



OPEN

# Availability to predators and a size structure of the Antarctic krill *Euphausia superba* in the 48.1 CCAMLR subarea

Anna Panasiuk<sup>1✉</sup>, Gabriela Gic-Grusza<sup>2</sup> & Małgorzata Korczak-Abshire<sup>3</sup>

The Antarctic krill *Euphausia superba* is a key species in Antarctic waters, mainly because it is a major component of the diet of dominant predators, including penguins. It is also a marine living resource that is commercially harvested. Since 2000, krill fishing has become more concentrated. On the basis of several years of data, it has been reported that up to 57% of the krill fishery harvests occur in the Bransfield Strait area. The distribution of krill in the Southern Ocean is not well described. Studies that compare the size of krill caught by commercial vessels with that recorded in the diet of predators are even rarer. The main objectives of this study were to assess the spatial diversity in the size and putative age of krill in the CCAMLR subarea 48.1, to investigate the spatial availability of krill and its size and age structure, and to assess whether the diet of *Pygoscelis* penguins reflects the size structure of krill present in the environment. The results implied that the size and age structure of the krill population were similar throughout the Bransfield Strait during the study period, although those in the eastern and southern parts of the strait and the Brabant Island region were the most similar. The Livingston Island and Drake Passage areas were clearly distinguishable from the above regions, where larger and therefore older krill were recorded. All *Pygoscelis* penguin species showed size preferences for consumed krill; therefore, their diet is likely not a reliable indicator of the size of krill in the environment. Krill that had not yet reached sexual maturity, and thus not yet started reproducing were commercially caught in the Bransfield Strait during the investigated years.

**Keywords** Antarctic krill, *Pygoscelis* penguins, Western Antarctic, Predator diet, Commercial fishery, Krill fishery management

On the basis of data from research expeditions in the years 1926–2004, the krill *Euphausia superba* biomass in Antarctic waters has been estimated at 379 million tonnes, of which approximately 30% are located in the Atlantic sector of the Southern Ocean<sup>1,2</sup>. The Antarctic krill fishery has been in operation for approximately 50 years, with the largest catches occurring in the 1980s<sup>2</sup>. To protect krill stocks and control fishing, an international treaty called the Convention for the Conservation of Antarctic Marine Living Resources was established in the early 1980s. The Convention recommends the establishment of precautionary catch limits (PCLs), i.e., the amount of krill that can be caught without causing significant damage to the functioning of the environment. Between 1993 and 2010, there was a decline in interest, followed by an increase in fishing, and in 2020, reported catches reached a historically highest level of 450 781 tonnes in the CCAMLR subarea 48<sup>3</sup>. Currently, 9.3% of all estimated krill biomass can be harvested, which is considered by CCAMLR to have no potential negative impact on species dependent on this crustacean<sup>4</sup>. The West Antarctic Peninsula (WAP), including the South Shetland Islands, is an important habitat for numerous breeding colonies of penguins of the genus *Pygoscelis*<sup>5,6</sup>. The local availability of krill is especially important during the breeding season, when nesting penguins do not forage far from their colonies<sup>7</sup>. When incubating eggs and feeding chicks, birds depend more on local food resources, however this depends on the size of the colony<sup>8,9</sup>. For example, breeding chinstrap penguins usually feed approximately 30–70 km from their colonies<sup>10–13</sup>, and Adélie penguins at King George Island usually forage

<sup>1</sup>Faculty of Oceanography and Geography, Department of Marine Biology and Biotechnology, Laboratory of Plankton Biology, University of Gdańsk, Al. M. Piłsudskiego 46, 81-378 Gdynia, Poland. <sup>2</sup>Faculty of Oceanography and Geography, Department of Physical Oceanography and Climate Research, Laboratory of Physical Oceanography, University of Gdańsk, Al. M. Piłsudskiego 46, 81-378 Gdynia, Poland. <sup>3</sup>Institute of Biochemistry and Biophysics, Polish Academy of Sciences, Pawińskiego 5a, 02-106 Warsaw, Poland. ✉email: anna.panasiuk@ug.edu.pl

less than 30–40 km from their colonies<sup>9</sup>. However, the availability of krill on a large scale is also crucial during penguins' winter migrations, before and after the breeding season, when they tend to migrate long distances during winter from their breeding grounds, up to 1000 km for Adélie penguins from the South Orkney Islands<sup>14</sup>, and up to 4782 km for chinstrap penguins from Livingston Island<sup>15</sup>.

Krafft et al.<sup>16</sup> estimated that the total krill biomass in subarea 48 was 62.9 megatonnes in 2018–2019 and that, compared with that found in the historical CCAMLR 2000 survey, the krill biomass in the South Shetland region was two times lower (2000 survey – 6.615.000 t., 2018–19 survey – 3.325.000 t.). However, an estimate of total krill biomass is somewhat unreliable for areas where penguins and other predators feed during the breeding season and where fishing vessels operate. Until the 1990s, the Antarctic krill fishery operated mainly in the Indian Ocean sector and then intensified in the Atlantic sector, around the Antarctic Peninsula and the South Shetland Islands<sup>17</sup>. Recently, krill fishing has shifted southward to the Drake Passage area and farther<sup>18</sup>. Santa Cruz et al.<sup>18</sup> reported, on the basis of data from several years, that up to 57% of fishing occurs in the Bransfield Strait area. The main reason for the southern shift in fishing is believed to be the reduction in ice cover, especially its subsequent formation in autumn and winter, which makes the South Shetland Islands area more accessible to trawlers<sup>17,19,20</sup>. Shifts in fishing farther south of shelf areas intensify competition for food resources between commercial vessels and seabirds breeding in these regions. *Pygoscelis* penguins in the investigated region depend on the distribution and biomass of krill, as krill constitute almost 100% of their diet<sup>6,21</sup>; this is because as the relatively high sea surface temperature and melting sea ice in recent decades have caused a decrease in the abundance of the silverfish *Pleurogramma antarctica*, which can also be an important food source for penguins<sup>22,23</sup>. The distribution of Antarctic krill in the Southern Ocean – on large- and small-scale bases – is not well described, and the size structure of this crustacean on the basis of fishing vessel data in these studies is rarely considered<sup>24</sup>. Even less common are studies comparing the size of krill caught by commercial vessels with that recorded in the diet of predators, e.g., Juarez et al.<sup>25</sup>, Fraser and Hofmann<sup>26</sup>, during their studies near Palmer Station, western Antarctic Peninsula, indicated that there is a clear temporal variability between, for example, the intensity of ice cover in this area and the qualitative and quantitative structure of krill, which is also reflected in the diet of krill-dependent predators.

