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Changing the focus: the need for cross-scale dynamic management in the Southern Ocean and implications for holistic conservation of Antarctic marine living resources

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1. INTRODUCTION

Waters surrounding the Antarctic Peninsula hold one of the most productive marine ecosystems, with populations of Antarctic krill (*Euphausia superba*) sustaining a diverse array of predators (Atkinson *et al*., 2019; Trathan and Hill, 2016). However, this region is facing increasing challenges due to the impacts of climate change and human activities. The West Antarctic Peninsula (WAP) is presently one of the fastest-warming regions on Earth (Siegert *et al*., 2019; Hogg *et al*., 2020). Contemporary warming on the WAP is related to both atmospheric changes and increased transport of warm upper circumpolar deep water onto the shelf (Henley *et al*., 2019), evidenced by observed temperature increases of 3°C in the air and roughly 1°C in surface ocean temperatures from 1955 to 2004 (Moffat and Meredith, 2018). Furthermore, the WAP is witnessing the dramatic retreat of ice shelves and marine glaciers, coupled with a decline in sea-ice concentration and duration, particularly in the WAP and southern Bellingshausen Sea area (Stammerjohn *et al*., 2008). On June 27, 2023, Antarctic sea-ice extent reached a new historic low at 11.7 million km^2, plummeting 2.6 million km^2 below the 1981–2010 average for that time of year and falling 1.2 million km^2 below the previous lowest record registered in 2022 (Purich and Doddridge, 2023).

The WAP concentrates most of human activities in Antarctica, including infrastructure related to scientific research, station operations, transport logistics, tourism, and fishing (Hogg *et al*., 2020; Znój *et al*., 2017). These activities often overlap in both space and time. Nineteen permanent stations plus twenty-five seasonal facilities are located along the Antarctic Peninsula (COMNAP 2017), including 6 year-round stations in the Fildes Peninsula region, in the southwest corner of King George Island (Braun *et al*., 2014). For these reasons, this area displays the largest human footprint (human spatial pressure) in the Antarctic Peninsula region (Pertierra *et al*., 2017). Furthermore, in recent decades the krill fishery has grown to meet rising demand for omega-3 dietary supplements and fishmeal, and relocated from a circumpolar distribution to local hotspots. In the Southern Ocean, 99% of this fishery has concentrated in hotspots within the central Bransfield Strait and the northern Gerlache Strait, the west of the South Orkney Islands and at the northeast of the South Georgia Islands (Subareas 48.1, 48.2 and 48.3 respectively, Fig. 1), predominantly in coastal areas (Watters *et al*., 2020; Trathan *et al*., 2022; Warwick-Evans *et al*., 2022). In this area, the majority of krill is currently caught in autumn and, to a lesser extent, in the north of the South Shetland Islands during summer (Warwick-Evans *et al*. 2022). In the Bransfield Strait and Drake Passage regions, annual krill catches rose from 34,000 tons/year before 2010 to 121,000 tons/year during 2010-2016 (Watters *et al*., 2020). Due to rapid regional warming the distribution of krill has contracted southward and towards shallower waters over the past 90 years

(Atkinson *et al.,* 2019). For these reasons, the krill fishery is also expected to shift southwards in tandem with the krill's movement towards cooler waters (Atkinson *et al.*, 2019), potentially increasing spatial overlap between vessels and penguin and marine mammal foraging areas in the coastal areas of the AP (Hogg *et al.*, 2020; Trathan *et al.*, 2022).

The Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR) plays a pivotal role in the conservation and sustainable use of marine resources within the Southern Ocean. CCAMLR adopts a science based precautionary and ecosystem-based approach to conservation, mandating the consideration of ecosystem effects in managing marine resource harvesting. In doing so, it is considered the world's most successful international management body for marine living resources (Brooks *et al.*, 2020a). CCAMLR's decisions establish the regulatory framework governing fisheries management, encompassing aspects like catch limits, seasonal and area closures, measures to mitigate potential impacts on non-target species and the ecosystems, as well as the establishment of Marine Protected Areas (MPAs) (CCAMLR, 2023). MPAs have been discussed within CCAMLR since the 1990s, but the formal commitment to establish a Southern Ocean MPA network was not made until 2002 in an effort to meet global targets (Brooks *et al.*, 2020b). Since then, some states with jurisdiction over sub-Antarctic islands have been designating MPAs (i.e. at Crozet and Kerguelen Islands, Heard Island and McDonald Islands, South Georgia and South Sandwich Islands and Prince Edward islands), but the first high sea MPA (South Orkney Islands Southern Shelf, hereafter SOISS) was finally approved in 2009. This followed years of scientific workshops and identification of priority areas, crossed by geopolitical and economic discussions, with no evaluation criteria or rules to guide the process (Brooks *et al.*, 2020a,b). The legal framework to guide the establishment of CCAMLR´s MPAs (Conservation Measure 91-04) was adopted in 2011, during the development of other MPA proposals for the Ross Sea (which was adopted in 2016 and represents the world's largest international MPA) and the East Antarctic (Brooks *et al.*, 2020b). Currently, the East Antarctic proposal is still under negotiation, along with others for the Weddell Sea (aimed at protecting over 2 million km^2, Teschke *et al.*, 2021) and the WAP (Hogg *et al.*, 2020). If implemented, the Domain 1 (WAP) MPA is expected to increase the number of whales by about 5% and of penguins by 10% in the Scotia Sea (Klein and Watters, 2020).

CCAMLR also regulates fisheries, by limiting overall catch (primarily to conserve the krill stock) and spatially distributing the catches (to conserve krill-dependent predators) (Klein and Watters, 2020; Warwick-Evans *et al.*, 2022). CCAMLR's primary management outcomes for conserving krill predators are included in the Conservation Measures 51–01 and 1–07 (CCAMLR, 2021), including, for example, the consideration of an interim limit (“krill trigger level”), of 620,000 tons in Area 48, as well as subdividing it amongst Statistical Subareas (Constable *et al*., 2023). Currently, several CCAMLR members wish to increase the allowable catch of krill (Watters and Hinke 2022) and small-scale management of the krill fishery (i.e., the use of smaller or finer scale management units/spatial sub-sections over which catch/effort is distributed) is under discussion. As catches have become more concentrated and closer to predator breeding colonies, CCAMLR has recognized the need for a framework that ensures precautionary protection at scales used by krill predators and now by the fishery (Trathan *et al*., 2022; Watters and Hinke 2022; Warwick-Evans *et al*., 2022). This is because catch limits set for large geographic areas facilitate concentration of catch, which can increase the risks of ecological impacts at smaller scales, through depletion of local krill populations (Klein and Watters 2020). By spreading the fishing effort across small scale management units the fishery would be forced to spread effort, thereby diminishing local impact on krill and predators foraging within the small management areas. If CCAMLR succeeds in implementing a small-scale approach to management, it would allow setting specific spatio-temporal catch limits according to fine scale ecosystem processes, such as consumption by predators, or important areas for krill (Warwick-Evans *et al*., 2022). The revision of krill management is particularly relevant for CCAMLR subarea 48.1, where seasonal sea ice has been retreating due to regional warming, leaving more space for fishing to grow (Watters *et al*., 2020; Trathan *et al*., 2022). In 2019, CCAMLR’s Working Group on Ecosystem Monitoring and Management (WG-EMM) agreed on a work program to implement a revised management strategy for the krill fishery, which incorporates risk assessment, recognizing the need to consider information on the structure and function of the wider krill-based ecosystem, including krill-dependent predator species (Warwick-Evans *et al*., 2022). Within the private sector, in 2018 some krill harvesting companies, members of the Association of Responsible Krill Harvesting (ARK), agreed on a set of voluntary measures to aid in the protection of the Antarctic ecosystems, which include voluntary restricted zones, trans-shipment and vessel safety (https://www.ark-krill.org/ark-voluntary-measures). Yet, these are voluntary agreements between private stakeholders, not legally-binding regulations agreed by Parties to ensure the fulfillment of the objectives of an international convention for the joint management of common resources.

