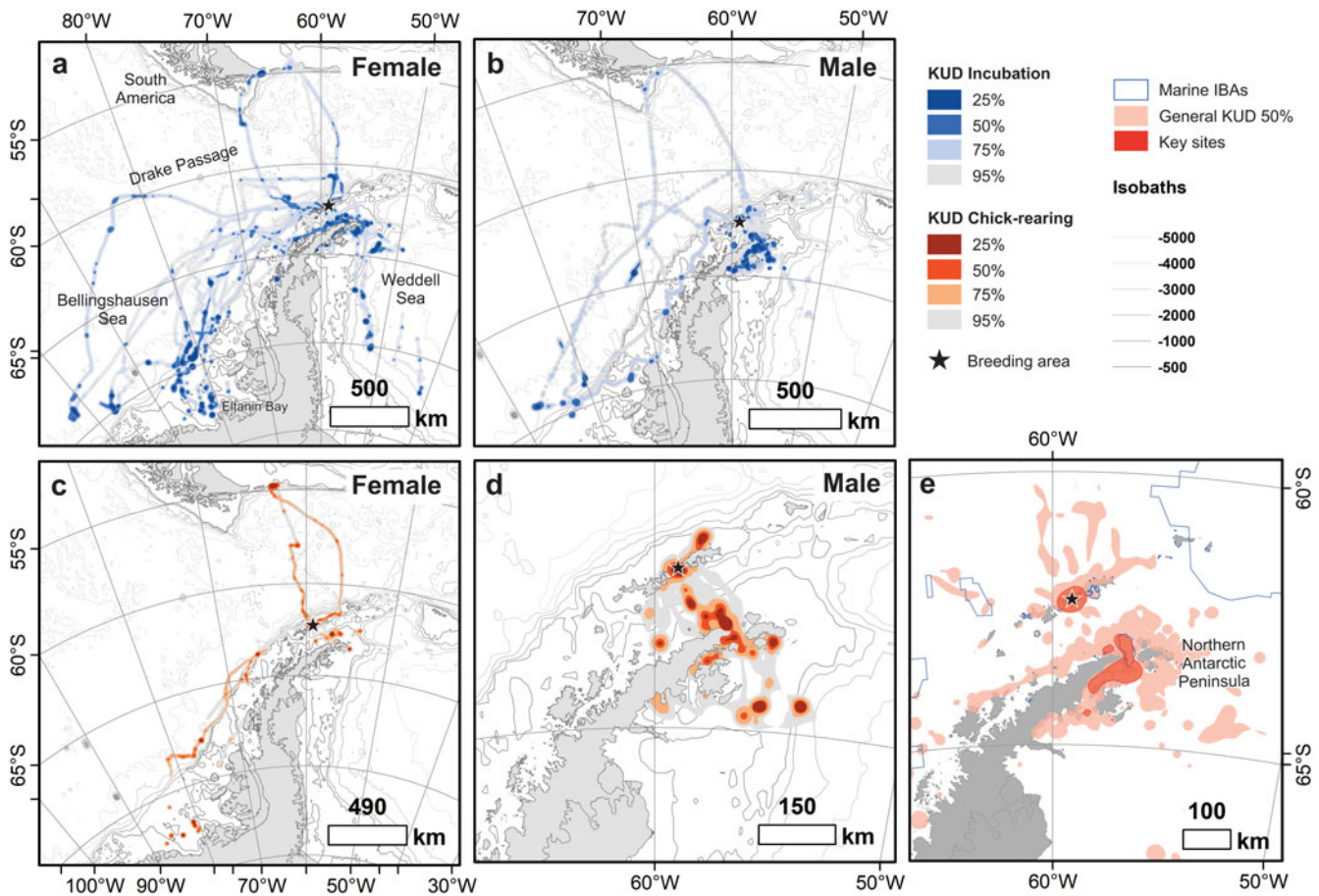
Fig. 1. Kernel usage density (KUD) of (**a. & c.**) female (*n* = 21) and (**b. & d.**) male (*n* = 26) breeding southern giant petrels (*Macronectes giganteus*) from Harmony Point, Nelson Island (black stars), tracked between December 2019 and January 2020 and between December 2021 and January 2022. Incubation and chick-rearing stages are depicted in blue and orange colours, respectively. Population-level 50% KUD and marine Important Bird Areas (IBAs; https://maps.birdlife.org/marineibas/) are depicted in **e**. Dark red polygons are key sites for the tracked population. Antarctic coastline polygons and bathymetric isolines were obtained from Gerrish *et al.* (2021) and The International Bathymetric Chart of the Southern Ocean Version 2 (Dorschel *et al.* 2022), respectively.

(*Pygoscelis papua*) colonies in Antarctica. Penguin colony distribution data in southern South America were obtained as published maps and then georeferenced in *ArcMap* 10.3 (ESRI, Redlands, CA, USA). Data were obtained for southern rockhopper penguins (*Eudyptes c. chrysocome*; Baylis *et al.* 2013b), gentoo penguins (Baylis *et al.* 2013a), king penguins (*Aptenodytes patagonicus*; Pistorius *et al.* 2012) and Magellanic penguins (*Spheniscus magellanicus*; Global Penguin Society; https://www.globalpenguinsociety. org/portfolio-species-15.html). Euclidean distances to penguin colonies were calculated with the Spatial Analyst tool in *ArcMap* 10.3. SST gradients were calculated as the standard deviation of SST in a 0.3° × 0.3° moving filter in Spatial Analyst. NetCDF files were first converted to raster files and then averaged into 2 month composites. Ice concentration data were first averaged into monthly composites and then averaged into a single mean composite for each summer. Each environmental variable was resampled to the same spatial grid of 0.06° (~6 km,

the coarsest scale of the environmental datasets) to allow spatial comparison and combined modelling. All environmental variables were scaled using the 'scale' function in *R*. Processing of variables was done using the 'raster' *R* package (Hijmans & Van Etten 2021).