A detailed spatial analysis of the size and putative age of krill in the CCAMLR subarea 48.1 was carried out to test the following hypotheses: (1) the size of krill in the Bransfield Strait varies spatially, which is the result of its different areas of origin; (2) in the Bransfield Strait, there are mainly smaller krill that have not begun reproduction; and (3) the size of the krill dominating the penguins' diet does not differ from the size of krill dominant in commercial fishing. For a more detailed analysis, the area was divided into sectors that may be influenced by different water masses and, therefore, harbor krill populations with different structures. Diet samples of three *Pygoscelis* penguins species were collected during the corresponding Antarctic summers. The results presented in this work are based on a two-year study.

## Materials and methods

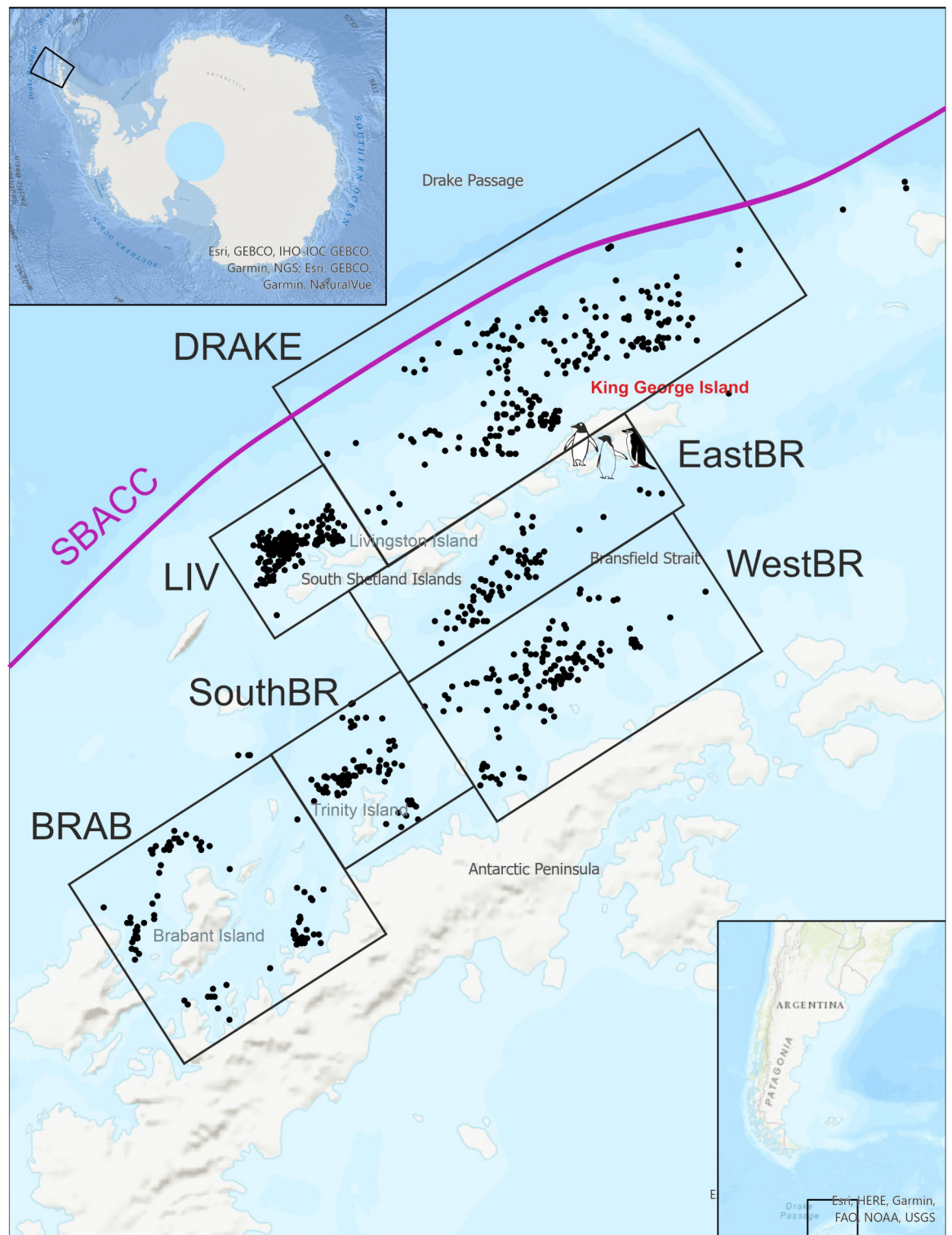
### Data sources

The size data for the Antarctic krill *E. superba* in the CCAMLR subarea 48.1 (Fig. 1 – a black frame on a smaller map and an enlarged area next to it) were made available by the CCAMLR secretariat (SISO database) ([www.ccamlr.org/](http://www.ccamlr.org/)). A total of 810 commercial hauls of Antarctic krill were made during this period. In 2011, fishing took place in January, April, May and December; in 2012, it took place in January, February, March, April, May, June, October, November, and December; and in 2013, the research period included January, February and March. For each catch, between January 2011 and March 2013, the green weight was estimated, and 100 to 500 individuals of Antarctic krill were measured.