Ice-obligate Adélie penguins (*Pygoscelis adeliae*) are a key indicator species in Antarctic ecosystems (Cusset e*t al*., 2023). Although Adélie penguins are the most abundant penguin species in Antarctica, with 10 million mature individuals (IUCN, 2020), populations in the WAP are shrinking and the future is not promising. WAP colonies have decreased by over 50% since the 1970s (Trivelpiece *et al*., 2011; Lynch *et al*., 2012) and an example of this is the Copacabana Field Station colony (at Admiralty Bay, King George Island), that has reduced by 79% in 25 years (Hinke *et al*., 2017). Population declines are predicted at ~30% of Adélie colonies by 2060 and ~60% by 2099 in the WAP (Cimino *et al*., 2016). Population declines are attributed to reduced krill biomass and availability due to regional sea-ice declines, fishing, and the proliferation of natural competitors such as seals and whales (Trivelpiece *et al*., 2011; Lynch *et al*., 2012; Watters *et al*., 2020; Warwick-Evans *et al*., 2022). Shifts in the duration and spatial extent of ice coverage are expected to be important drivers of population change for ice-obligate species, as a positive correlation between ice extent and survival rates has been observed in Adélie populations from the Antarctic Peninsula (Hinke *et al*., 2014; Hinke *et al*., 2017).

However, most studies on this species were conducted during the summer, when adult Adélie penguins are accessible in their colonies (Machado-Gaye *et al*., 2024). During this period, birds perform sex-specific foraging strategies, when females tend to forage farther, longer, and dive shallower, while males exploit waters closer to the colony and dive deeper (Chappell *et al*., 1993; Clarke *et al*., 1998; Lescroël *et al*., 2010; Widmann *et al.,* 2015; Riaz *et al.,* 2020). These differences in foraging behavior were linked to differences in diet, with females from Hope Bay (Antarctic Peninsula) consuming greater amounts of krill in more offshore/pelagic waters, while males feed equally on krill and fish in more inshore, benthic waters (Clarke *et al*., 1998; Colominas-Ciuró *et al*., 2018). In the vicinity of the Antarctic Peninsula, South Shetland Islands, and South Orkney Islands, Adélie penguins consume fishes *Pleuragramma antarcticum* and *Lepidonotothen squamifrons* during the summer (Polito *et al*., 2011). According to Juáres *et al.* (2017), summer diet at Stranger Point (King George Island, close to our study site) has been krill-dominated for the last 27 years, with minor fish consumption of *P. antarcticum* and *Electrona antarctica*.

Several knowledge gaps still persist regarding the Adélie penguin WAP populations, particularly concerning their non-breeding distribution, movements and feeding habits (Erdmann *et al*., 2011). Tracked adult and juvenile Adélie penguins from other colonies in the South Shetland Islands travel to the NW Weddell Sea after breeding, molt on the ice, and also used the southern Scotia Sea before returning to the breeding colonies by late September (Hinke *et al*., 2015, 2020; Polito *et al.,* 2017). Erdmann *et al.* (2011) explored the partitioning of foraging resources between sexes during the non-breeding period, registering an increase in foraging area overlap in females during a year with heavy ice cover. Adélie penguins from Signy Island (South Orkney Islands), a colony close to WAP, also headed to the Weddell Sea to molt after breeding, foraging near and molting on sea-ice (Dunn *et al.,* 2011; Warwick-Evans *et al.*, 2019). The study of δ13C stable isotopes also revealed that Adélie penguins disperse widely and forage in more pelagic/offshore habitats during the post-breeding season in comparison with the breeding season (Herman *et al.,* 2017), and that currently they forage further south and/or closer to the sea ice edge than in the 1980s, possibly due to climate change (Negrete *et al.,* 2016). For the pre-breeding season, Gorman *et al*. (2014) reported no sex-related differences in the trophic niche, while Polito *et al*. (2011) found that high trophic-level prey such as fish and/or squid comprised a significant portion (46.8 - 62.9%) of female Adélie penguin diets. In turn, Juáres *et al*. (2016) reported that krill dominated the diet of Adélie penguins in Stranger Point over their annual cycle, but found a mean contribution of 16 and 14% of pelagic and benthonic fish during the post-breeding stage, which rose to 23% and 10% during the pre-breeding stage. Given the significant changes observed in the Antarctic Peninsula region in the last two decades, these studies are of high value for comparative purposes, as most of them represent a base-line elaborated with data collected between 10 and 20 years ago. In order to facilitate evidence-based policymaking, more information is needed on the non-breeding ecology of Adélie penguins, including sex-disaggregated data as several studies have found differences between males and females across many penguin species.

Being highly dependent on sea ice during the winter season, and given the massive reduction observed in sea-ice extension in recent years, understanding the spatial dynamics of and dietary resources utilized by Adélie penguins during the non-breeding season is vital to understand the effects of environmental changes, on overall population persistence. Lack of resources in critical periods throughout the year may have a profound impact on juvenile and adult survival and subsequent breeding success (Black *et al.,* 2018; Hinke *et al.,* 2020). This is particularly relevant for Adélie penguins, that migrate long distances after breeding, to molt and forage in the pack ice (Ballard *et al*., 2010; Hinke *et al*., 2015), hundreds of km away from the colony (Dunn *et al*., 2011). Overall, winter migration is the major source of adult mortality, with about 25% of penguins not returning to their breeding grounds (Ainley & DeMaster 1980; Davis 1988).

Key stages during the Adélie penguins non-breeding season include: 1) immediately after their chicks fledge, as penguins have to recover body condition from the breeding stage; 2) before and after molting, as they have to generate and regain reserves to prepare and recover from a highly energy-intensive molt (when molting, Adélie penguins lose and regrow their entire plumage at one time, spending a mean of 16-19 days fasting on the ice; Hinke *et al*., 2015; Schmidt *et al*., 2023; this study); 3) before starting the breeding season, as they have to accumulate reserves to endure the energetic demands of incubation and chick-rearing. Identifying the areas used by these animals during those critical stages of the non-breeding season, and understanding what resources they exploit during the wintering season is key to ensure that human-induced impacts are diminished to a minimum during these time-periods. This information is in turn valuable to assess whether current MPAs proposals provide a valuable contribution to diminishing those impacts.

Here we seek to provide updated information on the spatial use and the trophic niche of WAP Adélie penguins during the non-breeding period and across two seasons, with special emphasis on critical periods such as pre and post molting, and prior to the start of the reproductive season. Using geolocators we identify molting and wintering areas used by Adélie penguins breeding at Ardley Island. We asses trophic niche using Stable Isotope Analysis (SIA) of carbon and nitrogen on feathers. With our results, we expect to contribute to the discussion on the design and implementation of dynamic and effective Marine Protected Areas and sustainable fishery management in the Southern Ocean.

2. METHODS

2.1 Study site

We studied Adélie penguins breeding at Ardley Island (62°13'00.1" S, 58°55'59.9" W), located in Maxwell Bay, King George Island (South Shetland Islands). Ardley Island is a small ice-free island (~2 km long by 1 km wide), connected to the Fildes Peninsula by an isthmus which is submerged during high tides. The island has been designated as an Antarctic Specially Protected Area (ASPA 150), a CCAMLR Ecosystem Monitoring Program (CEMP) site, and Important Bird Area (IBA AQ048). The colony currently hosts approximately 209 breeding pairs of Adélie penguins (census November 2023, this study) and has experienced a sharp decline in the number of breeding pairs since the 1980s (Braun *et al*., 2017).