As SGPs are known to interact with fisheries (Otley *et al.* 2007, Jiménez *et al.* 2011), we obtained data on daily fishing effort (hours, all gear types) from the Global Fishing Watch database (https://globalfishingwatch.org) with a spatial resolution of 0.01° (~1 km). Fishing effort was only available for the 2019/2020 summer, and population-level overlap was too little to include this variable in the habitat selection analysis. We thus visually investigated the overlap of foraging areas (KUD 50%) and polygons of krill fishing areas obtained from Krüger *et al.* (2019b) and with areas where toothfish (*Dissostichus* spp.) research-driven exploratory fisheries are allowed in Antarctica (Commission for the Conservation of Antarctic Marine Living Resources

(CCAMLR), https://gis.ccamlr.org/). Toothfish fishing usually occurs during periods of low sea-ice coverage, and its occurrence is evaluated on a yearly basis depending on the trends of toothfish populations (e.g. Hanchet *et al.* 2015). Longline fishing effort is relatively low compared with longline fishing elsewhere (e.g. Clay *et al.* 2019), and, given the strict measures adopted for longline fishing in the area, seabird bycatch is also very low (Hanchet *et al.* 2015, Collins *et al.* 2021). Therefore, the impact of toothfish fisheries is expected to be low and restricted within those areas. Krill fishing polygons encompass the summed area of fishing activity during the summers of 2013–2017. We also investigated whether SGP foraging areas were within confirmed marine Important Bird Areas (IBAs; BirdLife International, https://maps.birdlife.org/marineibas/), which are areas of significant importance for birds and therefore are priority areas for conservation.

Habitat selection

Habitat selection was evaluated as the probability of individuals choosing a specific step (two consecutive observed positions) among other available locations (random steps) in relation to the environmental covariates available within reach.
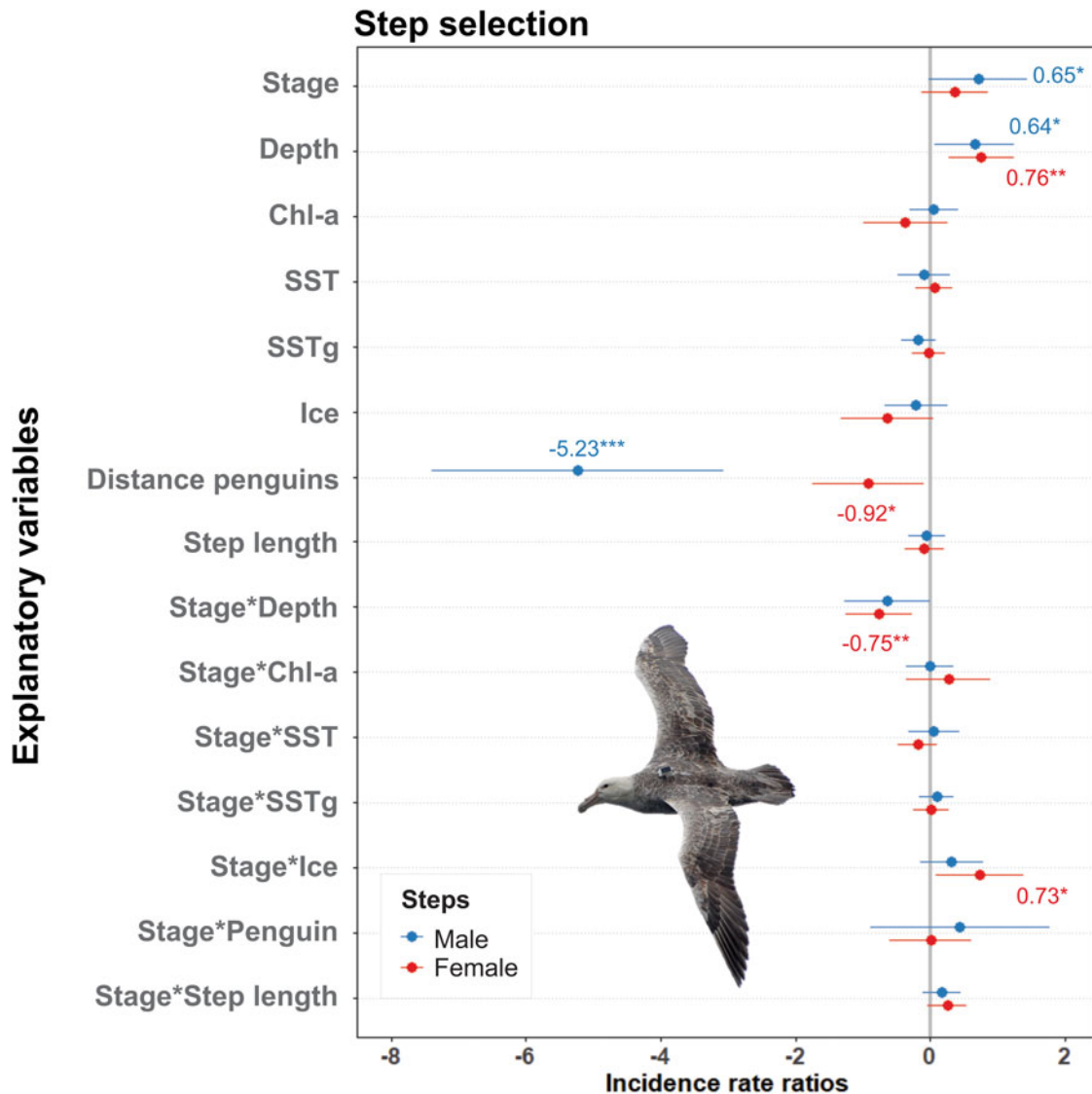
Firstly, geographical positions were translated into a step, which is composed of the step length and turning angle (deviation from previous bearings), using the '*steps_by_burst*' function in the '*amt*' *R* package. We then fitted gamma distributions to the step lengths and von Mises distributions to turn angles using maximum likelihood to generate nine random steps for each observed step based on these distributions (Signer *et al.* 2019). Random steps were generated using the '*random_step*' function of the '*amt*' *R* package. Environmental variables were extracted at the end of all steps to evaluate which variables were responsible for the animal choosing a specific habitat.