Diet samples were collected in the austral summers (December–February) of 2011/2012 and 2012/2013. Field work was conducted at King George Island, South Shetland Islands (62° 10' S, 58° 30' W), within Antarctic Specially Protected Area (ASPA) No. 128, where Adélie, chinstrap, and gentoo penguins breed in five colonies. Field protocols were approved by the University of California San Diego Institutional Animal Care and Use Committee permit# S05480. The samples were collected via the water-offloading technique<sup>27,28</sup> following a modification of the CCAMLR CEMP (CCAMLR Ecosystem Monitoring Program) standard methods. Krill were measured for total length according to the CCAMLR standard protocol (<https://www.ccamlr.org/>): from the anterior side of the eyeball to the tip of the telson<sup>29</sup>. The results of the penguin diet study were originally published by Panasiuk et al.<sup>28</sup> and Wawrzynek-Borejko et al.<sup>21</sup>.

### Statistical analysis

ArcGIS Pro software was used to analyze the availability of krill sizes preferred by penguins in the Bransfield Strait and Drake Passage areas. This geographic information system (GIS) software enables the integration of several environmental elements, such as location, season, and month, as well as a thorough analysis of spatial patterns. The use of GIS software not only made managing and visualizing complex datasets easier but also improved the accuracy of the analytical processes, highlighting the crucial role that geospatial technology plays in clarifying intricate ecological dynamics. Krill data from fishing vessels were investigated in five research areas: Brabant Island (BRAB), Livingston Island (LIV), southern Bransfield Strait (sSouthBR), western Bransfield Strait (wWestBR), Eastern Bransfield Strait (eEastBR), and Southern parts of the Drake Passage (DRAKE). The putative (i.e., acknowledging environmentally induced geographic discrepancies in growth rates<sup>30</sup>) age of krill was determined on the basis of Candy and Kawaguchi<sup>31</sup> size ranges: 0–25.9 mm – year 0, 26–39.9 mm – year 1+, 40–47.9 mm – year 2+, 48–50.9 mm – year 3+, 51–52.9 mm – year 4+, 53–54.9 mm – year 5+, and 55–70 mm – year 6+. To compare the sizes of krill from fishing vessels and from the diets of the studied penguins, data from fishing vessels in the Bransfield Strait, which were collected from December 2011 to March 2012 and from December 2012 to March 2013, were extracted. This occurred because data related to the diet of the analyzed



**Fig. 1.** Locations of commercial fishing stations of the Antarctic krill *Euphausia superba* in subarea 48.1 of CCAMLR divided into sectors: *LIV* Livingston Island, *DRAKE* Southern parts of the Drake Passage, *EastBR* Eastern parts of the Bransfield Strait, *WestBR* Western parts of the Bransfield Strait, *SouthBR* Southern part of the Bransfield Strait, *SBACC* the estimated southern boundary of the ACC. The breeding areas of populations of the three investigated *Pygoscelis* (*P. adeliae*, *P. antarcticus*, *P. papua*) penguin species on King George Island (South Shetland Islands) are marked by penguin drawings; *SBACC* the estimated southern boundary of the ACC.

penguins were also collected during analogous summer periods. The sizes of krill from fishing vessels and from the diet of *Pygoscelis* penguins were compared via ANOVA and Tukey tests.

## Results

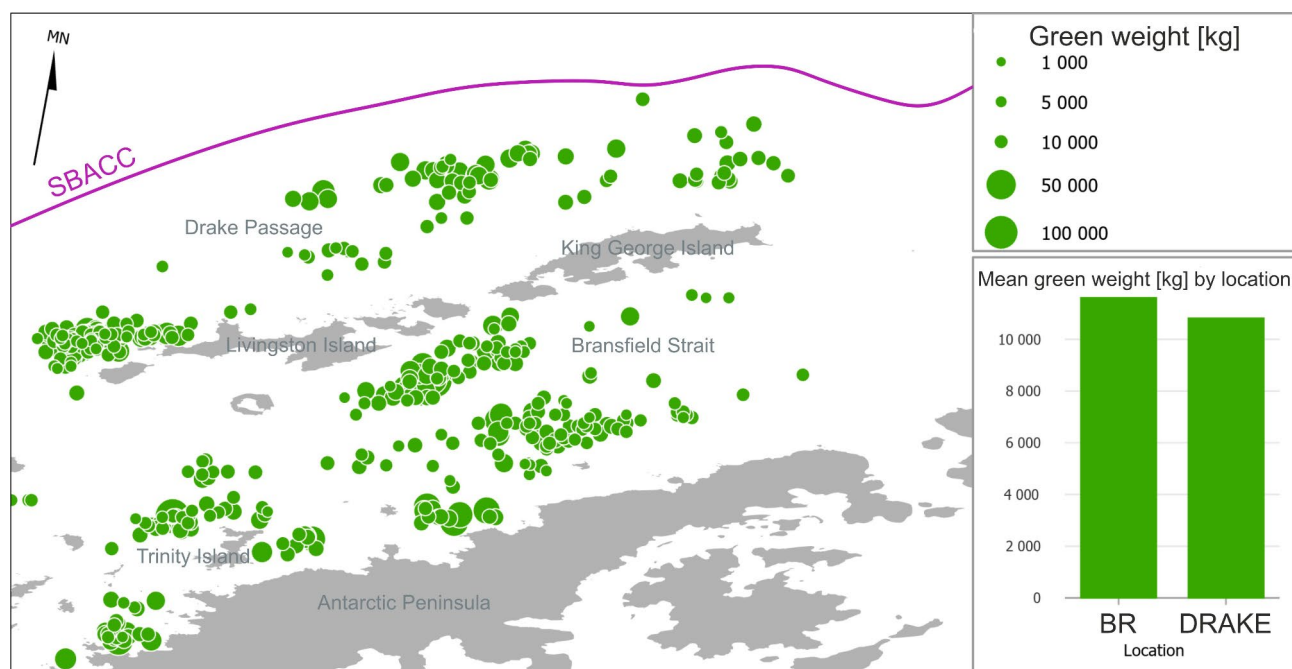
### Green weight of the Antarctic krill *Euphausia superba* commercial catches

