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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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► To cite this version:

N. Zaldúa, Z. Zajková, A.L. Machado-Gaye, V. Franco-Trecu, M. Cosse, et al.. Changing the focus: The need for cross-scale dynamic management in the Southern Ocean and implications for holistic conservation of Antarctic marine living resources. *Marine Policy*, 2024, 170, pp.106361. 10.1016/j.marpol.2024.106361 . hal-04701356

HAL Id: hal-04701356

<https://hal.science/hal-04701356v1>

Submitted on 18 Sep 2024

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

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19 DECLARATIONS OF INTEREST: None

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21 ACKNOWLEDGMENTS

22 This work was supported by 1) Ecos Sud Program (project PU20B01/U20B03), 2) Commission
23 for the Conservation of Antarctic Marine Living Resources (CCAMLR) General Capacity Building
24 Fund and Scientific Scholarship Scheme, 3) Agencia Nacional de Investigación e Innovación's
25 (ANII) Clemente Estable Fund (project FCE_1_2021_1_166587), National System of
26 Researchers and National Postgraduate Scholarship Programme POS_FCE_2021_1_1010792
27 and POS_NAC_2021_1_169785, and 4) Basic Science Development Programme (PEDECIBA).
28 Logistic support was provided by the Uruguayan Antarctic Institute (IAU). ZZ was funded by the
29 Ministry of Science, Innovation and Universities (PID2021-124831OA-I00). The funding sources
30 had no involvement in the study design; the collection, analysis and interpretation of data; the
31 writing of the report or in the decision to submit the article for publication.

32 The authors would like to thank Noelia Gobel, Javier Menéndez-Blázquez, Philip Miller, Joaquín
33 Muñoz, Maryam Raslan, Mauro Rozas Sia, Alex Valdes, Pablo Vaz-Canosa, Ariel Farías and
34 Coline Marciau for assistance with fieldwork, Ana Laura Rodales for assistance during lab work,
35 as well as Simeon Lisovski, Melina Barrionuevo and Samantha Dodino for software technical
36 recommendations.

37 This article is part of Natalia Zaldúa's doctoral thesis. This work is a contribution to the Integrated
38 Science to Inform Antarctic and Southern Ocean Conservation Scientific Research Programme
39 (Ant-ICON) of SCAR.

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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 km², plummeting 2.6 million km² below the 1981–2010 average for that time of year and falling 1.2 million km² 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

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(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 km², 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),

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4 68 including, for example, the consideration of an interim limit (“krill trigger level”), of 620,000 tons in
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6 69 Area 48, as well as subdividing it amongst Statistical Subareas (Constable *et al.*, 2023). Currently,
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8 70 several CCAMLR members wish to increase the allowable catch of krill (Watters and Hinke 2022)
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10 71 and small-scale management of the krill fishery (i.e., the use of smaller or finer scale management
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12 72 units/spatial sub-sections over which catch/effort is distributed) is under discussion. As catches
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14 73 have become more concentrated and closer to predator breeding colonies, CCAMLR has
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16 74 recognized the need for a framework that ensures precautionary protection at scales used by krill
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18 75 predators and now by the fishery (Trathan *et al.*, 2022; Watters and Hinke 2022; Warwick-Evans
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20 76 *et al.*, 2022). This is because catch limits set for large geographic areas facilitate concentration of
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22 77 catch, which can increase the risks of ecological impacts at smaller scales, through depletion of
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24 78 local krill populations (Klein and Watters 2020). By spreading the fishing effort across small scale
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26 79 management units the fishery would be forced to spread effort, thereby diminishing local impact
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28 80 on krill and predators foraging within the small management areas. If CCAMLR succeeds in
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30 81 implementing a small-scale approach to management, it would allow setting specific spatio-
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32 82 temporal catch limits according to fine scale ecosystem processes, such as consumption by
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34 83 predators, or important areas for krill (Warwick-Evans *et al.*, 2022). The revision of krill
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36 84 management is particularly relevant for CCAMLR subarea 48.1, where seasonal sea ice has been
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38 85 retreating due to regional warming, leaving more space for fishing to grow (Watters *et al.*, 2020;
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40 86 Trathan *et al.*, 2022). In 2019, CCAMLR’s Working Group on Ecosystem Monitoring and
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42 87 Management (WG-EMM) agreed on a work program to implement a revised management
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44 88 strategy for the krill fishery, which incorporates risk assessment, recognizing the need to consider
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46 89 information on the structure and function of the wider krill-based ecosystem, including krill-
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48 90 dependent predator species (Warwick-Evans *et al.*, 2022). Within the private sector, in 2018 some
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50 91 krill harvesting companies, members of the Association of Responsible Krill Harvesting (ARK),
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52 92 agreed on a set of voluntary measures to aid in the protection of the Antarctic ecosystems, which
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54 93 include voluntary restricted zones, trans-shipment and vessel safety ([https://www.ark-krill.org/ark-
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56 94 voluntary-measures](https://www.ark-krill.org/ark-voluntary-measures)). Yet, these are voluntary agreements between private stakeholders, not
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58 95 legally-binding regulations agreed by Parties to ensure the fulfillment of the objectives of an
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60 96 international convention for the joint management of common resources.