We then applied a SSF by fixing a mixed conditional Poisson model with individual-specific random slopes for each variable. We used steps of foraging points as the binary response variable (observed step = 1, random step = 0), environmental variables, stage and step length as covariates and individual ID as a random effect (following Muff *et al.* 2020). We fixed the random effect variance to 10^6 because small values that could be selected by models tend to shrink the intercepts (Muff *et al.* 2020). Models were run separately for each sex. Analysis was conducted in the *glmmTMB R* package (Brooks *et al.* 2017), which uses a frequentist GLMM approach.

We used AICc model selection to distinguish among a set of candidate models describing the relationship between environmental variables, step length and step selection and the interaction between stage and

Table I. Foraging trip metrics of breeding female and male southern giant petrels (*n* = 47). Results for metrics are given as median [quartile 1–quartile 3], with ranges given in parentheses.

Stage	2019–2020		2021–2022	
	Female (*n* = 10)	Male (*n* = 11)	Female (*n* = 11)	Male (*n* = 15)
Incubation trips				
Duration (days)	*n* = 10	*n* = 14	*n* = 16	*n* = 28
	7.8 [3.5–9.1]	6.2 [3.7–7.5]	6.6 [3.4–8.1]	4.1 [1.8–5.7]
	(1.2–12.1)	(0.01–13.2)	(1.2–14.6)	(0.1–10.2)
Maximum cumulative distance (km)	1648.2 [60.5–2054.7]	603.9 [150.3–1119.6]	2317.5 [926.6–4326.5]	919.1 [229.4–1049.2]
	(31.5–3498.2)	(5.9–1625.9)	(122.2–5293.5)	(2.0–5797.4)
Maximum range (km)	295.1 [12.5–522.7]	191.2 [28.4–271.9]	301.9 [228.5–1037.7]	202.7 [33.6–248.7]
	(8.0–1401.3)	(2.9–662.0)	(10.3–2099.7)	(1.0–1491.4)
Chick-rearing trips				
Duration (days)	*n* = 3	*n* = 7	*n* = 10	*n* = 14
	1 [1.0–1.25]	1.3 [0.8–1.95]	1.1 [1.0–1.85]	0.8 [0.4–1.5]
	(1.0–1.5)	(0.4–3.0)	(0.4–3.5)	(0.01–4.9)
Maximum cumulative distance (km)	272.7 [175.7–275.45]	147.1 [82.4–249.7]	253.2 [154.5–536.1]	194.2 [34.3–323.1]
	(78.7–278.2)	(14.9–315.2)	(120.3–2419)	(1.6–1540.1)
Maximum range (km)	46.9 [31.9–46.7]	18.8 [17.35–95.8]	56.6 [27.2–86.1]	22.5 [11.2–126.1]
	(16.8–106.4)	(7.4–113.8)	(22.0–872.2)	(0.8–385.7)

Fig. 2. Estimates and confidence intervals (95%) from the binomial step-selection model of breeding southern giant petrels. Significance codes: ***$P = 0.001$, **$P = 0.01$, *$P = 0.05$. Chl-a = chlorophyll a; SST = sea-surface temperature; SSTg = gradients of sea-surface temperature.

environmental variables. The best-fit model for both was the most complex. Variables used in the final model were sea-surface chlorophyll a, SST, SSTg, distance from known penguin colonies, SIC and depth. Distance from ice-free areas was not included in the analysis as it was strongly correlated with distance from known penguin colonies (Pearson correlation, $r = 0.73$).

The probability of movement in relation to seal haul-out sites was not evaluated due to the lack of a complete dataset of these sites in the Antarctic Peninsula. However, the occurrence of SGPs on haul-out sites was verified by cross-checking Google Earth Pro satellite and drone imagery (only for Harmony Point) of terrestrial ice-covered areas overlapped by SGP foraging fixes. Cloud-free images of these sites, when existent, were

inspected for the presence of seals, which can be identified as long black spots over the ice (LaRue *et al.* 2011). Drone images of Harmony Point were taken with a Mavic Pro II drone (DJI, Shenzhen, China) as part of another study (see Corá *et al.* 2020). Drone flight was authorized by a permit from Instituto Antártico Chileno (No. 1046/2019).