The Antarctic krill catch green weight throughout the study period was greater in the Bransfield Strait than in the southern parts of the Drake Passage (Fig. 2). The highest catch values [kg] were recorded in the eastern and western parts of the Bransfield Strait and in the area of Livingston Island (Fig. 3). Fishing activity was clearly concentrated closer to the shores, both in the case of the South Shetland Islands and the Antarctic Peninsula. Until the end of the Antarctic summer, most fishing vessels were concentrated in the eastern part of the Bransfield Strait, and at the beginning of winter, their activity moved toward the western shores of the study area (Fig. 3).

### Size and age of commercial catches of the Antarctic krill *Euphausia superba*

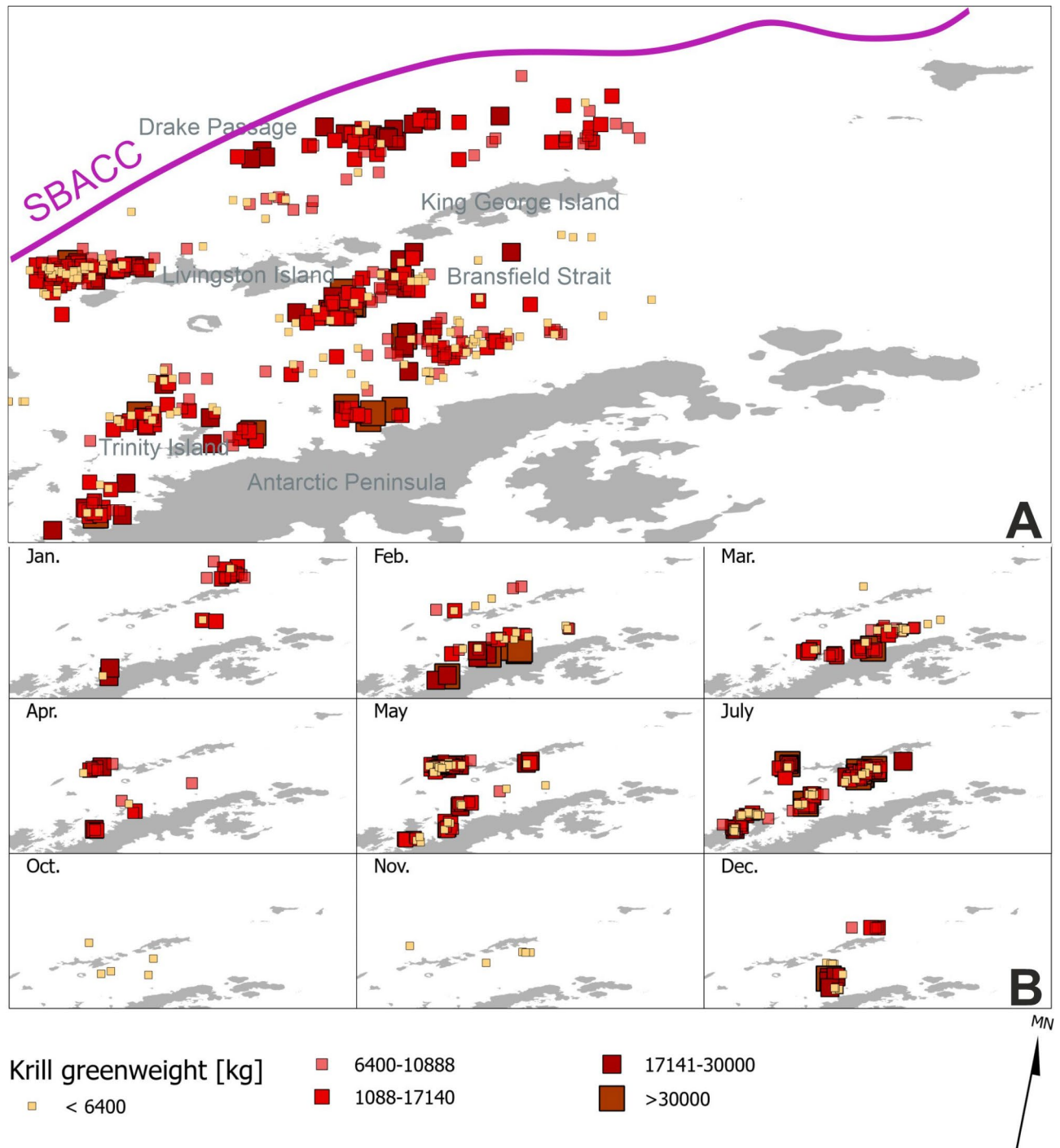
Data from commercial fishing vessels were analyzed from January 2011 to March 2013 in the CCAMLR 48.1 subarea. Spatially, the largest krill (above 4 cm) were observed on the border of the continental shelf north of the South Shetland Islands and close to Livingston Island (Table 1, Fig. 4). Smaller krill (less than 3.8 cm in size) were recorded throughout the entire Bransfield Strait. In the Bransfield Strait, the krill population was diverse, but relatively small krill dominated. Generally, krill smaller than 4 cm in size were observed in the Bransfield Strait throughout the year, with the exception of May and June. During these months, larger individuals were observed in the Brabant Islands area, as well as to the south of Livingston Island (Fig. 4). Notably, throughout the study period, the highest levels of fishing activity were recorded north of the South Shetland Islands and in the area of Livingston Island. Therefore, the data on the number of krill size measurements varied between areas. North of the South Shetland Islands, 42 566 krill individuals were measured, whereas in a small area of Livingston Island, 43 751 individuals were measured during the same period. In the eastern part of the Bransfield Strait, there were more than 25 000 individuals; in the western part, there were more than 12 000 individuals; and in the southern part, there were more than 13 000 individuals (Table 1, Fig. 3).