2.2 Deployment of devices and data collection

Adult Adélie penguins were captured during the 2020/2021 and 2021/2022 breeding seasons (November-December) and fitted with MK3005-series archival geolocators (hereafter GLS; Lotek UK Ltd, Dorset, United Kingdom) to study dispersal and space utilization. We took care to minimize stress by covering the penguin´s head during handling and ensuring that handling time was always below 5 minutes. The GLS were fitted with cable-lined plastic seals to the penguin’s tarsus following Ratcliffe *et al.* (2014). Each GLS weighed 2.5 g, representing approx. 0.06% of body mass of adult Adélie penguins (mean for Ardley Island 3847 ± 392.3 g, Machado-Gaye *et* *al*., 2024). Twenty-one GLS were deployed in 2020 and 20 in 2021, on different individuals observed breeding. GLS were recovered at the onset of the following breeding season in November/December. The GLS measures light intensity every minute and saves to memory the maximum light measurement recorded in 10 minutes. Additionally, the device records the exact time of change (within 3 seconds) and duration of wet/dry state; but the new state is recorded only if it is sensed for 6 seconds or more. Temperature is recorded after 25 min of continuous exposure to water. Temperature wet timer will reset anytime device goes dry for >6 seconds.

2.3 Location estimations

Light level data were processed in R (v 4.3.0) (R Core Team 2023). Locations were estimated following the approach of Merkel *et al*. (2016), using a probabilistic algorithm included in the package probGLS (Merkel *et al.,* 2016) that relies on timing of twilight events (sunsets and sunrises). This approach can incorporate various sources of uncertainty (e.g. uncertainty in solar angle), knowledge of the behavior and habitat use of the species (e.g. travel speed), by defining associated parameter values *a priori*.

Twilight events from raw light intensities were computed with the preprocessLight function (TwGeos package; Lisovski *et al.*, 2019), considering a light threshold of 2.5, incorporating uncertainty and unknown solar angle. Uncertainty in twilight events was assumed to follow a log-normal distribution and the error parameters for this uncertainty were generated using twilight_error_estimation function (package probGLS). Twilight events were filtered manually (preprocessLight function) and automatically (twilightEdit function, window = 4, outlier.mins = 45, stationary.mins = 25), before estimating locations.

Values set to run probGLS were k-loess = 3; particle.num = 1200 and iteration.num = 100. We also used daily mean sea surface temperature (SST) and daily SST error data for 2021 and 2022, provided by the NOAA Physical Sciences Laboratory (https://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.highres.html) and daily estimates of SST based on the temperature recorded by the GLS tags to improve the precision of location estimations.

Once latitude and longitude were estimated, locations were further filtered considering latitude residuals dispersion (k-loess = 1.5) and using the ‘sdafilter’ algorithm (argosfilter package, Freitas *et al.*, 2008) to remove unrealistic locations based on horizontal traveling speed. The sdafilter function is based on the traveling speed of the tracked animal, distance between successive locations and turning angle. We used a threshold of 2.0 m/s based on the maximum of Adélie penguin horizontal speeds reported in Machado-Gaye *et al.* (2024). Finally, 19 unrealistic locations were filtered through visual inspection (interactive map), as the previous or subsequent location was located across the Antarctic Peninsula. After applying the aforementioned filters, 5324 positions (86.3%) were retained. All analyses were performed using locations from 1 January to 15 November of each year.

2.3 Environmental covariates

We used daily sea-ice concentration values, reported on a 6.25 km grid, available from the University of Bremen (Spreen *et al.*, 2008; https://seaice.uni-bremen.de/data/amsr2/asi_daygrid_swath/s6250/netcdf/) to calculate mean monthly sea-ice concentration and to estimate the contour of 15% sea-ice concentration (effective ice edge). We also extracted the mean sea-ice concentration within a buffer of 100 km around each location for all the individuals to infer sea-ice concentration preferences of Adélie penguins throughout the year.

2.4 Molt period identification

We used GLS wet/dry data to identify long continuous dry periods as molt, as animals do not enter water during this phase (e.g., Schmidt *et al*., 2023). The period of 30 days previous to the onset of molt, corresponding to pre-molt foraging trips, was considered the time-window of the feather's stable isotope incorporation (see below, Whitehead *et al.*, 2016). We estimated the individual centroids of these 30-days pre-moult locations using the st_centroid function in sf R package (Pebesma 2018).

2.5 Laboratory analysis

2.5.1 Stable Isotopes Analysis (SIA)

Feathers are a metabolically inert tissue after growth, thus they potentially reflect food consumption of penguins during their pre-moult foraging trips (Tierney *et al* 2008; Hinke *et al*., 2015). We estimated carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope ratios of body feathers to assess for intraspecific foraging niche partitioning between year and sex (yet, because of the small sample size we did not perform statistical analysis by sex). δ^{15}N primarily increases as the trophic level of individuals rises (Post 2002), while δ^{13}C provides information about the origin of primary productivity, enabling the inference of foraging habitat (France 1995). In the marine environment, for instance, ^{13}C distinguishes between the utilization of benthic and pelagic prey and pelagic and offshore food webs (France 1995), integrating both a horizontal (inshore/offshore) and a vertical (benthic/pelagic) component (Cherel and Hobson 2007).

Feathers were collected in November-December of the year of its synthesis, after the GLS recovery. Up to 6 body feathers were plucked from the legs of 11 and 9 adult penguins carrying GLS during the 2021 and 2022, respectively. To increase the sample size and representation of the colony, in 2022 feathers from another 7 individuals (without GLS) were included in the analysis. Feathers were stored in plastic bags at ambient temperature until processing. They were cleaned with a chloroform: methanol (2:1) mixture, sonicated for 3 min, rinsed twice with 100% methanol and dried at 50°C for 24 hrs. Four feathers per individual were cut with precision scissors to obtain a homogenous grind.

Nitrogen and carbon isotope ratios were measured on feather homogenates (0.5–1.0 mg) by Elemental Analyzer Continuous Flow Isotope Ratio Mass Spectrometry in the Center for Stable Isotopes, University of New Mexico using a Costech ECS 4010 Elemental Analyzer coupled to a ThermoFisher Scientific Delta V Advantage mass spectrometer via a CONFLO IV interface. Isotope ratios are reported using the standard delta notation relative to V-AIR and to Vienna Pee Dee Belemnite (V-PDB), respectively. Three internal, laboratory standards were run at the beginning, at intervals between samples, and at the end of analytical sessions. Analytical precision calculated from the standards is ± 0.1 ‰ (1 standard deviation) for both $\delta^{15}N$ and $\delta^{13}C$. Analyses were normalized to the laboratory standards (more information in Supp. material).

2.5.2 Sex determination

For sex identification, we used molecular techniques from blood and feather samples. Blood samples were drawn using a 5ml syringe from the leg vein of individuals with GLS. A droplet of 2ml – 3ml of blood was dropped onto the ring of an FTA card and allowed to dry for one hour. The FTA cards were then placed in a plastic bag and brought back to the laboratory. These cards were then kept at room temperature. DNA isolation was performed using the QIAamp®DNA Blood Mini Kit (QIAGEN, Hilden, Germany) based on a nucleated blood protocol with a few modifications. To start, a 3mm disc from the FTA card was punched using an autoclaved ticket puncher and placed in a 1.5 ml tube. A total of 280 µL ATL buffer and 20 µL Proteinase K were added to each sample tube containing an FTA card piece, following the manufacturer's instructions.