Results

We were able to recover 58 tags and retrieve data from 47 (21 in 2019–2020 and 26 in 2021–2022), a 70% data recovery rate success. Seven devices that were attached with tapes were lost, all of them attached to females. No device that was attached with a harness backpack was lost.
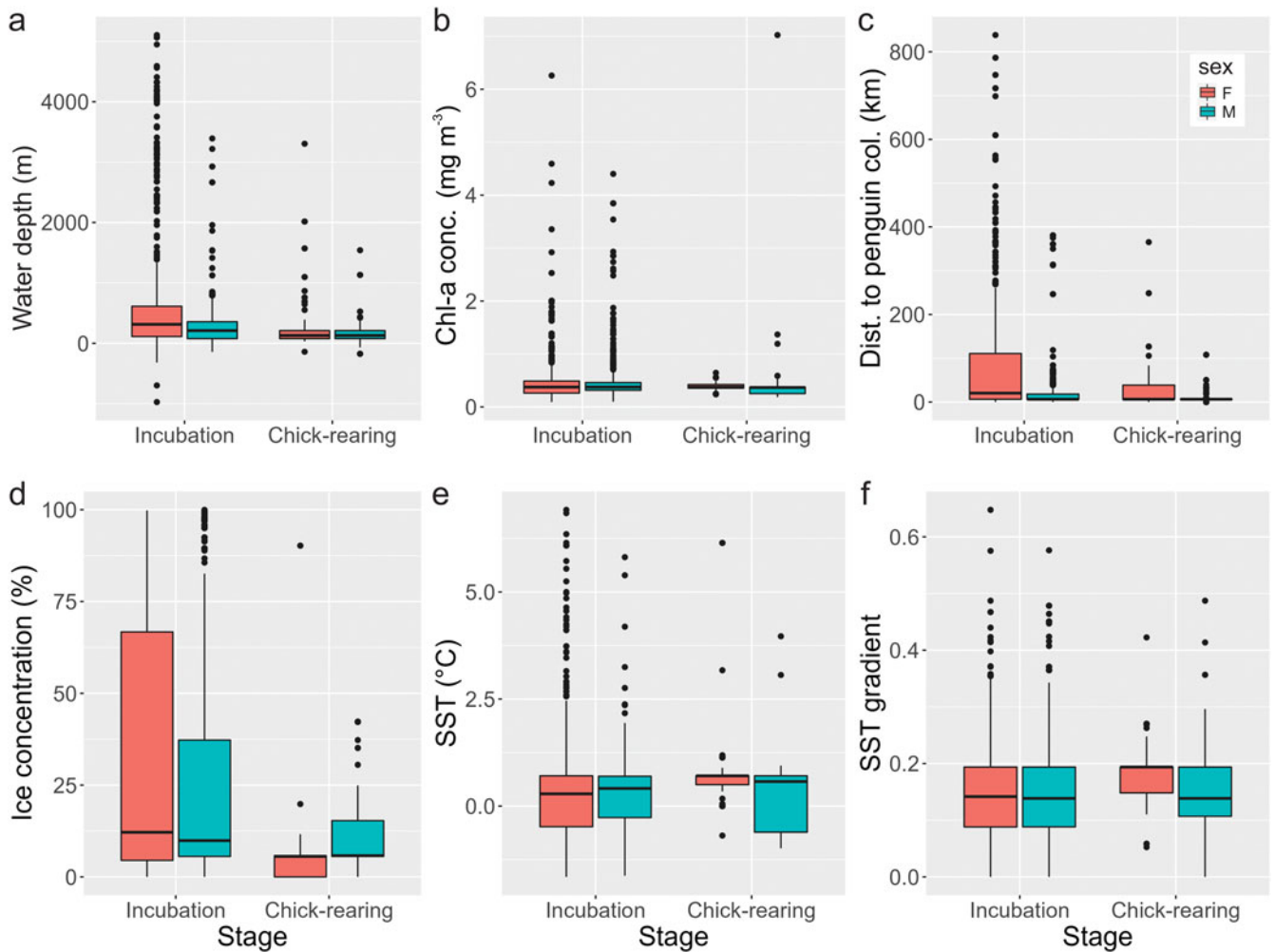
Fig. 3. Median values for the different environmental variables characterizing foraging areas of female (red) and male (blue) southern giant petrels from Nelson Island, Maritime Antarctica, during the incubation and chick-rearing stages. **a.** Water depth; **b.** chlorophyll *a* (Chl-a) concentration; **c.** distance to penguin colonies; **d.** sea-ice concentration; **e.** sea-surface temperature (SST); **f.** gradient of SST.