The research findings showed that the areas north of the South Shetland Islands and around Livingston Island, as well as subareas within the Bransfield Strait, were grouped in terms of the size of the krill caught (Fig. 5). Despite this, no statistically significant differences in krill length were found between any of the areas within the Bransfield Strait region, although the areas of the southern and eastern straits, as well as the eastern and western parts, were characterized by similar values in terms of the size of the krill caught (Table 2). During the analyses, the krill were divided into individual years of life on the basis of their size. Throughout the year, 2+ krill dominated north of the South Shetland Islands, whereas 1+ and 2+ krill dominated in the Bransfield Strait (Fig. 4). An interesting situation occurred in May and June, when two distinct groups of krill, 5+ and 6+, were observed in the areas of the Brabant Island and Anvers Island and in the Boyd Strait. In area 48.1, 4+ krill were recorded sporadically (Fig. 6). The results of the analyses clearly indicated that young krill were caught throughout the Bransfield Strait. The most diverse population structure of caught krill occurred in the area of Livingston Island, and in this area, large quantities of the oldest krill (over 6 years old) were recorded, accounting



**Fig. 2.** Green weight [kg] of the Antarctic krill *Euphausia superba* harvested in the CCAMLR subarea 48.1 between December 2011 and March 2013; SBACC the estimated southern boundary of the ACC.





**Fig. 3.** Green weight [kg] of the Antarctic krill *Euphausia superba* harvested in the CCAMLR subarea 48.1 between December 2011 and March 2013 for the entire study period (**A**) and for each month (**B**); SBACC the estimated southern boundary of the ACC.

for more than 11% of the catches (Fig. 7). A similar population structure was observed in the southern part of the Drake Passage; however, in this case, slightly younger (three- and four-year-old) individuals were recorded, and half of the population consisted of two-year-old individuals (Fig. 7). The opposite pattern was observed in the Bransfield Strait region, where krill over one year of age dominated, constituting approximately 70% of all caught individuals. However, the structures of the krill populations in the Brabant Island area and eastern part of the Bransfield Strait were the most similar to each other, as were the structures of the krill populations in the southern and western parts of the strait. Taking the above findings into account, very young krill, i.e., those over one year old, are clearly caught in significant quantities in the Bransfield Strait.

	DRAKE	LIV	BRAB	EastBR	WestBR	SouthBR
Mean	4.59	4.74	3.71	3.78	3.75	38.01
SD	0.58	6.42	0.72	0.50	0.72	6.23
Med.	4.6	47.47	3.6	3.7	3.7	37.17
Mode	5	52	3.6	3.5	3.7	34
Min.	2.07	16	1.6	1.7	2	18
Max.	6.7	65	6.2	6.1	6	59
Q25	4.21	42.9	3.3	3.47	3.2	3.4
Q50	4.6	47.47	3.6	3.7	3.7	3.72
Q75	5	52	4.1	4.09	4.2	4.2
Number of krill size records	42 566	43 751	14 880	25 142	12 153	13 089

**Table 1.** Basic statistics describing the differences in the size of the Antarctic krill *Euphausia superba* between six study areas (DRAKE, LIV, BRAB, EastBR, WestBR, and SouthBR) in the CCAMLR subarea 48.1 between December 2011 and March 2013.