Feather samples were used for sex identification of those individuals with no GLS (therefore, no blood sample). Each feather sample consisted of 4-6 segments of 2.5 mm from the basal part of the quill (tip). We used the rest of the feathers for the isotopic analysis. The DNA extraction from feathers was carried out with the prepGEM Universal (PUN) DNA extraction Kit (Zygem, Hamilton, New Zealand) following the manufacturing procedure for Solid Tissue.

A fragment of the CHD1 gene, located on the bird's sex chromosomes, was amplified by PCR with P2 and P8 primers (Griffiths *et al*., 1998). This PCR produces fragments (CHD1W and CHD1Z) that differ in 18 bp length among sex chromosomes on *Pygoscelis* penguins (Polito *et al.,* 2012; Valenzuela-Guerra *et al.,* 2013; Zhang *et al*., 2013). Chromosome Z occurs in both sexes while chromosome W is unique to females. Therefore, a single fragment size is amplified in males (ZZ) and two fragments of different sizes in females (ZW).

The PCR reaction was carried out following Rabinovich *et al.* (2024), the PCR consisted of a final volume of 20uL with 1x of Platinum Multiplex Master Mix (Invitrogen Life Technologies, Carlsbad, California), 0.5 uL of each primer and 50 ng of genomic DNA template. We incorporated a fluorescent dye (FAM) on the P2 primer to analyze the fragments size by capillary electrophoresis. PCR profile consisted of an initial denaturing step at 94ºC for 10 min, followed by 35 cycles of 94ºC for 30 sec, 47ºC for 1 min, and 72ºC for 1 min, and a final extension of 72ºC for 10 min. Positive and negative controls were included in each PCR. Positive controls consisted of samples of *Gubernatrix cristata* of known sex. PCR amplification was confirmed by electrophoresis on 1% agarose gel and products were sent to the Unidad de secuenciación Sanger at Hospital de Clínicas, Uruguay, for fragment analysis. Genotype assignment was carried out with GeneMarker 2.4.0 (Softgenetics LLC, State College, Pennsylvania). Males were homozygotes (370/370 pb) and females, heterozygotes (370/388 pb).

SIA sex-disaggregated results are presented in Table 1 and supplementary material (Table 1 Supp). No further analysis was done because of small female sample size.

2.6 Analysis of isotopic data

ANOVAs were performed to evaluate differences in δ^{13}C and δ^{15}N values between years. We did not include sex in models due to the small number of females sampled (see Table 1). Stable Isotope Bayesian Ellipses in R (SIBER, Jackson *et al*., 2011) were employed to delineate the isotopic niche space for each year. This methodology, a Bayesian adaptation of Layman metrics

(Layman *et al*., 2007), accommodates uncertainties like sampling biases and limited sample sizes in the assessment of niche metrics (Jackson *et al*., 2011). Through Markov Chain Monte Carlo (MCMC) simulations, this approach assigns measures of uncertainty to compute ellipse parameters, akin to a bootstrap procedure. Standard ellipse areas, adjusted for small sample sizes (SEA_C), were utilized to estimate the breath of the isotopic niche, employing Bayesian standard ellipse areas (SEA_B) at 40%, with 1000 replicates. The derived values included the modes and the 95% confidence interval (CI). Ellipses area overlap between years were estimated with the function maxLikOverlap in the package *SIBER* (Jackson *et al*., 2011).

3. RESULTS

3.1 Non-breeding distribution range

Eleven tags were retrieved in 2021 and 9 tags in 2022 after almost one year of deployment, providing records of ambient light intensity, wet/dry status and sea surface temperature. Our results revealed migration routes across the Bransfield Strait, north of the Antarctic Peninsula, and the Wedell and Scotia seas, encompassing three different CCAMLR management subareas, two proposed Marine Protected Areas (MPA) and one MPA (Fig. 1).

Penguins depended on resources available in CCAMLR subareas 48.1 and 48.5 during the post-breeding and molting stage (January-March), and resources distributed across the subarea 48.5 during the post-molting stage (April) and subareas 48.1, 48.2 and 48.5 during the pre-breeding stage (September-October). On the other hand, both the proposed Domain 1 MPA (D1MPA) and the Weddell Sea MPA (WSMPA), as well as the already extant South Orkney Islands Southern Shelf Marine Protected Area (SOISS) MPA, include a significant portion of Adélie´s non-breeding areas. Remarkably, part of the areas used by some individuals during the late non-breeding (September and October), and breeding stages (November and January) fall outside the limits of the CCAMLR convention (Figs. 1 and 2).

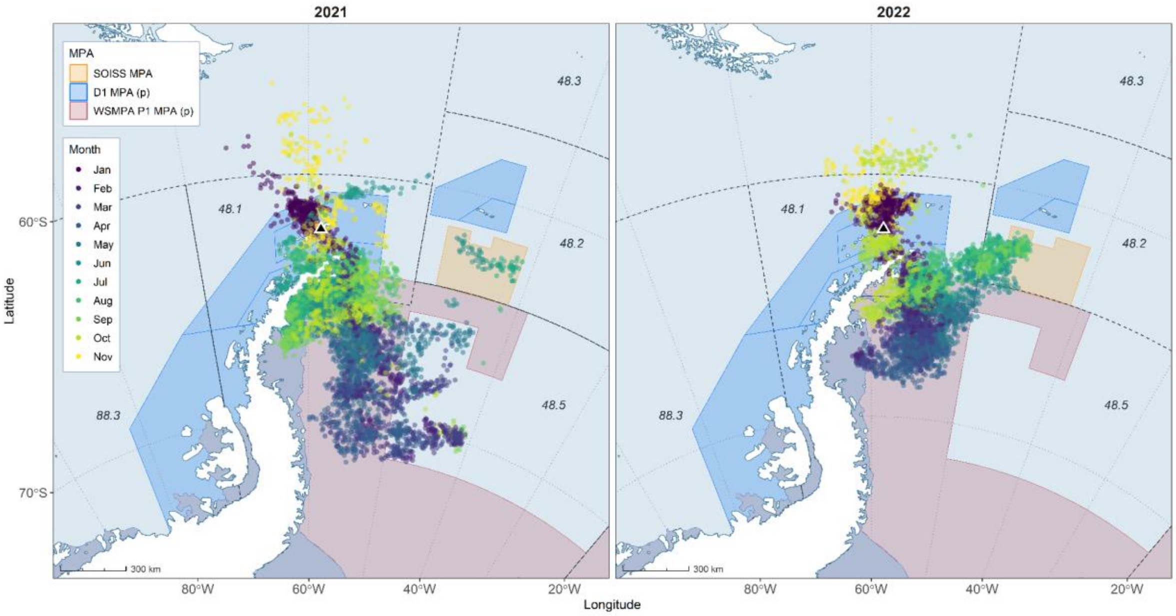

Figure. 1. Year-round distribution of 20 Adélie penguins from Ardley Island in Antarctic Peninsula during the 2021 (left, n = 11) and 2022 (right, n = 9). Color shaded areas represent MPA/MPA proposals: Light orange corresponds to the South Orkney Islands Southern Shelf Marine Protected Area (SOISS MPA); light blue to the Domain 1 Marine Protected Area (D1MPA) proposal; and light red to the Weddell Sea Marine Protected Area (WSMPA Phase 1) proposal. Number codes in italics refer to CCAMLR management sub-areas. Colony is represented by a black triangle.