Foraging distribution and behaviour

A total of 34 complete foraging trips (13 from females and 21 from males) were obtained in 2019–2020 and 68 complete trips were obtained in 2021–2022 (26 from females and 42 from males). Individuals engaged in 1–14 days long trips between the Weddell and Bellingshausen seas and the southern tip of Tierra del Fuego, foraging up to ∼2100 km away from the colony to the west of the Antarctic Peninsula, 1317 km to the south-east and 950 km to the north (Fig. 1). As expected, breeding stage and sex, but not individual ID and year ($P = 0.303$ and $P = 0.301$, respectively), influenced the maximum range, cumulative distance of trips and trip duration. Females tended to engage in longer foraging trips than males (Table I), both in the number of days (GLMM: *t*-value = 2.294, df = 34, $P = 0.028$) and in the maximum trip range (GLMM: *t*-value = -2.690, df = 34, $P = 0.011$) and had higher

cumulative trip distances (GLMM: *t*-value = 3.041, df = 34, $P = 0.004$). For both sexes, incubation trips lasted longer (GLMM, days: *t*-value = -7.292, df = 34, $P = 0.000$) and reached greater distances (GLMM, maximum distance: *t*-value = -5.206, df = 34, $P = 0.000$) than in the chick-rearing stage (Fig. 1 & Table I).

Males fed extensively in the surroundings of their breeding colony, the nearby islands, the Bransfield Strait and the Trinity Peninsula, Graham Land (Fig. 1). Only one male foraged out of Antarctica, over waters to the south of Tierra del Fuego and in the same trip foraged up to -70°S (Fig. 1c). Females, despite also foraging near the colony and by the northern Antarctic Peninsula, showed a more widespread distribution, and many foraging locations were parallel to the Antarctic Peninsula. Eight females foraged south of -70°S in waters facing the Eltanin Bay in the Bellingshausen Sea and in the Weddell Sea. During incubation, one female
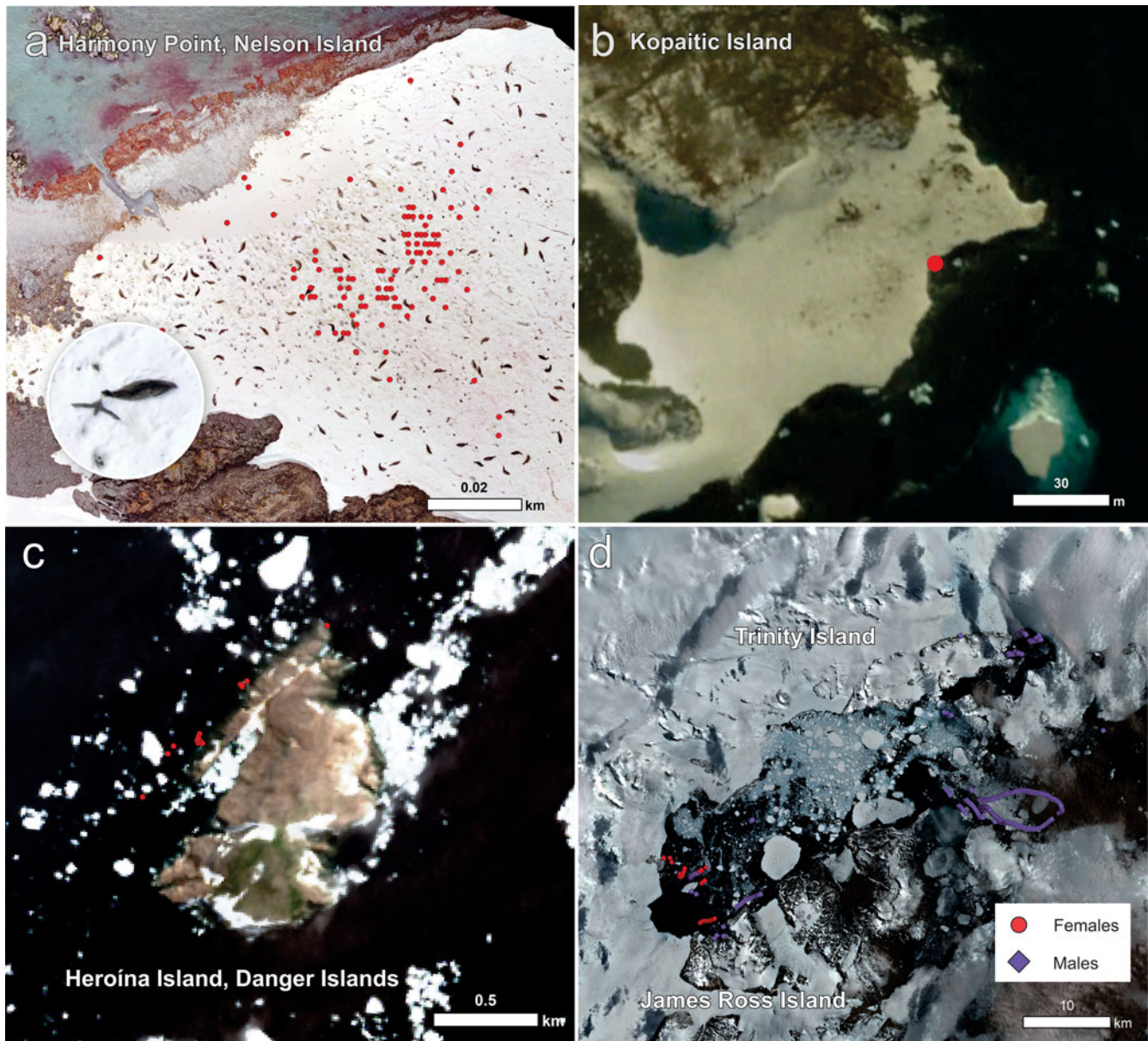
Fig. 4. Distinct habitats used by breeding southern giant petrels. **a.** Glacier edge at Harmony Point, Nelson Island, a haul-out site of Weddell seals (aerial drone image taken in January 2020); in detail is a southern giant petrel feeding on seal faeces. **b.** Ice-covered coast of Kopaitic Island where hauled-out seals are visible (Google Earth Pro image from 14 March 2015). **c.** Breeding colonies of Adélie penguins at Heroína Island (Danger Islands) in the Weddell Sea, where 292 363 breeding pairs were counted in 2015 (Borowicz *et al.* 2018). **d.** Open water amid fast ice in the Prince Gustav channel, Weddell Sea (satellite image from 30 December 2019 freely obtained from Sentinel2, https://apps.sentinel-hub.com/eo-browser).