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97 Ice-obligate Adélie penguins (*Pygoscelis adeliae*) are a key indicator species in Antarctic
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99 ecosystems (Cusset *et al.*, 2023). Although Adélie penguins are the most abundant penguin
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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

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101 the 1970s (Trivelpiece *et al.*, 2011; Lynch *et al.*, 2012) and an example of this is the Copacabana
102 Field Station colony (at Admiralty Bay, King George Island), that has reduced by 79% in 25 years
103 (Hinke *et al.*, 2017). Population declines are predicted at ~30% of Adélie colonies by 2060 and
104 ~60% by 2099 in the WAP (Cimino *et al.*, 2016). Population declines are attributed to reduced krill
105 biomass and availability due to regional sea-ice declines, fishing, and the proliferation of natural
106 competitors such as seals and whales (Trivelpiece *et al.*, 2011; Lynch *et al.*, 2012; Watters *et al.*,
107 2020; Warwick-Evans *et al.*, 2022). Shifts in the duration and spatial extent of ice coverage are
108 expected to be important drivers of population change for ice-obligate species, as a positive
109 correlation between ice extent and survival rates has been observed in Adélie populations from
110 the Antarctic Peninsula (Hinke *et al.*, 2014; Hinke *et al.*, 2017).

111 However, most studies on this species were conducted during the summer, when adult Adélie
112 penguins are accessible in their colonies (Machado-Gaye *et al.*, 2024). During this period, birds
113 perform sex-specific foraging strategies, when females tend to forage farther, longer, and dive
114 shallower, while males exploit waters closer to the colony and dive deeper (Chappell *et al.*, 1993;
115 Clarke *et al.*, 1998; Lescroël *et al.*, 2010; Widmann *et al.*, 2015; Riaz *et al.*, 2020). These
116 differences in foraging behavior were linked to differences in diet, with females from Hope Bay
117 (Antarctic Peninsula) consuming greater amounts of krill in more offshore/pelagic waters, while
118 males feed equally on krill and fish in more inshore, benthic waters (Clarke *et al.*, 1998;
119 Colominas-Ciuró *et al.*, 2018). In the vicinity of the Antarctic Peninsula, South Shetland Islands,
120 and South Orkney Islands, Adélie penguins consume fishes *Pleuragramma antarcticum* and
121 *Lepidonotothen squamifrons* during the summer (Polito *et al.*, 2011). According to Juárez *et al.*
122 (2017), summer diet at Stranger Point (King George Island, close to our study site) has been krill-
123 dominated for the last 27 years, with minor fish consumption of *P. antarcticum* and *Electrona*
124 *antarctica*.

125 Several knowledge gaps still persist regarding the Adélie penguin WAP populations, particularly
126 concerning their non-breeding distribution, movements and feeding habits (Erdmann *et al.*, 2011).
127 Tracked adult and juvenile Adélie penguins from other colonies in the South Shetland Islands
128 travel to the NW Weddell Sea after breeding, molt on the ice, and also used the southern Scotia
129 Sea before returning to the breeding colonies by late September (Hinke *et al.*, 2015, 2020; Polito
130 *et al.*, 2017). Erdmann *et al.* (2011) explored the partitioning of foraging resources between sexes
131 during the non-breeding period, registering an increase in foraging area overlap in females during
132 a year with heavy ice cover. Adélie penguins from Signy Island (South Orkney Islands), a colony
133 close to WAP, also headed to the Weddell Sea to molt after breeding, foraging near and molting

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134 on sea-ice (Dunn *et al.*, 2011; Warwick-Evans *et al.*, 2019). The study of $\delta^{13}\text{C}$ stable isotopes
135 also revealed that Adélie penguins disperse widely and forage in more pelagic/offshore habitats
136 during the post-breeding season in comparison with the breeding season (Herman *et al.*, 2017),
137 and that currently they forage further south and/or closer to the sea ice edge than in the 1980s,
138 possibly due to climate change (Negrete *et al.*, 2016). For the pre-breeding season, Gorman *et*
139 *al.* (2014) reported no sex-related differences in the trophic niche, while Polito *et al.* (2011) found
140 that high trophic-level prey such as fish and/or squid comprised a significant portion (46.8 - 62.9%)
141 of female Adélie penguin diets. In turn, Juárez *et al.* (2016) reported that krill dominated the diet
142 of Adélie penguins in Stranger Point over their annual cycle, but found a mean contribution of 16
143 and 14% of pelagic and benthonic fish during the post-breeding stage, which rose to 23% and
144 10% during the pre-breeding stage. Given the significant changes observed in the Antarctic
145 Peninsula region in the last two decades, these studies are of high value for comparative
146 purposes, as most of them represent a base-line elaborated with data collected between 10 and
147 20 years ago. In order to facilitate evidence-based policymaking, more information is needed on
148 the non-breeding ecology of Adélie penguins, including sex-disaggregated data as several studies
149 have found differences between males and females across many penguin species.

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

160 Key stages during the Adélie penguins non-breeding season include: 1) immediately after their
161 chicks fledge, as penguins have to recover body condition from the breeding stage; 2) before and
162 after molting, as they have to generate and regain reserves to prepare and recover from a highly
163 energy-intensive molt (when molting, Adélie penguins lose and regrow their entire plumage at
164 one time, spending a mean of 16-19 days fasting on the ice; Hinke *et al.*, 2015; Schmidt *et al.*,
165 2023; this study); 3) before starting the breeding season, as they have to accumulate reserves to
166 endure the energetic demands of incubation and chick-rearing. Identifying the areas used by

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167 these animals during those critical stages of the non-breeding season, and understanding what
168 resources they exploit during the wintering season is key to ensure that human-induced impacts
169 are diminished to a minimum during these time-periods. This information is in turn valuable to
170 assess whether current MPAs proposals provide a valuable contribution to diminishing those
171 impacts.