In 2022, the non-breeding range exhibited a notably more coastal pattern compared to 2021, during which Adélie penguins displayed more prominent incursions into the Weddell Sea and Drake Passage. Figure 2 illustrates the non-reproductive locations per month relative to the ice edge (15% sea-ice concentration). In January, Adélie penguins departed from the Ardley Island colony, initially heading north into the Drake Passage and the Scotia Sea before turning towards the tip of the Antarctic Peninsula. By February, the majority of the tracked individuals had already reached the pack-ice region of the Weddell Sea, where they molt. From March to May, all the penguins remained within the Weddell Sea, and then in June, they began moving northward again, getting closer to the coast of the Antarctic Peninsula. As winter progressed, a noticeable shift occurred, with some individuals seemingly turning towards the South Orkney Islands, particularly in 2022, while others still stayed well south of the ice edge.

Only 2 penguins were registered near the colony (<100 km) during winter (July-August 2021). The first penguins returning to Ardley Island were recorded in October, even though other individuals were still in the Weddell Sea, while others were navigating the waters of the Drake

Passage, halfway between the South Shetland Islands and Tierra del Fuego. In November, the majority of individuals remained within the area spanning the Bransfield Strait and the Drake Passage, out of the pack ice.

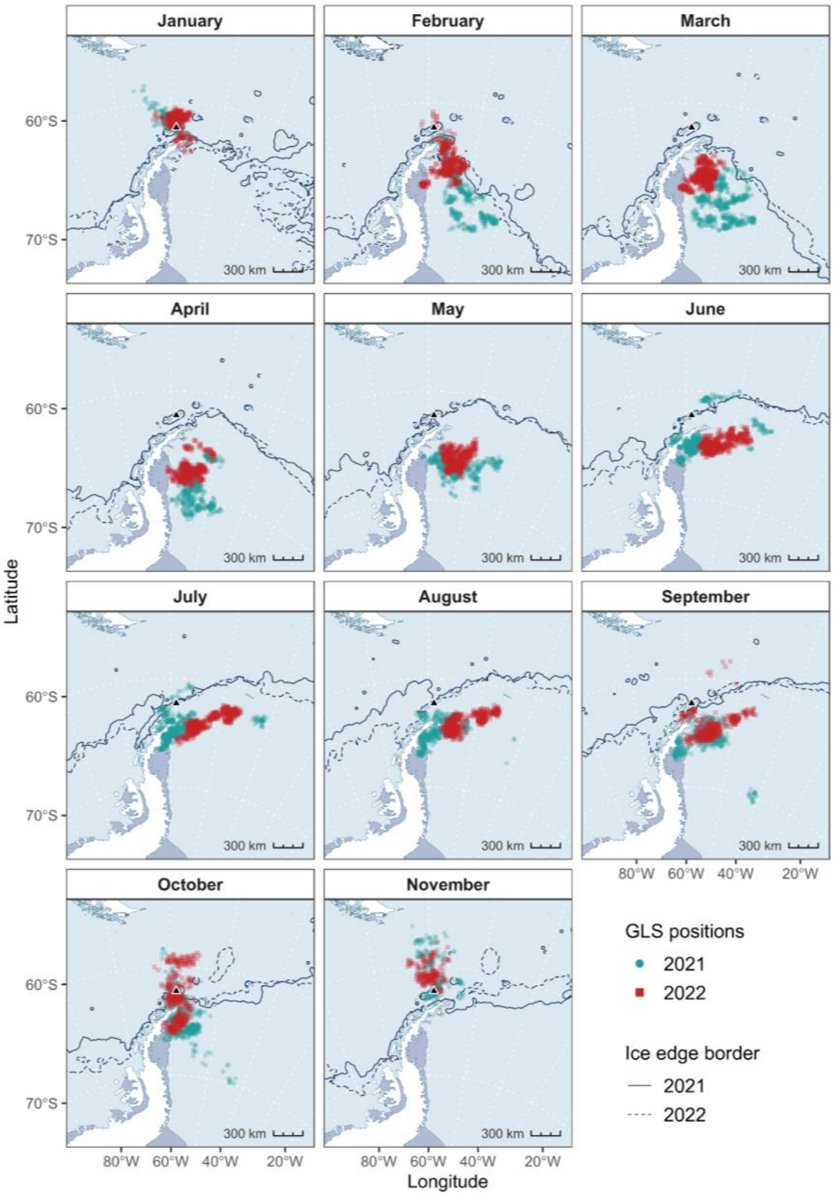

Figure 2. Locations of 20 Adélie penguins by month (January-November) in relation to ice edge. Solid and dashed black lines represent 15% sea-ice concentration (effective ice edge) in 2021 and 2022, respectively. Colony is represented by a black triangle.

Regarding the connection with sea ice throughout the year (as Adélie penguins are considered an ice-obligate species), we observed that the highest sea ice concentrations (SIC) were recorded in April and May for both years (Fig. 3). This corresponds to the post-molt period when most locations were situated on >90% SIC. The rest of the year shows great inter-individual variability, with similar patterns between years. A striking variability can be observed between years in February, March and October, reflecting different individual choices during molt and prior to the breeding season. This is also evident when latitude and longitude positions are compared between years (Fig. 4)