reached longitude -103°W (Fig. 1a,b), travelling the farthest distance (2009.7 km from the colony) and covering the greatest cumulative distance (5293.5 km) of all individuals. The trip lasted 7.2 days.

Our estimates show that 96.2% of the core foraging areas (KUD 50%) used by the general Harmony Point population are captured by the sample of 47 tracked birds. Despite the variability in the foraging distribution, key areas for the species, which are areas used by a substantial portion of the population, are located around the breeding colony and by the tip of the northern Antarctic Peninsula and the Prince Gustav Channel, between Trinity Peninsula and James Ross Island (Fig. 1e). About a third of this key area is within IBA 'Hope Bay Marine - Antarctic Sound', but it also overlaps with smaller IBAs, such as 'Duroch Islands' and 'Devil Island' (Fig. 1e).
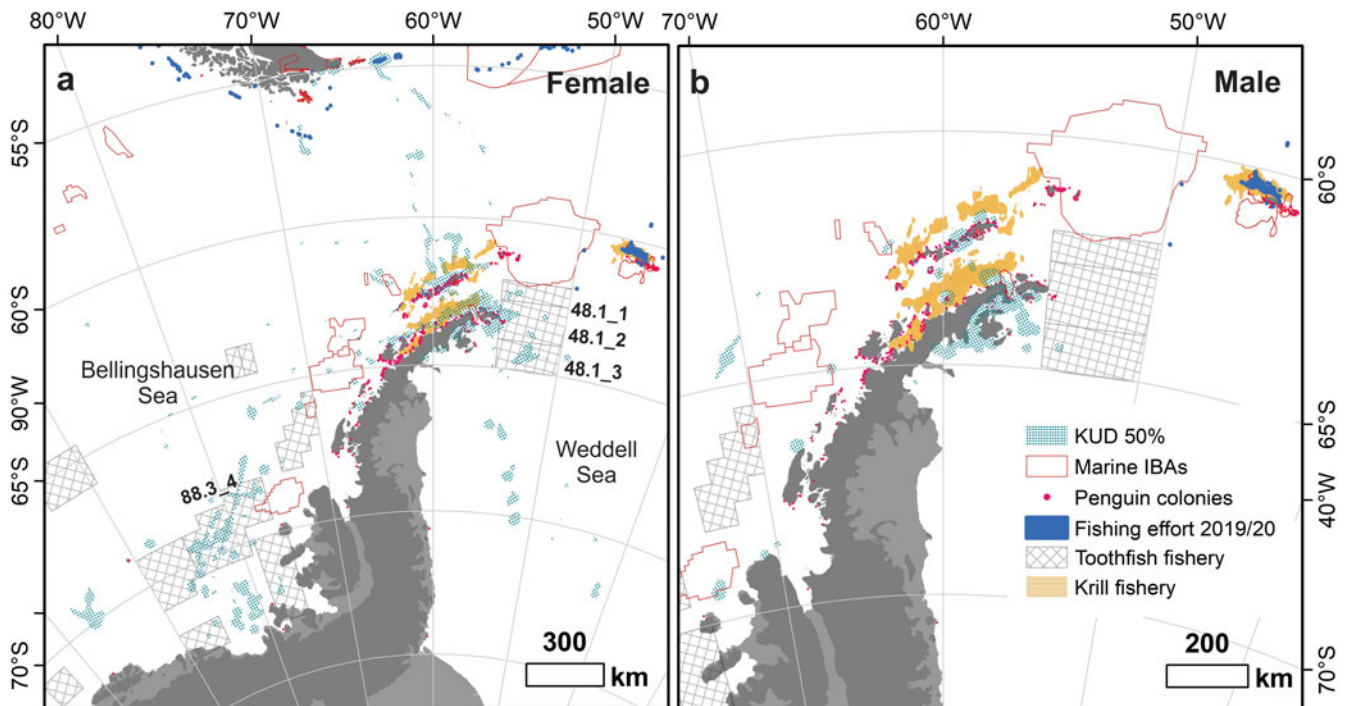
Fig. 5. Foraging areas (kernel usage density (KUD) 50%) of **a.** female and **b.** male southern giant petrels breeding at Harmony Point, Nelson Island, and the distribution of known penguin breeding colonies (Humphries *et al.* 2017), confirmed marine Important Bird Areas (IBAs; BirdLife International, https://maps.birdlife.org/marineibas/), research blocks of exploratory toothfish (*Dissostichus* spp.) fisheries (Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), https://gis.ccamlr.org/), areas used by Antarctic krill (*Euphausia superba*) fisheries in recent years (Krüger 2019b) and longline fishing effort during December 2019 and January 2020 (Global Fishing Watch, https://globalfishingwatch.org).