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

180 2. METHODS

181 2.1 *Study site*

182 We studied Adélie penguins breeding at Ardley Island (62°13'00.1" S, 58°55'59.9" W), located in
183 Maxwell Bay, King George Island (South Shetland Islands). Ardley Island is a small ice-free island
184 (~2 km long by 1 km wide), connected to the Fildes Peninsula by an isthmus which is submerged
185 during high tides. The island has been designated as an Antarctic Specially Protected Area (ASPA
186 150), a CCAMLR Ecosystem Monitoring Program (CEMP) site, and Important Bird Area (IBA
187 AQ048). The colony currently hosts approximately 209 breeding pairs of Adélie penguins (census
188 November 2023, this study) and has experienced a sharp decline in the number of breeding pairs
189 since the 1980s (Braun *et al.*, 2017).

190 2.2 *Deployment of devices and data collection*

191 Adult Adélie penguins were captured during the 2020/2021 and 2021/2022 breeding seasons
192 (November-December) and fitted with MK3005-series archival geolocators (hereafter GLS; Lotek
193 UK Ltd, Dorset, United Kingdom) to study dispersal and space utilization. We took care to
194 minimize stress by covering the penguin's head during handling and ensuring that handling time
195 was always below 5 minutes. The GLS were fitted with cable-lined plastic seals to the penguin's
196 tarsus following Ratcliffe *et al.* (2014). Each GLS weighed 2.5 g, representing approx. 0.06% of
197 body mass of adult Adélie penguins (mean for Ardley Island 3847 ± 392.3 g, Machado-Gaye *et*
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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

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234 locations and turning angle. We used a threshold of 2.0 m/s based on the maximum of Adélie
235 penguin horizontal speeds reported in Machado-Gaye *et al.* (2024). Finally, 19 unrealistic
236 locations were filtered through visual inspection (interactive map), as the previous or subsequent
237 location was located across the Antarctic Peninsula. After applying the aforementioned filters,
238 5324 positions (86.3%) were retained. All analyses were performed using locations from 1
239 January to 15 November of each year.

241 2.3 Environmental covariates

242 We used daily sea-ice concentration values, reported on a 6.25 km grid, available from the
243 University of Bremen (Spren *et al.*, 2008; [https://seaice.uni-
244 bremen.de/data/amr2/asi_daygrid_swath/s6250/netcdf/](https://seaice.uni-bremen.de/data/amr2/asi_daygrid_swath/s6250/netcdf/)) to calculate mean monthly sea-ice
245 concentration and to estimate the contour of 15% sea-ice concentration (effective ice edge). We
246 also extracted the mean sea-ice concentration within a buffer of 100 km around each location for
247 all the individuals to infer sea-ice concentration preferences of Adélie penguins throughout the
248 year.

31 2.4 Molt period identification

32 We used GLS wet/dry data to identify long continuous dry periods as molt, as animals do not
33 enter water during this phase (e.g., Schmidt *et al.*, 2023). The period of 30 days previous to the
34 onset of molt, corresponding to pre-molt foraging trips, was considered the time-window of the
35 feather's stable isotope incorporation (see below, Whitehead *et al.*, 2016). We estimated the
36 individual centroids of these 30-days pre-moult locations using the `st_centroid` function in `sf` R
37 package (Pebesma 2018).
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44 2.5 Laboratory analysis

48 2.5.1 Stable Isotopes Analysis (SIA)

49 Feathers are a metabolically inert tissue after growth, thus they potentially reflect food
50 consumption of penguins during their pre-moult foraging trips (Tierney *et al* 2008; Hinke *et al.*,
51 2015). We estimated carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope ratios of body feathers to assess
52 for intraspecific foraging niche partitioning between year and sex (yet, because of the small
53 sample size we did not perform statistical analysis by sex). $\delta^{15}\text{N}$ primarily increases as the trophic
54 level of individuals rises (Post 2002), while $\delta^{13}\text{C}$ provides information about the origin of primary
55 productivity, enabling the inference of foraging habitat (France 1995). In the marine environment,
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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 $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. 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.

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

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

313 The PCR reaction was carried out following Rabinovich *et al.* (2024), the PCR consisted of a final
314 volume of 20uL with 1x of Platinum Multiplex Master Mix (Invitrogen Life Technologies, Carlsbad,
315 California), 0.5 uL of each primer and 50 ng of genomic DNA template. We incorporated a
316 fluorescent dye (FAM) on the P2 primer to analyze the fragments size by capillary electrophoresis.
317 PCR profile consisted of an initial denaturing step at 94°C for 10 min, followed by 35 cycles of
318 94°C for 30 sec, 47°C for 1 min, and 72°C for 1 min, and a final extension of 72°C for 10 min.
319 Positive and negative controls were included in each PCR. Positive controls consisted of samples
320 of *Gubernatrix cristata* of known sex. PCR amplification was confirmed by electrophoresis on 1%
321 agarose gel and products were sent to the Unidad de secuenciación Sanger at Hospital de
322 Clínicas, Uruguay, for fragment analysis. Genotype assignment was carried out with GeneMarker
323 2.4.0 (Softgenetics LLC, State College, Pennsylvania). Males were homozygotes (370/370 pb)
324 and females, heterozygotes (370/388 pb).