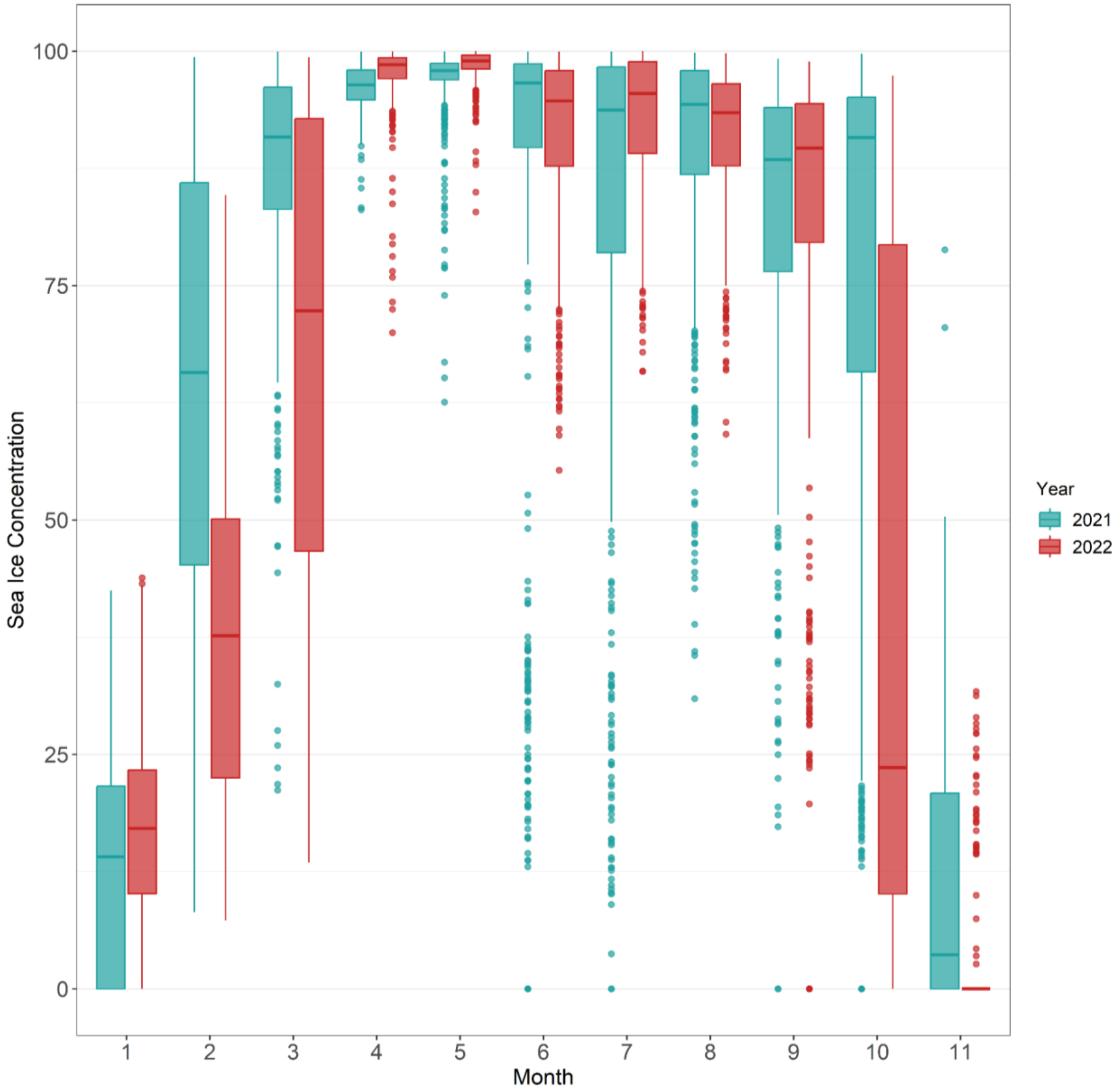

Figure 3. Mean sea-ice concentration (%) within 100 kms buffer around Adélie penguins GLS locations, per month/year.

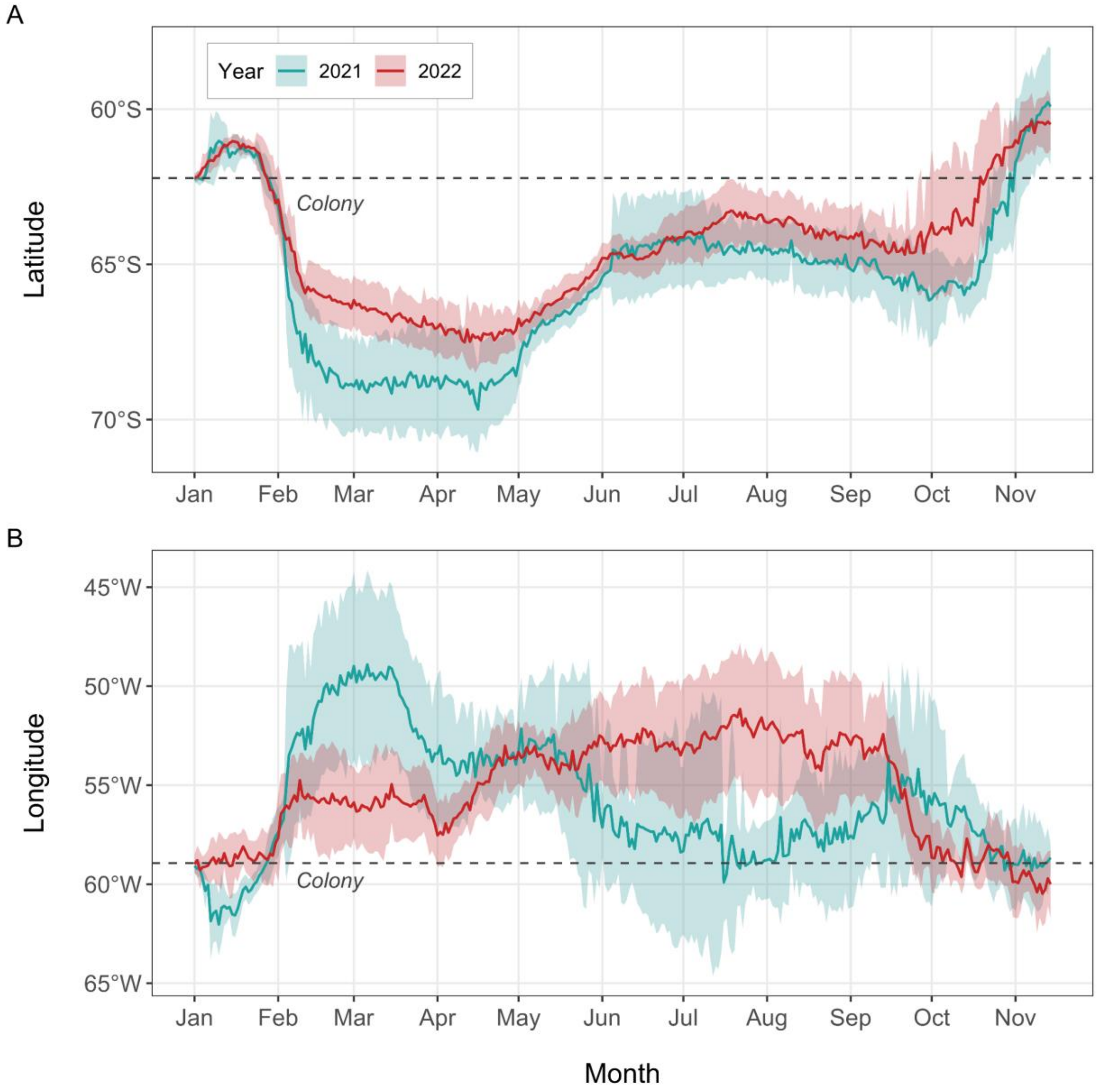

Figure 4. Changes in the (A) latitudinal and (B) longitudinal positions of Adélie penguins during two years of tracking (2021, n = 11, and 2022, n = 9). Lines indicate the mean and the shaded area the standard deviation of individual daily positions. Dash lines represent latitude and longitude of the colony.

3.2 Molt

Dates of first and last molt initiation in 2021 were February 9 and March 2, while in 2022 were February 11 and 22 respectively. Molt lasted on average 16.1 ± 2.7 d (range = 9 to 18 d) in 2021 and 18.7 ± 1.39 d (range = 17 to 21 d) in 2022. Onset of pre-molt periods (i.e. the isotopic incorporation period) were estimated between January 10 and January 31 for 2021, and January 12 and January 23 for 2022.

3.3 Isotopic niche

Mean δ^{13}C value for both sexes pooled together was -24.82 ± 0.34‰ in 2021, while in 2022 it was -24.23 ± 0.74‰. In the case of δ^{15}N, the means were 9.12 ± 0.21‰ and 9.32 ± 0.67‰, in 2021 and 2022, respectively (see Table 1 for sex-disaggregated values and Suppl. material for individual values). Statistical differences among years were detected only in δ^{13}C (p-value = 0.02), without differences in δ^{15}N (p-value = 0.36). The area of the Bayesian ellipses was used as a measure of isotopic niche width, which was greater in 2022 compared to 2021 (Fig. 5, Table 1). In 2022 δ13C signatures indicate more influence of coastal environments and there was greater diversity of trophic levels (δ15N) utilized compared to 2021. The overlap ellipse area was 0.14‰2, representing 60% for 2021 and 13% for 2022.

Table 1. δ^{13}C, δ^{15}N signatures (means ± SD and range, in ‰) disaggregated by year and sex and Bayesian standard ellipse area-SEA$_B$ (medianode and 95% IC, in ‰2) by year are shown for adult Adélie penguin feathers. n = number of individuals.