Habitat selection

Water depth had a weak but positive effect (0.65) on male habitat selection, while distance from penguin colonies had a strong negative effect (-5.38). Water depth and the interaction between breeding stage and SIC had positive effects (0.76 and 0.75, respectively) on female habitat selection. Distance from penguin colonies and the interaction between stage and depth had negative effects (-1.03 and -0.75, respectively), meaning that, although with a weaker effect, females were also attracted by proximity to penguin colonies and to shallower waters during the chick-rearing stage (see Fig. 2).

Males mainly selected areas with shallow to intermediate depths related to the coastal and continental shelf and foraged at shallower depths during the chick-rearing stage (Fig. 3a). They selected areas near penguin colonies with a median distance of 6.44 km during incubation and chick-rearing (see Figs 3c, 4c & 5). During incubation, females mainly selected areas with intermediate to deep depths related to the continental shelf, shelf slope and pelagic habitats, and, as with males, they foraged at shallower depths during the chick-rearing stage (Figs 1 & 3a). During incubation, females selected areas slightly more distant

from penguin colonies than males (median: 20.37 km), but during chick-rearing the distance was similar (Fig. 3c). Although ice concentration alone had a negligible effect on habitat selection, both sexes used areas with varied ice concentrations (Fig. 3d), using habitats ranging from 0% to 99.8% ice coverage during incubation. Females tended to select habitats with markedly lower ice concentrations during chick-rearing (Fig. 3d).

Evidence of overlap between seal haul-out sites and foraging fixes of both sexes was found (Fig. 4a,b). At Harmony Point, where drone imagery allowed closer inspection, it was possible to determine that, when at land, birds frequently used ice-covered areas where Weddell seals (*Leptonychotes weddellii*) hauled out to rest (Fig. 4a).

There was also substantial overlap with areas consistently used by krill fisheries in previous years and exploratory toothfish fisheries, especially by females (Fig. 5). Overlap with toothfish fishery areas was mainly on research block 88.3_4 located over the Bellingshausen Sea and blocks 48.1_1, 48.1_2 and 48.1_3 on the Weddell Sea (Fig. 5a). One female and one male also overlapped their foraging range with areas with low fishing effort at the southern Patagonian Shelf slope,

next to Isla de los Estados (Argentina), where trawlers and bottom longline vessels were fishing during the period when birds were using the area (Fig. 5a). The female foraged at this region during both the incubation and chick-rearing stage, while the male foraged there only during incubation.

Discussion

This study presented the fine-scale foraging distribution of a generalist marine top predator of the Antarctic, the SGP, and described its relationship with environmental variables during the breeding season. The survey, staged at Nelson Island, Maritime Antarctica, is the first to assess the fine-scale distribution of a SGP population breeding above 60°S.

Tracked birds used a wide area of the Antarctic Peninsula and adjacent islands, demonstrating that even by tracking a small number of individuals it is possible to assess conditions of a large area of the Antarctic, especially during the incubation period. The only previous tracking survey of SGPs breeding above 60°S was performed at Elephant Island (61°13'S, 55°21'W) using coarse-scale light-level geolocators (Krüger *et al.* 2017, 2018). SGPs from Elephant Island foraged mainly to the north of the island on the Drake Passage and less frequently in the northern Antarctic Peninsula. Birds from the present study, on the other hand, showed a marked southerly distribution in relation to their breeding colony (Nelson Island) and used a great share of the coast of the western and northern Antarctic Peninsula and the Bellingshausen and Weddell seas as foraging grounds, exploring ice-covered sea and land.

Previous studies tracking SGP populations across the Southern Ocean (e.g. Bird Island, South Georgia: González-Solís *et al.* 2008, Granroth-Wilding & Phillips 2019; Argentine Patagonia, Copello *et al.* 2011; Crozet Island, Thiers *et al.* 2014) in general showed that, during the breeding season, females made farther, longer and more pelagic trips than males and fewer coastal trips (Granroth-Wilding & Phillips 2019). This pattern is confirmed in the present study. Granroth-Wilding & Phillips (2019) suggest that females use terrestrial and coastal areas to scavenge, which has been previously assumed as a male-dominated behaviour (Hunter 1983, González-Solís 2004, Forero *et al.* 2005). The positive effect of proximity to penguin colonies on female habitat selection and consistent use of confirmed seal haul-out sites confirm this suggestion, but female coastal behaviour might also be related to coprophagy, a recently described behaviour for the species and specifically confirmed for the tracked population (Corá *et al.* 2020).

Males also showed a high probability of selecting foraging areas nearby penguin colonies. Males are

known to actively predate on penguins (Le Bohec *et al.* 2003, Ryan *et al.* 2008) and adults and chicks of other seabirds on breeding colonies (Dilley *et al.* 2013, Grohmann Finger *et al.* 2021, Risi *et al.* 2021). It is possible to infer that some of the land areas visited by males, whose habitat selection was also positively influenced by water depth and elevation, could represent areas with an unknown presence of penguin colonies. Small penguin colonies are less likely to be spotted in satellite images (Fretwell & Trathan 2021) such as Sentinel2 (which has an open-source interface). Therefore, the foraging tracks of SGPs could provide clues as to where to invest field effort or where to use paid-for high-definition satellite images to verify the presence of small penguin colonies and to identify seal haul-out sites.