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

2.6 Analysis of isotopic data

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

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

341 3. RESULTS

342 3.1 *Non-breeding distribution range*

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

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

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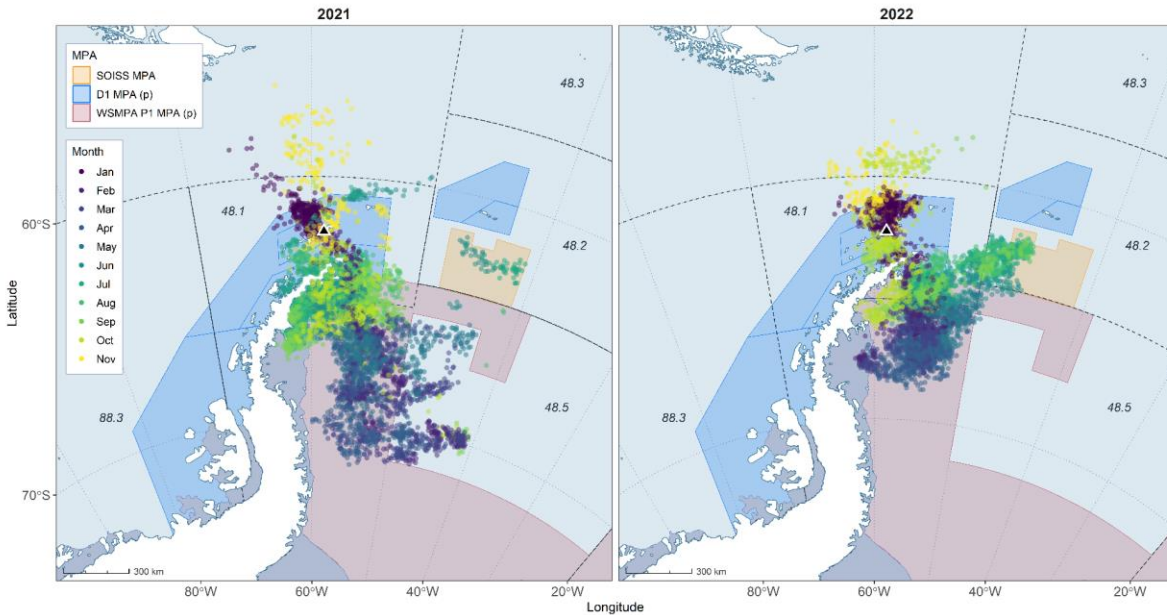
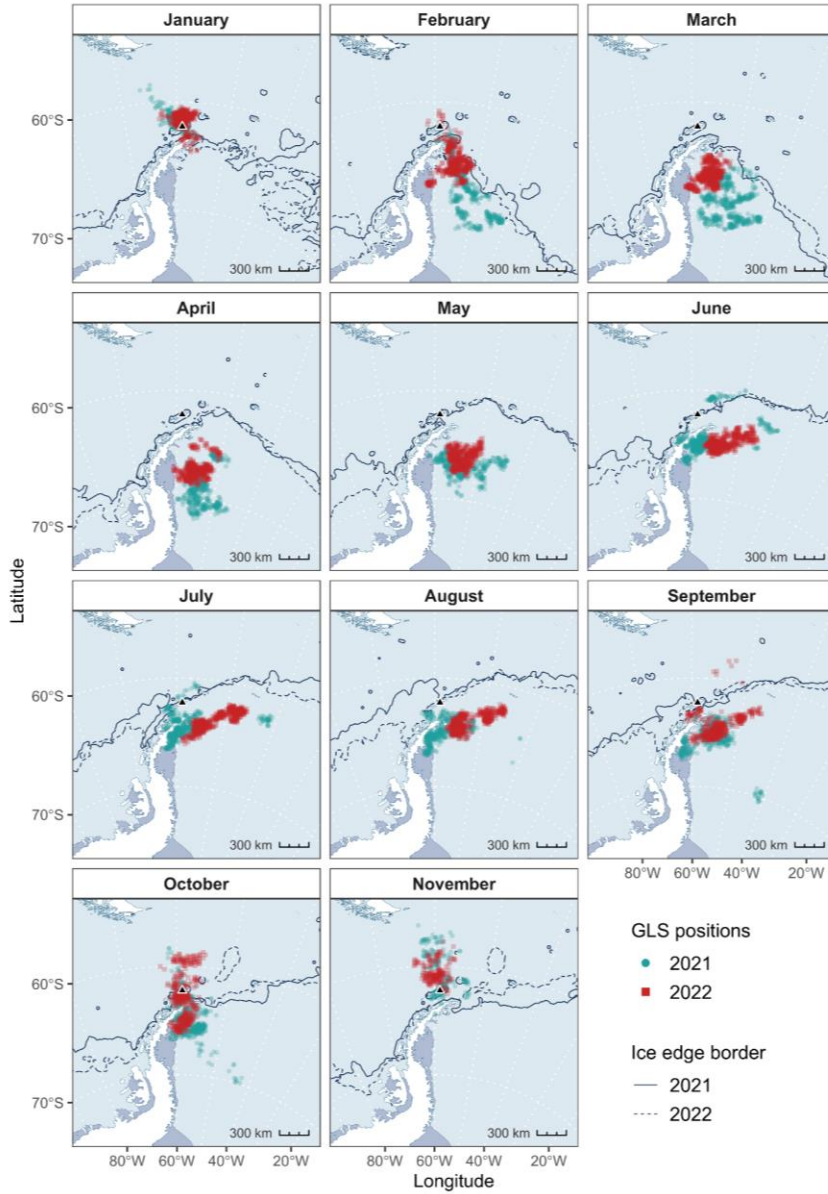


Figure. 1. Year-round distribution of 20 Adélie penguins from Ardley Island in Antarctic Peninsula during the 2021 (left, n = 11) and 2022 (right, n = 9). Color shaded areas represent MPA/MPA proposals: Light orange corresponds to the South Orkney Islands Southern Shelf Marine Protected Area (SOISS MPA); 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.