**Size of the Antarctic krill *Euphausia superba* in commercial catches vs. the diet of *Pygoscelis* penguins**

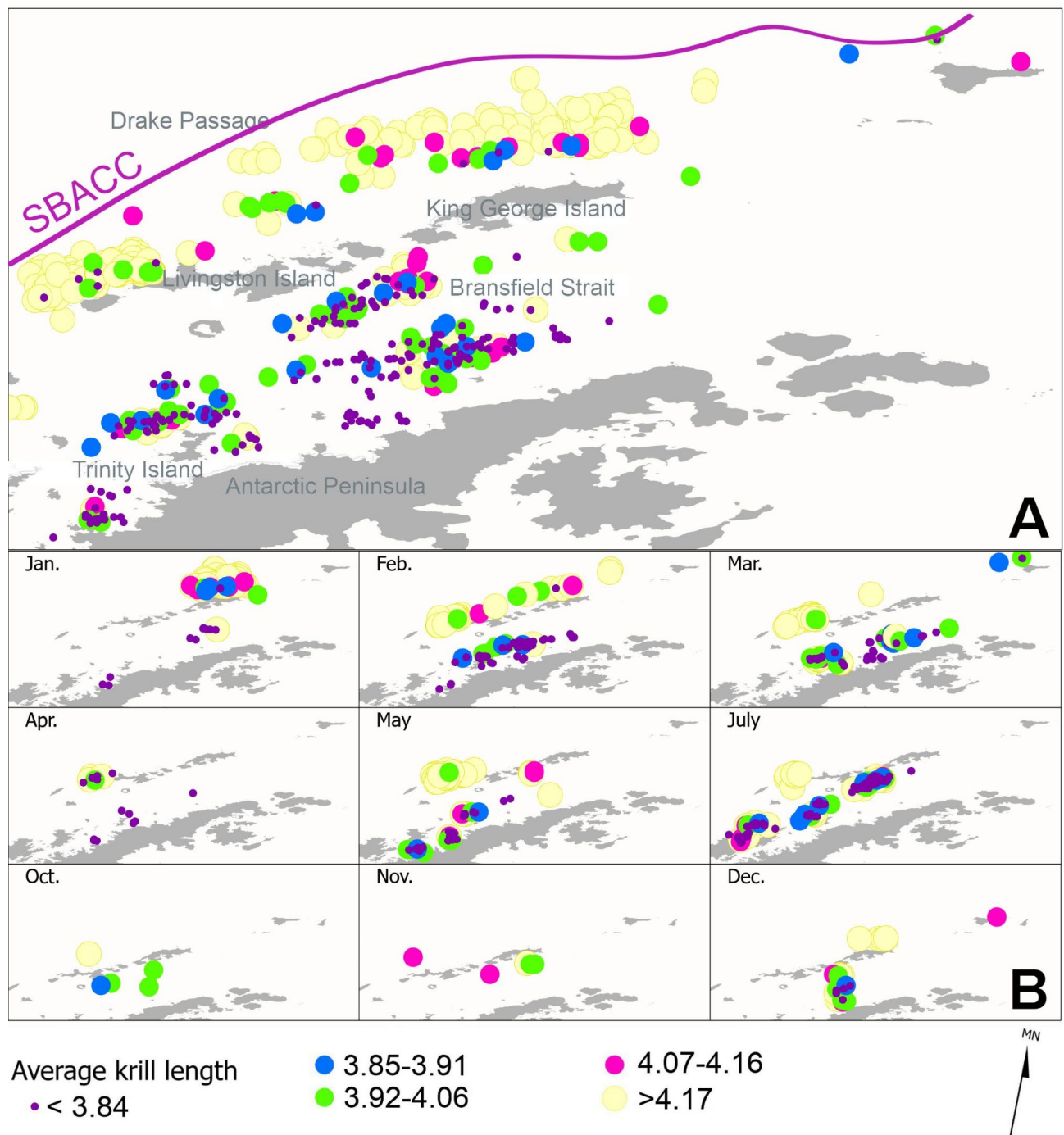
The size structure of krill caught in the Bransfield Strait was compared with the size structure of krill recorded in penguin diet samples. No statistically significant differences were detected for any of the three species of *Pygoscelis* tested (Fig. 8). However, on the basis of the results obtained, the size of krill caught in the Bransfield Strait was most similar to the size of krill consumed by Adélie penguins (Fig. 8, Table 3). Gentoo and chinstrap penguins prefer larger krill than those caught in the Bransfield Strait (Table 3).

**Discussion**

In recent decades, significant changes have been observed in the functioning of the Antarctic environment, including changes in the populations of key zooplankton species, such as the Antarctic krill *E. superba*, as well as dependent predators<sup>32–34</sup>. This is caused by e.g., ocean warming, changes in ocean circulation patterns, glacial melting or fishing<sup>35</sup>. To ensure the renewability of the pelagic krill stock and the availability of food for krill predators, Hinke et al.<sup>36</sup> investigated the overlap between the fishing and foraging areas of *Pygoscelis* penguins and reported that these areas mainly overlap north of the South Shetland Islands and in the area of the Bransfield Strait, including its southwestern regions. Since the beginning of CCAMLR, krill fishing has largely been concentrated in the area of the previously mentioned Orkney Islands or in the Bransfield Strait<sup>37</sup>. This fact certainly has consequences for the functions of predators, which depend on the availability, biomass and size structure of the Antarctic krill. *Pygoscelis* penguins constitute approximately 90% of the bird biomass in the Antarctic area<sup>38</sup>. Although Adélie, gentoo and chinstrap penguins inhabit the same areas, they have different migratory behaviors and habitat preferences or slightly different diet compositions<sup>39</sup>. These three penguin species respond very differently to climate change<sup>40</sup>. In the case of Adélie and chinstrap penguins, significant population declines have been observed, as Adélie are heavily dependent on sea ice, and while chinstraps are usually found outside the pack ice they are dependent on krill existing in the pack ice zone<sup>6,41–44</sup>. The situation is slightly different for gentoo penguins, which tend to avoid ice and cope better at slightly higher temperatures. The population of the gentoo species is growing, and new colonies are being observed<sup>42</sup>. Therefore, it is very important to study the potential overlap between fishing and colony areas, as well as the food preferences of predators in relation to, for example, the size of the consumed krill.