The same areas used by SGPs from Nelson Island have been identified as Areas of Ecological Significance (AESs) of the Southern Ocean (Hindell *et al.* 2020, fig. 1 of that study). Several confirmed marine IBAs (Fig. 5; https://maps.birdlife.org/marineibas/) were also visited, especially IBA 'Hope Bay Marine - Antarctic Sound', which was created due to large foraging aggregations of breeding Adélie penguins. AESs are areas preferred by multiple predator species and indicate high levels of lower trophic biomass and biodiversity (Hindell *et al.* 2020). Due to their high productivity, they can also be targeted by fishing activities throughout the year (Fig. 4; Grémillet *et al.* 2018, Krüger 2019b). SGP mortality associated with longline fishery, although low, has been recorded outside Antarctica (Sullivan *et al.* 2006, Gianuca *et al.* 2017). The consistent use of usual fishing areas in the southern Patagonian Shelf by breeding SGPs shows that even during the breeding season the species could be interacting with fishing boats outside the CCAMLR management areas. While seabird bycatch in longline fisheries has been reduced to a minimal within the CCAMLR areas due to strict measures and regulations (SC-CAMLR-40/BG/23, https://www.ccamlr.org/en/sc-camlr-40/bg/23), seabird mortality associated with krill fisheries (warp strikes and bycatch) has become a recent issue, with records of SGPs attending fishing nets and feeding on mammal bycatch (SC-CAMLR-40/BG/23, SC-CAMLR-40/BG/26, https://www.ccamlr.org/en/sc-camlr-40/bg/26, SC-CAMLR-40/BG/27, https://www.ccamlr.org/en/sc-camlr-40/bg/27). Krill fisheries have been recently changing their period of activity on the western Antarctic Peninsula towards the end of summer and early autumn (Krüger 2019b, Krüger *et al.* 2021); therefore, further data would be necessary to quantify any potential interaction of SGPs with krill fishing vessels. Although IUU longline fishing within the CCAMLR areas is currently not a great concern, unidentified fishing gear is retrieved from time to time (CCAMLR-40/06, https://www.ccamlr.org/en/ccamlr-40/06),

indicating that such activity does occur. In this case, as IUU fisheries are unregulated, they might pose more risks to seabirds. SGPs, therefore, could be used as a means of monitoring any suspicious activity throughout the western Antarctic Peninsula; for instance, using the Automatic Identification Systems from vessels and radar detection tracking devices (Votier *et al.* 2010, Weimerskirch *et al.* 2020) and bird-borne cameras (Votier *et al.* 2013).

Due to the large spatial scale of the Antarctic Peninsula, challenging field conditions and high logistical costs, monitoring the environment and the state and distribution of seabird and mammal populations is a challenge for researchers. In this sense, marine top predators have already been used as oceanographic platforms (Fedak 2013, Ohshima *et al.* 2013) and as indicators of past and current environmental change by tracking shifts in dietary (Carpenter-Kling *et al.* 2019), foraging (Miller & Trivelpiece 2008), demographic (Trivelpiece *et al.* 2011) and phenological parameters (Lynch *et al.* 2012). Optimal sentinel species should be conspicuous and easy to access and be sensitive and respond to changes in the environment in a timely and a detectable manner, which is usually associated with a reliance on a small diversity of or singular prey species (Hazen *et al.* 2019). SGPs are, however, a highly opportunistic and generalist species (Hunter 1984, Granroth-Wilding & Phillips 2019, Grohmann Finger *et al.* 2021), whose status in Antarctica seems to be stable or increasing (e.g. Petry *et al.* 2018, Krüger 2019a). Populations of the southern Atlantic Ocean, including the mid-latitudes of the Antarctic, have been favoured by climate change (Petry *et al.* 2018, Gianuca *et al.* 2019) and the consumption of discards associated with increased fishing activity (Krüger *et al.* 2017). However, in a few sites, local population declines have been recorded and attributed to the stress caused by constant human activities, such as scientific activities and tourism (e.g. Nelson Island: Silva *et al.* 1998; Signy Island: Conroy 1972). But as for populations breeding in higher latitudes or with more southerly breeding distributions, such as the one from Harmony Point, major causes of population variability are yet to be investigated. Therefore, although demographic studies of SGPs still might not be optimal tools for investigating environmental changes in the Antarctic, the large size, conspicuousness, accessibility of colonies and wide and diverse spatial distribution of SGPs make them useful monitoring platforms. Females can be particularly useful for investigating IUU fisheries, while both sexes can be used to investigate seal haul-out sites and penguin colonies. A long-term study joining GPS tracking, animal-borne cameras and diet analysis should provide researchers with a large amount of data on the condition and occurrence of penguin colonies, Weddell seal haul-out sites and IUU fisheries at different spatial and temporal scales.

Ethics approval

Animal study ethics were evaluated and approved by Instituto Antártico Chileno and the Comité Ético Científico de la Universidad de Magallanes. Entrance to Harmony Point Antarctic Specially Protected Area was authorized by Instituto Antártico Chileno (Permits No 1045/2019, No 662/2021 and No 433/2022). Sampling was authorized by Instituto Antártico Chileno (Permits No 1046/2019 and No 654/2021).

Author contributions

JVGF and LK conceived the ideas and designed the study; JVGF, LK and DHC collected the data; JVGF and LK analysed the data; JVGF led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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