Year	**2021**		**2022**	
Sex	**Female**	**Male**	**Female**	**Male**
δ^{13}C	-24.72 ± 0.35	-24.88 ± 0.35	-24.36 ± 0.87	-24.20 ± 0.75
Range δ^{13}C	-25.1 to -24.3	-25.4 to -24.3	-25.1 to -23.4	-25.1 to -22.6
δ^{15}N	9.25 ± 0.26	9.05 ± 0.17	9.20 ± 0.61	9.35 ± 0.71
Range δ^{15}N	8.89 to 9.49	8.85 to 9.29	8.77 to 9.88	8.57 to 11.21
SEA$_B$	0.22 (0.13- 0.42)		1.15 (0.72-2.00)	
n	4	7	3	13

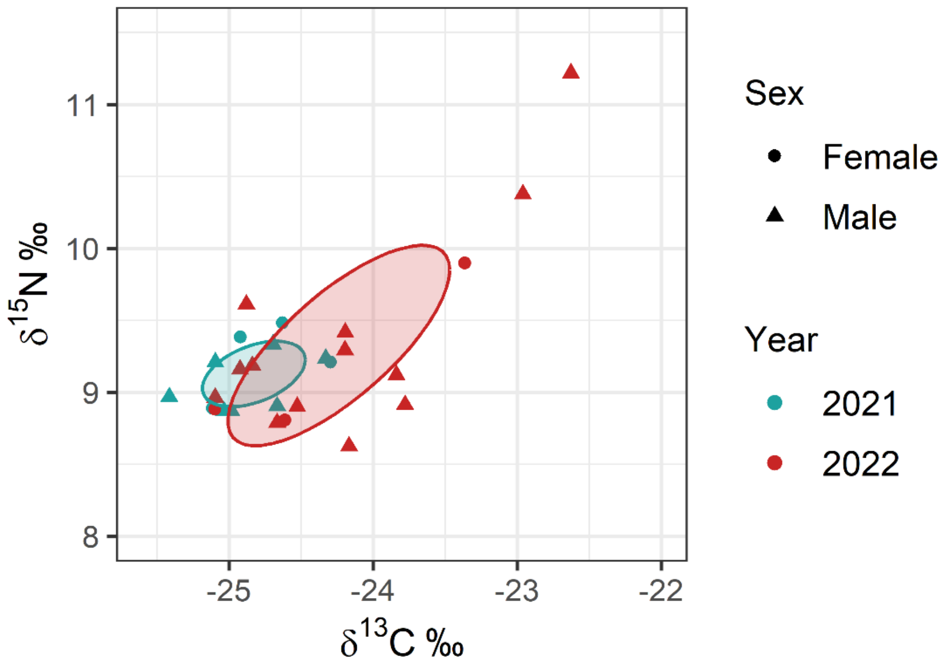

Fig.5. Bayesian ellipses representing Adélie penguin isotopic niches (Group Ellipses p.interval = 0.40).

4. DISCUSSION

After breeding, Adélie penguins from Ardley Island headed towards the Drake Passage and the Scotia Sea. By February, the majority had reached the Weddell Sea, where they molt, and afterwards, they remained within the pack ice of the Weddell Sea recovering from molting. As winter progressed, Adélie penguins got closer to the ice edge and the coast of the Antarctic Peninsula, while some individuals used the SOISS MPA. These general movement patterns are similar to those previously documented by Hinke *et al*. (2015) for other colonies in the South Shetland Islands (even though Adélie penguins from Admiralty Bay reached waters further north, especially in August and September) and show that these winter areas and their resources are key for recovering penguin body reserves (Trathan *et al*., 1996).

Three CCAMLR subareas (48.1, 48.2 and 48.5) and areas located outside the convention area were extensively used by Adélie penguins during key stages of the non-breeding season. Our results show the relevance of resources located within the two MPA proposals, the Domain 1, comprising the WAP and South of the Scotia Arc, and the Weddell Sea (Phase 1), for Adélie penguins during the non-breeding stage, but particularly during critical periods such as post-breeding/pre-molting, post-molting and pre-breeding. The SOISS MPA was also extensively used, particularly in 2022.

Consistent with prior findings (Ballard *et al*., 2010; Dunn *et al*., 2011; Hinke *et al*., 2015; Schmidt *et al.,* 2023), our results underscore the significant reliance of Adélie penguins on ice conditions. Adélie penguins molted in February and March within the Weddell Sea (as reported by Dunn *et al*., 2011), in locations where the concentration of sea ice was 40-90%. Warwick-Evans *et al*. (2019) reported SIC of molting locations > 80%, also for the Weddell Sea. The Weddell sea ice region is an important molting habitat for other Adélie colonies as well, such as those in Admiralty Bay, King George Island (Hinke *et al*., 2015; Oosthuizen *et al*. 2022), in Signy Island (Dunn *et al*., 2011; Warwick- Evans *et al*., 2019); and also for Emperor penguins (*Aptenodytes forsteri*) (Kooyman *et al*., 2000). We report the shortest Adélie penguin molt duration (mean 16.1 ± 2.7 d, range = 9 to 18 d in 2021), comparing to those reported by Schmidt *et al*. (2023) (i.e. mean 19.3 d, range = 13 to 26, as well as previous findings between 17 and 20 d). After molting, Adélie penguins stayed in locations with >90% SIC through April and May, similar to those reported by Dunn *et al*. (2011) (i.e. 90.3 - 93.7%). All individuals remained continuously at sea, south of the ice-edge, from March to September/October, a period of approximately 7 months after the end of the molt, as also reported by Dunn *et al*. (2011).

Stable Isotopes Analysis (SIA) showed significant statistical differences between years in δ^{13}C signatures, with higher values in 2022. In addition, both the δ^{13}C range and the Bayesian ellipse area in 2022 were higher. This suggests that during that year, penguins utilized resources with a greater diversity of origins. The spatial accuracy of the determination of foraging areas of consumers using their δ^{13}C values ranges from tens to hundreds of km in latitude, and at the spatial scale of a subantarctic archipelago, the δ^{13}C values indicate the distance of their foraging areas from the coast (Cherel and Hobson 2007). Thus, our SIA results show the use of both coastal and offshore foraging areas in 2022, but principally off-shore areas in 2021, in accordance with the geolocation data. Overall, these results indicate higher resource diversity in 2022, possibly due to the inclusion of coastal/benthic items in the diet. Mean δ^{15}N signatures were also slightly higher in 2022, although not statistically significant. The δ15N values obtained in the present study are similar to the one reported by Juáres *et al.* (2016) for Stranger Point during the post-breeding stage (8.6 ± 0.5 ‰), when diet composition derived from SIA in feathers indicated 69% of krill, 16% pelagic fish and 14% of benthic fish. Thus, the incorporation of benthonic fish could explain the isotopic signatures seen in 2022. Compared to values reported by Cusset *et al.* (2023) in Adélie penguin feathers, the mean δ^{15}N values from our study are similar to those from Admiralty Bay between 2005 and 2011 (range = 8.70 – 9.03 ‰), and more recently, to those of Carlini and Esperanza´s colonies in 2019/2020 (8.95 and 8.72 ‰, respectively) and Signy Island in 2021/2022 (8.91 ‰). These results suggest that Adélie penguins from the AP had no major diet changes during the last 20 years, even when different colonies are considered.

Overall, our results identify areas used by Adélie penguins during the non-breeding season that are key for the viability of colonies in the WAP. A key element to ensure adult survival, the main determinant of population stability (Hinke *et al.*, 2014, 2017), is that individuals must be able to recover from the highly energetic demanding stages of breeding and molting, and gain reserves prior to the start of the next reproductive stage. These areas are also used by the krill fishery, possibly overlapping in space and time during the pre and post-breeding stages, as the majority of krill in the Bransfield and Gerlache Strait is currently caught in autumn (pre-breeding) and in summer (post-breeding) in the north of the South Shetland Islands (Warwick-Evans *et al.*, 2022).