**Size and age of the Antarctic krill *Euphausia superba* in commercial catches vs. food preferences of the *Pygoscelis* penguins**

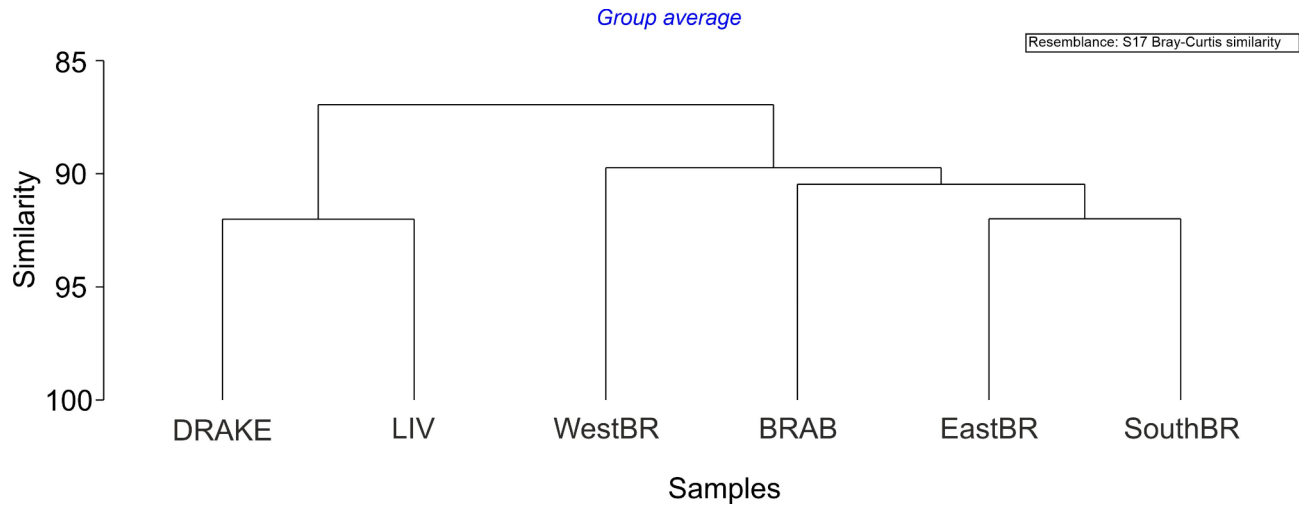
The average length of krill in commercial catches in the Bransfield Strait from December 2011 to March 2013 was 37.8 mm (in all studied sectors of the strait, the mean krill size ranged from 3.75 to 3.80 cm). Larger krill with average sizes ranging from 4.59 to 4.74 cm were recorded close to Livingston Island or in the Drake Passage. The results obtained in the Bransfield Strait area over two years suggested that 1- to – 3-year-old krill are caught in this area (with one-year-old krill dominating). It has been reported in the literature that the Bransfield Strait region is an area where smaller (i.e., younger) krill occur<sup>45,46</sup>, and according to the results of the research by Siegel and Loeb<sup>47</sup>, krill begin reproductive processes when individuals reach a size of 34.65–35.91 mm (L50) for females and 43.35–43.71 mm (L50) for males, which approximately corresponds to size class 2+ for females and 3+ for males. These findings clearly indicate that specimens that have not yet reached sexual maturity, and thus not yet started reproducing were commercially caught in the Bransfield Strait during the investigated seasons. These observations should be of particular interest for recommendations related to fishing quotas for this region of the Antarctic, as well as future plans related to significant restrictions on the catch of Antarctic krill. The results of our research were compared with the data published by the CCAMLR Secretariat (Fishery Report 2021: *Euphausia superba* in Area 48 - [https://fishdocs.ccamlr.org/FishRep\\_48\\_KRI\\_2021.pdf](https://fishdocs.ccamlr.org/FishRep_48_KRI_2021.pdf), Fishery Report 2022: *Euphausia superba* in Area 48 - [https://fishdocs.ccamlr.org/FishRep\\_48\\_KRI\\_2022.pdf](https://fishdocs.ccamlr.org/FishRep_48_KRI_2022.pdf)). CCAMLR analysis of the annual frequency distributions of krill catch lengths from 2011 to 2022 revealed that in most years, krill smaller than 4 cm were mostly caught in the Bransfield Strait region (481 S). In 2021, during the



**Fig. 4.** Average length [cm] of the krill *Euphausia superba* in subarea 48.1 of CCAMLR between December 2011 and March 2013 for the entire study period (A) and for each month (B); SBACC the estimated southern boundary of the ACC.

summer, catches were dominated by krill, which were approximately 3.5 cm in size, and similar results were also obtained by CCAMLR in 2022. Lower values for the size of recorded krill were obtained during standard research surveys using RMT 1 + 8 nets. For example, Siegel et al.<sup>48</sup> recorded the largest quantities of krill smaller than 30 mm in the same region in 2011.

Presented findings suggest that the structure of the krill population is consistent throughout the Bransfield Strait, although those in the eastern and southern parts of the strait and the Brabant Island region are the most similar. However, the structure in these areas was slightly different from that in the western part of Bransfield. The Livingston Island and Drake Passage areas were clearly distinguishable from the above regions, where larger and therefore older krill were recorded. However, this can be explained by the hydrology of the area. According



**Fig. 5.** Cluster analysis of krill size in communities recorded between December 2011 and March 2013 in the CCAMLR subarea 48.1 was divided into sectors: *LIV* Livingston Island, *BRAB* Brabant Island, *DRAKE* Southern parts of the Drake Passage, *EastBS* Eastern parts of the Bransfield Strait, *WestBS* Western parts of the Bransfield Strait, *SouthBS* Southern part of the Bransfield Strait.