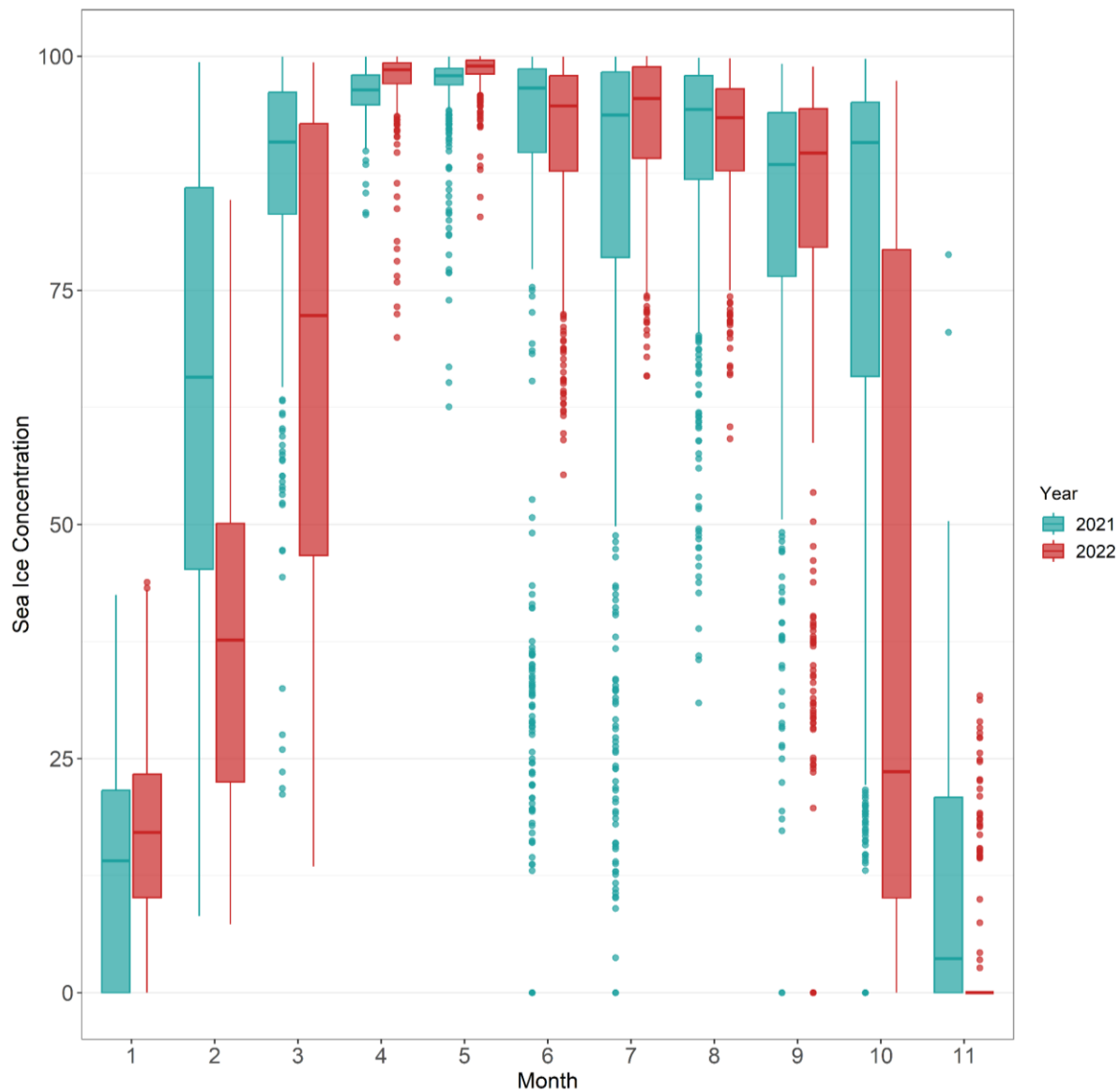
Only 2 penguins were registered near the colony (<100 km) during winter (July-August 2021). The first penguins returning to Ardley Island were recorded in October, even though other individuals were still in the Weddell Sea, while others were navigating the waters of the Drake

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4 385 Passage, halfway between the South Shetland Islands and Tierra del Fuego. In November, the
5 majority of individuals remained within the area spanning the Bransfield Strait and the Drake
6 386 Strait, out of the pack ice.
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53 390 Figure 2. Locations of 20 Adélie penguins by month (January-November) in relation to ice edge.
54 391 Solid and dashed black lines represent 15% sea-ice concentration (effective ice edge) in 2021
55 392 and 2022, respectively. Colony is represented by a black triangle.
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4 394 Regarding the connection with sea ice throughout the year (as Adélie penguins are considered
5 an ice-obligate species), we observed that the highest sea ice concentrations (SIC) were recorded
6 395 in April and May for both years (Fig. 3). This corresponds to the post-molt period when most
7 locations were situated on >90% SIC. The rest of the year shows great inter-individual variability,
8 396 with similar patterns between years. A striking variability can be observed between years in
9 397 February, March and October, reflecting different individual choices during molt and prior to the
10 breeding season. This is also evident when latitude and longitude positions are compared
11 398 between years (Fig. 4)
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404 Figure 3. Mean sea-ice concentration (%) within 100 kms buffer around Adélie penguins GLS
405 locations, per month/year.