CCAMLR consultative parties have committed to the conservation of Antarctic marine living resources (Article 2 of the Convention). This commitment takes into account the direct and indirect impacts of harvesting, associated activities, and environmental changes. Harvesting must hence be designed to avoid generating irreversible changes in the ecosystem, considering both the activity itself and other ongoing changes in the area (e.g., regional warming). This implies two types of conservation measures: 1) measures aimed at reducing the impact of fishing activity, including effects on components of the marine ecosystem beyond the harvested populations, and 2) measures aimed at increasing the system's resilience to ongoing changes. Small-scale management and MPAs are examples of conservation measures that address each of these two approaches.

Our results highlight the importance of employing both approaches simultaneously. Minimizing the impacts of changes occurring in the Antarctic Peninsula on species associated with or dependent on krill, such as penguins, requires actions that respond to the various pressures these species face throughout their annual cycle. These vary between locations and times. Regarding fishing, there is a clear need to reduce potential conflicts around reproductive colonies in summer (Hinke *et al.*, 2017), especially in Subareas 48.1 and 48.2, where krill fishing is currently concentrated. Hence, the relevance of small-scale management of fisheries. However, our results also emphasize the importance of reducing pressures at other times of the year in areas located far from breeding colonies (e.g., Subarea 48.5) and thus the need to adopt a seascape ecosystem management approach in order to manage widely distributed resources and interactions in a highly dynamic system (e.g., Murphy *et al*., 2021; Kavanaugh *et al.*, 2016). A reasonable approach to implement this could be to use finer scale management units in areas of higher risk, and larger scale managements in areas of reduced risk (Warwick-Evans *et al*., 2022). During post-breeding and pre-molt, when Adélie penguins need to build energy reserves, they were predominantly distributed within the proposed Weddell Sea MPA, highlighting the potential of a conservation measure aimed at minimizing interaction between krill fisheries and predators in that region during that specific time of the year (i.e., January-February). This is for example not currently ensured by krill harvesters' measures, as they are voluntary and not binding.

Another critical moment to consider is the pre-breeding stage, as body condition at arrival affects the decision to breed and determines the conditions with which adults undergo incubation and breeding, impacting breeding success (Vleck and Vleck 2002). Depletion of winter concentrations of krill by the fishery may lead to impacts on predators in the following spring (Warwick-Evans *et al*., 2022). In this way, ensuring that penguins initiate the reproductive season in the best possible body conditions requires measures aimed at reducing potential conflicts in September/October. During this stage part of the area used by Adélie penguins overlaps with the proposed Domain 1 MPA. During part of the reproductive period (in November and January, after the chick-rearing stage), some penguins use areas outside the CCAMLR area, with additional implications for marine resources management within the convention area. In these cases, protection is not currently ensured by krill harvesters' voluntary measures, either.

All of this reinforces the importance of advancing in the designation of MPAs as a complementary measure to small-scale management of fisheries. Currently, almost 12% of the CCAMLR area comprise MPAs and 4.6% falls under strict no-take protection, while another 10% is under negotiation (Brooks *et al.*, 2020a). In terms of the MPAs approach promoted by CCAMLR, achieving effective conservation also implies the need to consider innovative measures and other spatially and temporally explicitly protective measures. This includes limitations on activities in specific locations and times of the year (e.g., Thiebot *et al*., 2019), but not necessarily outside those periods. These results also highlight the relevance of accounting for connectivity when designing and managing MPAs, and hence the relevance of network-level considerations when designing and managing individual MPAs (Grorud-Colvert *et al*., 2014).

Adélie penguins’ dependence on resources from different subareas in different times of the year emphasizes the need of incorporating the temporal dimension of resources utilization when designing conservation measures in the Southern Ocean. With an increasing pressure on Adélie penguin colonies in the WAP coming from a range of sources, long-term protection of Adélie penguins in the area might depend both on 1) well designed and managed MPAs in the Domain 1 (Hogg *et al*., 2020) and the Weddell Sea (Teschke *et al*., 2021), and 2) small-scale management of fisheries (Watters and Hinke 2022) that simultaneously consider activities being undertaken in different small-scale management units. Without ecosystem management that considers both small and large scales, in a region undergoing significant environmental changes, there is a high risk that CCAMLR will fail to achieve agreed upon conservation objectives, as well as global targets set to protect marine biodiversity and ecosystem functions and services. In addition, long-term monitoring of the non-breeding stage could be important to assess consistency in foraging behavior over the years, especially considering potential shifts in prey distribution due to climate change.

ETHICS APPROVAL

All penguin handling procedures were reviewed and approved by the Honorary Commission of Animal Experimentation of Uruguay (CHEA protocol N° 1312).

DECLARATIONS OF INTEREST: None

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SUPPLEMENTARY MATERIAL

Methods - SIA

Analyses were normalized to the laboratory standards which were calibrated against IAEA N1, IAEA N2, and USGS 43 for δ^{15}N and NBS 21, NBS 22, and USGS 24 for δ^{13}C. The 3 internal laboratory standards are: UNM-CSI Protein std#1, casein purchased from Sigma Aldrich with d^{15}N and d^{13}C values of 6.43 and -26.52; UNM-CSI Protein std#2, soy protein purchased from Sigma Aldrich with d^{15}N and d^{13}C values of 0.98 and -25.78; UNM-CSI protein Std#4, house-made tuna protein with d^{15}N and d^{13}C values of 13.32 and -16.7.

Results – SIA

Table 1 Supp. Individual information and δ^{13}C and δ^{15}N signatures (‰) of adult Adélie penguin body feathers. ID corresponds to individual identification. Isotopic incorporation corresponds to the geometric center (centroid) of the locations from the 30 days previous to the molt (expressed in latitude and longitude decimal coordinates), this information is only available for individuals tracked with GLS

ID	Year	Sex	δ^{13}C	δ^{15}N	Centroid of isotopic incorporation
A1623_2021	2021	M	-24.3	9.2	-53.4414, -69.91577

A1625_2021	2021	M	-25.0	8.9	-53.77057, -66.48329
A1628_2021	2021	M	-25.4	9.0	-56.45354, -64.54308
A1631_2021	2021	M	-24.7	8.9	-53.97762, -66.19945
A1632_2021	2021	M	-25.1	9.2	-58.57656, -63.15674
A1633_2021	2021	M	-24.7	9.3	-55.22709, -64.62103
A1634_2021	2021	F	-24.9	9.4	-
A1637_2021	2021	M	-25.0	8.9	-59.0092, -62.9463
A1638_2021	2021	F	-24.3	9.2	-57.03649, -64.7358
A1639_2021	2021	F	-25.1	8.9	-45.3662, -69.73344
A1641_2021	2021	F	-24.6	9.5	-42.81799, -69.76863
A1623_2022	2022	M	-24.2	9.3	-57.77182, -62.93887
A1625_2022	2022	-	-	-	-55.77482, -64.11029
A1631_2022	2022	M	-23.8	9.1	-58.03188, -62.56977
A1632_2022	2022	M	-22.6	11.2	-58.38086, -63.22418
A1638_2022	2022	-	-	-	-56.91543, -64.30979
A1813_2022	2022	M	-25.1	9.0	-57.43817, -63.28128
A1824_2022	2022	F	-24.6	8.8	-56.94916, -63.36695
A1832_2022	2022	M	-24.9	9.2	-57.10452, -63.78352
A1833_2022	2022	F	-25.1	8.9	-55.24159, -64.27912
A1623_2023	2022	M	-24.8	9.2	-
A1625_2023	2022	M	-24.7	8.8	-
A1631_2023	2022	M	-24.9	9.6	-
A1632_2023	2022	M	-24.2	8.6	-
A1638_2023	2022	M	-23.0	10.4	-
A1813_2023	2022	M	-24.2	9.4	-
A1824_2023	2022	F	-23.4	9.9	-
A1832_2023	2022	M	-24.5	8.9	-
A1833_2023	2022	M	-23.8	8.9	-