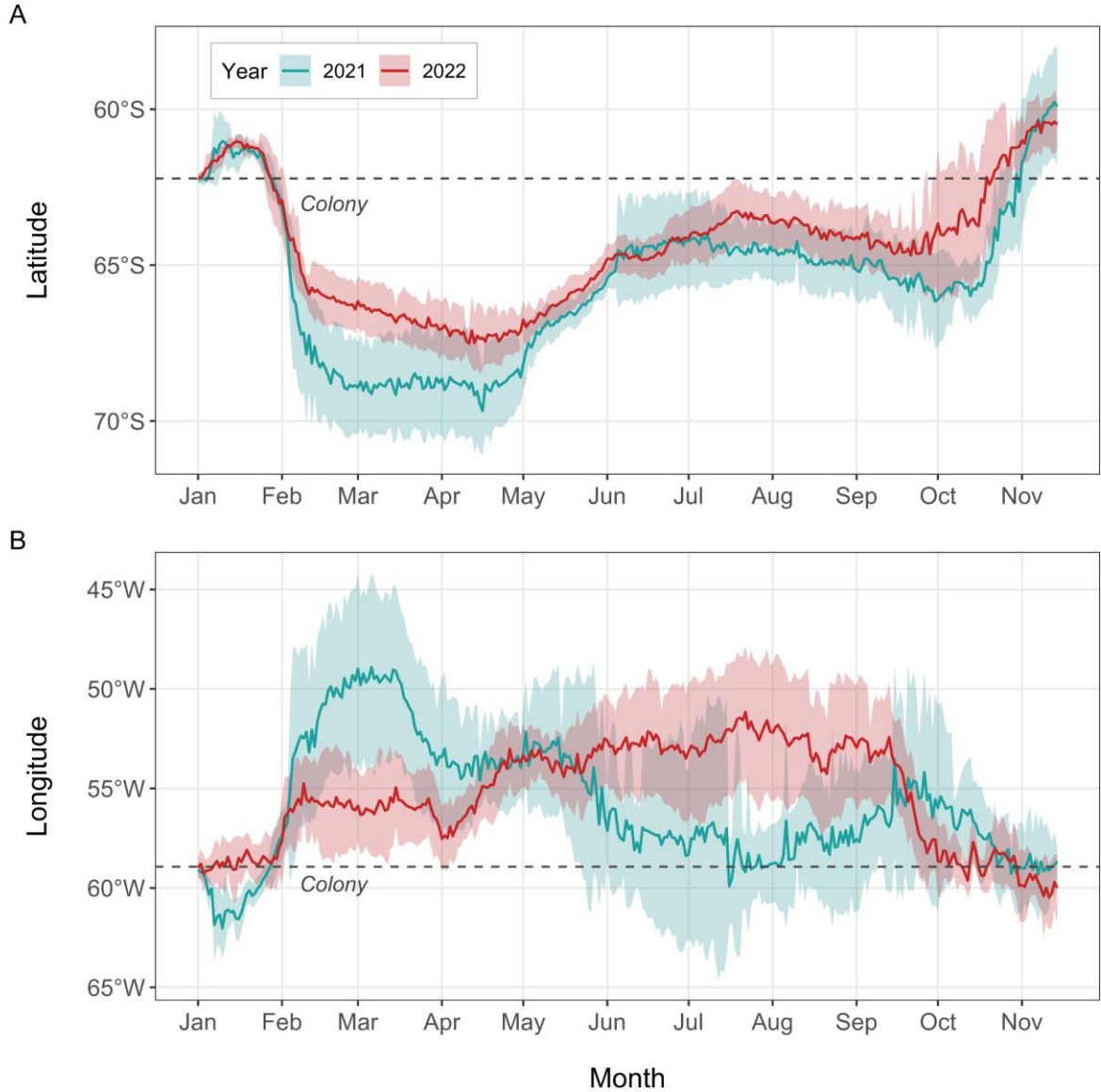


Figure 4. Changes in the (A) latitudinal and (B) longitudinal positions of Adélie penguins during two years of tracking (2021, $n = 11$, and 2022, $n = 9$). Lines indicate the mean and the shaded area the standard deviation of individual daily positions. Dash lines represent latitude and longitude of 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 $\delta^{13}\text{C}$ value for both sexes pooled together was $-24.82 \pm 0.34\text{‰}$ in 2021, while in 2022 it was $-24.23 \pm 0.74\text{‰}$. In the case of $\delta^{15}\text{N}$, the means were $9.12 \pm 0.21\text{‰}$ and $9.32 \pm 0.67\text{‰}$, 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 $\delta^{13}\text{C}$ (p -value = 0.02), without differences in $\delta^{15}\text{N}$ (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 $\delta^{13}\text{C}$ signatures indicate more influence of coastal environments and there was greater diversity of trophic levels ($\delta^{15}\text{N}$) utilized compared to 2021. The overlap ellipse area was 0.14‰^2 , representing 60% for 2021 and 13% for 2022.

Table 1. $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ signatures (means \pm SD and range, in ‰) disaggregated by year and sex and Bayesian standard ellipse area- SEA_B (median 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
$\delta^{13}\text{C}$	-24.72 ± 0.35	-24.88 ± 0.35	-24.36 ± 0.87	-24.20 ± 0.75
Range $\delta^{13}\text{C}$	-25.1 to -24.3	-25.4 to -24.3	-25.1 to -23.4	-25.1 to -22.6
$\delta^{15}\text{N}$	9.25 ± 0.26	9.05 ± 0.17	9.20 ± 0.61	9.35 ± 0.71
Range $\delta^{15}\text{N}$	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

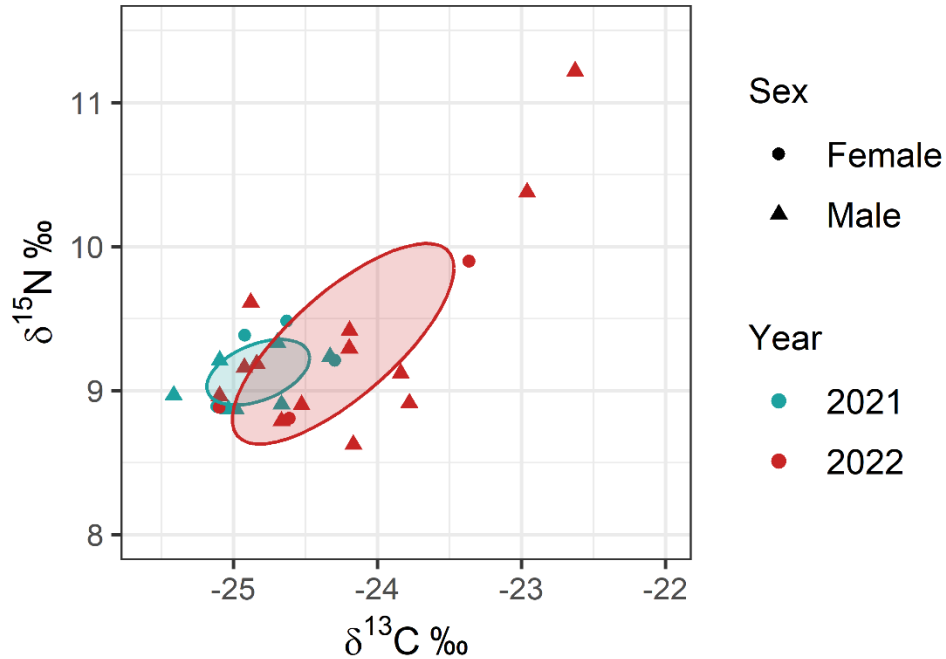


Fig.5. Bayesian ellipses representing Adélie penguin isotopic niches (Group Ellipses p.interval = 0.40).

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

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459 penguins during the non-breeding stage, but particularly during critical periods such as post-
460 breeding/pre-molting, post-molting and pre-breeding. The SOISS MPA was also extensively
461 used, particularly in 2022.

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463 Consistent with prior findings (Ballard *et al.*, 2010; Dunn *et al.*, 2011; Hinke *et al.*, 2015; Schmidt
464 *et al.*, 2023), our results underscore the significant reliance of Adélie penguins on ice conditions.
465 Adélie penguins molted in February and March within the Weddell Sea (as reported by Dunn *et*
466 *al.*, 2011), in locations where the concentration of sea ice was 40-90%. Warwick-Evans *et al.*
467 (2019) reported SIC of molting locations > 80%, also for the Weddell Sea. The Weddell sea ice
468 region is an important molting habitat for other Adélie colonies as well, such as those in Admiralty
469 Bay, King George Island (Hinke *et al.*, 2015; Oosthuizen *et al.* 2022), in Signy Island (Dunn *et al.*,
470 2011; Warwick- Evans *et al.*, 2019); and also for Emperor penguins (*Aptenodytes forsteri*)
471 (Kooyman *et al.*, 2000). We report the shortest Adélie penguin molt duration (mean 16.1 ± 2.7 d,
472 range = 9 to 18 d in 2021), comparing to those reported by Schmidt *et al.* (2023) (i.e. mean 19.3
473 d, range = 13 to 26, as well as previous findings between 17 and 20 d). After molting, Adélie
474 penguins stayed in locations with >90% SIC through April and May, similar to those reported by
475 Dunn *et al.* (2011) (i.e. 90.3 - 93.7%). All individuals remained continuously at sea, south of the
476 ice-edge, from March to September/October, a period of approximately 7 months after the end of
477 the molt, as also reported by Dunn *et al.* (2011).

478
479 Stable Isotopes Analysis (SIA) showed significant statistical differences between years in $\delta^{13}\text{C}$
480 signatures, with higher values in 2022. In addition, both the $\delta^{13}\text{C}$ range and the Bayesian ellipse
481 area in 2022 were higher. This suggests that during that year, penguins utilized resources with a
482 greater diversity of origins. The spatial accuracy of the determination of foraging areas of
483 consumers using their $\delta^{13}\text{C}$ values ranges from tens to hundreds of km in latitude, and at the
484 spatial scale of a subantarctic archipelago, the $\delta^{13}\text{C}$ values indicate the distance of their foraging
485 areas from the coast (Cherel and Hobson 2007). Thus, our SIA results show the use of both
486 coastal and offshore foraging areas in 2022, but principally off-shore areas in 2021, in accordance
487 with the geolocation data. Overall, these results indicate higher resource diversity in 2022,
488 possibly due to the inclusion of coastal/benthic items in the diet. Mean $\delta^{15}\text{N}$ signatures were also
489 slightly higher in 2022, although not statistically significant. The $\delta^{15}\text{N}$ values obtained in the
490 present study are similar to the one reported by Juárez *et al.* (2016) for Stranger Point during the
491 post-breeding stage (8.6 ± 0.5 ‰), when diet composition derived from SIA in feathers indicated
492 69% of krill, 16% pelagic fish and 14% of benthic fish. Thus, the incorporation of benthonic fish

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493 could explain the isotopic signatures seen in 2022. Compared to values reported by Cusset *et al.*
494 (2023) in Adélie penguin feathers, the mean $\delta^{15}\text{N}$ values from our study are similar to those from
495 Admiralty Bay between 2005 and 2011 (range = 8.70 – 9.03 ‰), and more recently, to those of
496 Carlini and Esperanza’s colonies in 2019/2020 (8.95 and 8.72 ‰, respectively) and Signy Island
497 in 2021/2022 (8.91 ‰). These results suggest that Adélie penguins from the AP had no major diet
498 changes during the last 20 years, even when different colonies are considered.

499
500 Overall, our results identify areas used by Adélie penguins during the non-breeding season that
501 are key for the viability of colonies in the WAP. A key element to ensure adult survival, the main
502 determinant of population stability (Hinke *et al.*, 2014, 2017), is that individuals must be able to
503 recover from the highly energetic demanding stages of breeding and molting, and gain reserves
504 prior to the start of the next reproductive stage. These areas are also used by the krill fishery,
505 possibly overlapping in space and time during the pre and post-breeding stages, as the majority
506 of krill in the Bransfield and Gerlache Strait is currently caught in autumn (pre-breeding) and in
507 summer (post-breeding) in the north of the South Shetland Islands (Warwick-Evans *et al.*, 2022).

508
509 CCAMLR consultative parties have committed to the conservation of Antarctic marine living
510 resources (Article 2 of the Convention). This commitment takes into account the direct and indirect
511 impacts of harvesting, associated activities, and environmental changes. Harvesting must hence
512 be designed to avoid generating irreversible changes in the ecosystem, considering both the
513 activity itself and other ongoing changes in the area (e.g., regional warming). This implies two
514 types of conservation measures: 1) measures aimed at reducing the impact of fishing activity,
515 including effects on components of the marine ecosystem beyond the harvested populations, and
516 2) measures aimed at increasing the system's resilience to ongoing changes. Small-scale
517 management and MPAs are examples of conservation measures that address each of these two
518 approaches.

519 Our results highlight the importance of employing both approaches simultaneously. Minimizing
520 the impacts of changes occurring in the Antarctic Peninsula on species associated with or
521 dependent on krill, such as penguins, requires actions that respond to the various pressures these
522 species face throughout their annual cycle. These vary between locations and times. Regarding
523 fishing, there is a clear need to reduce potential conflicts around reproductive colonies in summer
524 (Hinke *et al.*, 2017), especially in Subareas 48.1 and 48.2, where krill fishing is currently
525 concentrated. Hence, the relevance of small-scale management of fisheries. However, our results

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526 also emphasize the importance of reducing pressures at other times of the year in areas located
527 far from breeding colonies (e.g., Subarea 48.5) and thus the need to adopt a seascape ecosystem
528 management approach in order to manage widely distributed resources and interactions in a
529 highly dynamic system (e.g., Murphy *et al.*, 2021; Kavanaugh *et al.*, 2016). A reasonable
530 approach to implement this could be to use finer scale management units in areas of higher risk,
531 and larger scale managements in areas of reduced risk (Warwick-Evans *et al.*, 2022). During
532 post-breeding and pre-molt, when Adélie penguins need to build energy reserves, they were
533 predominantly distributed within the proposed Weddell Sea MPA, highlighting the potential of a
534 conservation measure aimed at minimizing interaction between krill fisheries and predators in that
535 region during that specific time of the year (i.e., January-February). This is for example not
536 currently ensured by krill harvesters' measures, as they are voluntary and not binding.

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

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

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558 Adélie penguins' dependence on resources from different subareas in different times of the year
559 emphasizes the need of incorporating the temporal dimension of resources utilization when
560 designing conservation measures in the Southern Ocean. With an increasing pressure on Adélie
561 penguin colonies in the WAP coming from a range of sources, long-term protection of Adélie
562 penguins in the area might depend both on 1) well designed and managed MPAs in the Domain
563 1 (Hogg *et al.*, 2020) and the Weddell Sea (Teschke *et al.*, 2021), and 2) small-scale management
564 of fisheries (Watters and Hinke 2022) that simultaneously consider activities being undertaken in
565 different small-scale management units. Without ecosystem management that considers both
566 small and large scales, in a region undergoing significant environmental changes, there is a high
567 risk that CCAMLR will fail to achieve agreed upon conservation objectives, as well as global
568 targets set to protect marine biodiversity and ecosystem functions and services. In addition, long-
569 term monitoring of the non-breeding stage could be important to assess consistency in foraging
570 behavior over the years, especially considering potential shifts in prey distribution due to climate
571 change.

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573 ETHICS APPROVAL

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

576

577 DECLARATIONS OF INTEREST: None

578

579 ACKNOWLEDGMENTS

580 This work was supported by 1) Ecos Sud Program (project PU20B01/U20B03), 2) Commission
581 for the Conservation of Antarctic Marine Living Resources (CCAMLR) General Capacity Building
582 Fund and Scientific Scholarship Scheme, 3) Agencia Nacional de Investigación e Innovación's
583 (ANII) Clemente Estable Fund (project FCE_1_2021_1_166587), National System of
584 Researchers and National Postgraduate Scholarship Programme POS_FCE_2021_1_1010792
585 and POS_NAC_2021_1_169785, and 4) Basic Science Development Programme (PEDECIBA).
586 Logistic support was provided by the Uruguayan Antarctic Institute (IAU). ZZ was funded by the
587 Ministry of Science, Innovation and Universities (PID2021-124831OA-I00) and with the

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588 institutional support of the grant ‘Severo Ochoa Centre of Excellence’ accreditation (CEX2019-
589 000928-S) funded by AEI 10.13039/501100011033. The funding sources had no involvement in
590 the study design; the collection, analysis and interpretation of data; the writing of the report or in
591 the decision to submit the article for publication.

592 The authors would like to thank Noelia Gobel, Javier Menéndez-Blázquez, Philip Miller, Joaquín
593 Muñoz, Maryam Raslán, Mauro Rozas Sía, Alex Valdes, Pablo Vaz-Canosa, Ariel Farías and
594 Coline Marciau for assistance with fieldwork, Ana Laura Rodales for assistance during lab work,
595 as well as Simeon Lisovski, Melina Barrionuevo and Samantha Dodino for software technical
596 recommendations.

597 This article is part of NZ's doctoral thesis. This work is a contribution to the Integrated Science to
598 Inform Antarctic and Southern Ocean Conservation Scientific Research Programme (Ant-ICON)
599 of SCAR.

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836 SUPPLEMENTARY MATERIAL

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838 *Methods - SIA*

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

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846 *Results – SIA*

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

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

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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	-

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