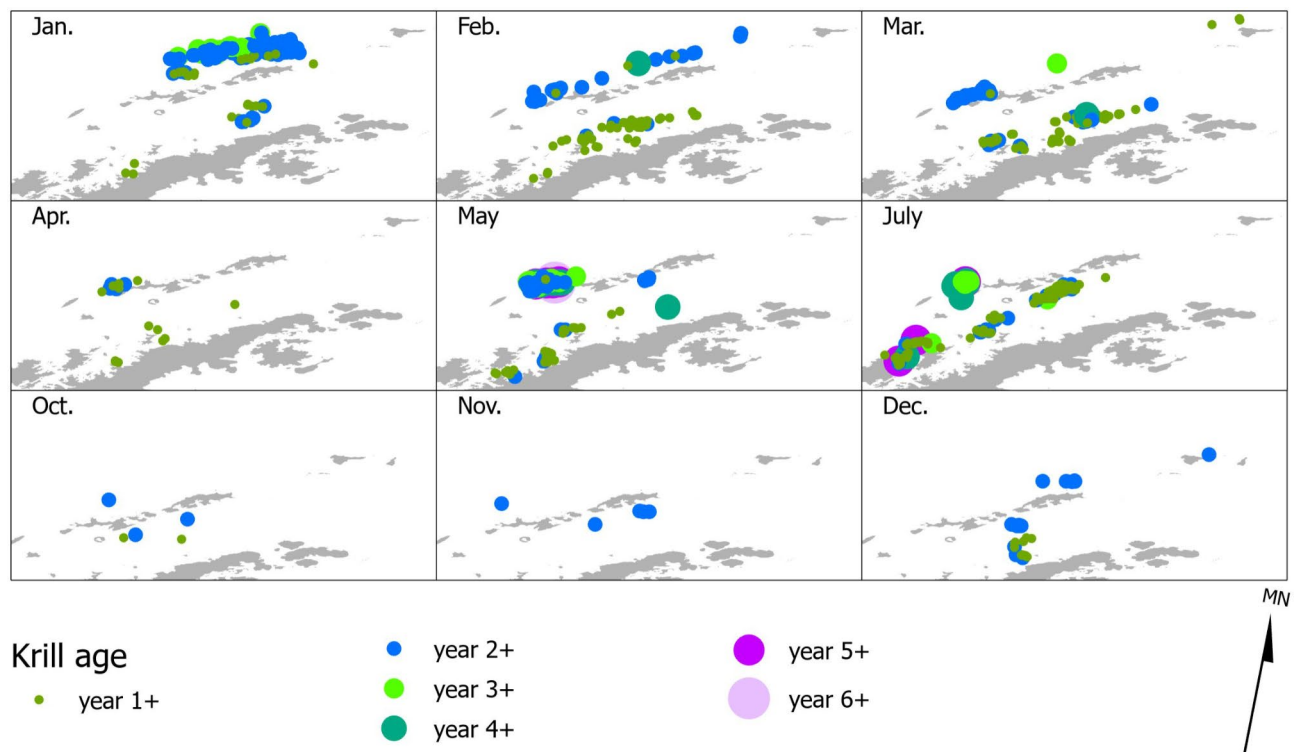
ANOVA $p < 0.05$				
Region	diff	lwr	upr	p adj
DRAKE-BRAB	0.88895024	0.871812258	0.906088231	0.0000000
EastBR-BRAB	0.07635746	0.057744556	0.094970374	0.0000000
LIV-BRAB	0.97264498	0.955748210	0.989541754	0.0000000
SouthBR-BRAB	0.10047491	0.078909884	0.122039944	0.0000000
WestBR-BRAB	0.05122403	0.029221588	0.073226479	0.0000000
EastBR-DRAKE	-0.81259278	-0.826906484	-0.798279074	0.0000000
LIV-DRAKE	0.08369474	0.071697126	0.095692349	0.0000000
SouthBR-DRAKE	-0.78847533	-0.806461222	-0.770489438	0.0000000
WestBR-DRAKE	-0.83772621	-0.856234300	-0.819218121	0.0000000
LIV-EastBR	0.89628752	0.882263520	0.910311514	0.0000000
SouthBR-EastBR	0.02411745	0.004721003	0.043513895	0.0052985
WestBR-EastBR	-0.02513343	-0.045015060	-0.005251802	0.0042640
SouthBR-LIV	-0.87217007	-0.889926268	-0.854413868	0.0000000
WestBR-LIV	-0.92142095	-0.939705907	-0.903135990	0.0000000
WestBR-SouthBR	-0.04925088	-0.071920007	-0.026581753	0.0000000

**Table 2.** Results of ANOVA and Tukey’s post hoc tests comparing the sizes of the Antarctic krill *Euphausia superba* between December 2011 and March 2013 in the CCAMLR subarea 48.1 divided into sectors: *LIV* Livingston Island, *BRAB* Brabant Island, *DRAKE* Southern parts of the Drake passage, *EastBS* Eastern parts of the Bransfield Strait, *WestBS* Western parts of the Bransfield Strait, and *SouthBS* Southern part of the Bransfield Strait.

to Sangrá et al.<sup>49</sup> and Veny et al.<sup>50</sup>, the western part of the strait is influenced by the Bransfield Strait Current, and the eastern part is influenced by transitional zonal water with the influence of the Weddell Sea. This results in spatial differences in the structure of the krill population<sup>51</sup>. The obtained results, which also consider the prior studies of Moffat and Meredith 2018<sup>52</sup> and Trathan et al. 2022<sup>37</sup> assume that small krill in the Bransfield Strait flow mainly from the Weddell Sea region, which is why smaller individuals are recorded mainly in the eastern, southern and western parts of the Strait, whereas larger krill flow into the Strait from the western side, also from the area of the Antarctic Circumpolar Current. However, it should be noted that despite the different sources of krill in the Strait, their communities are relatively well mixed in the studied area, but may change seasonally and spatially, as the circulation patterns of water masses in the Strait are seasonal<sup>53</sup>. Warwick-Evans et al.<sup>54</sup> also noted that there are many underwater canyons in the Strait, which may isolate krill despite the existence of strong currents.

In this study, we also examined the size of krill in the diets of three species of penguins of the genus *Pygoscelis*, Adélie, chinstrap and gentoo, during two summer Antarctic seasons, 2011/2012 and 2012/2013, to compare the

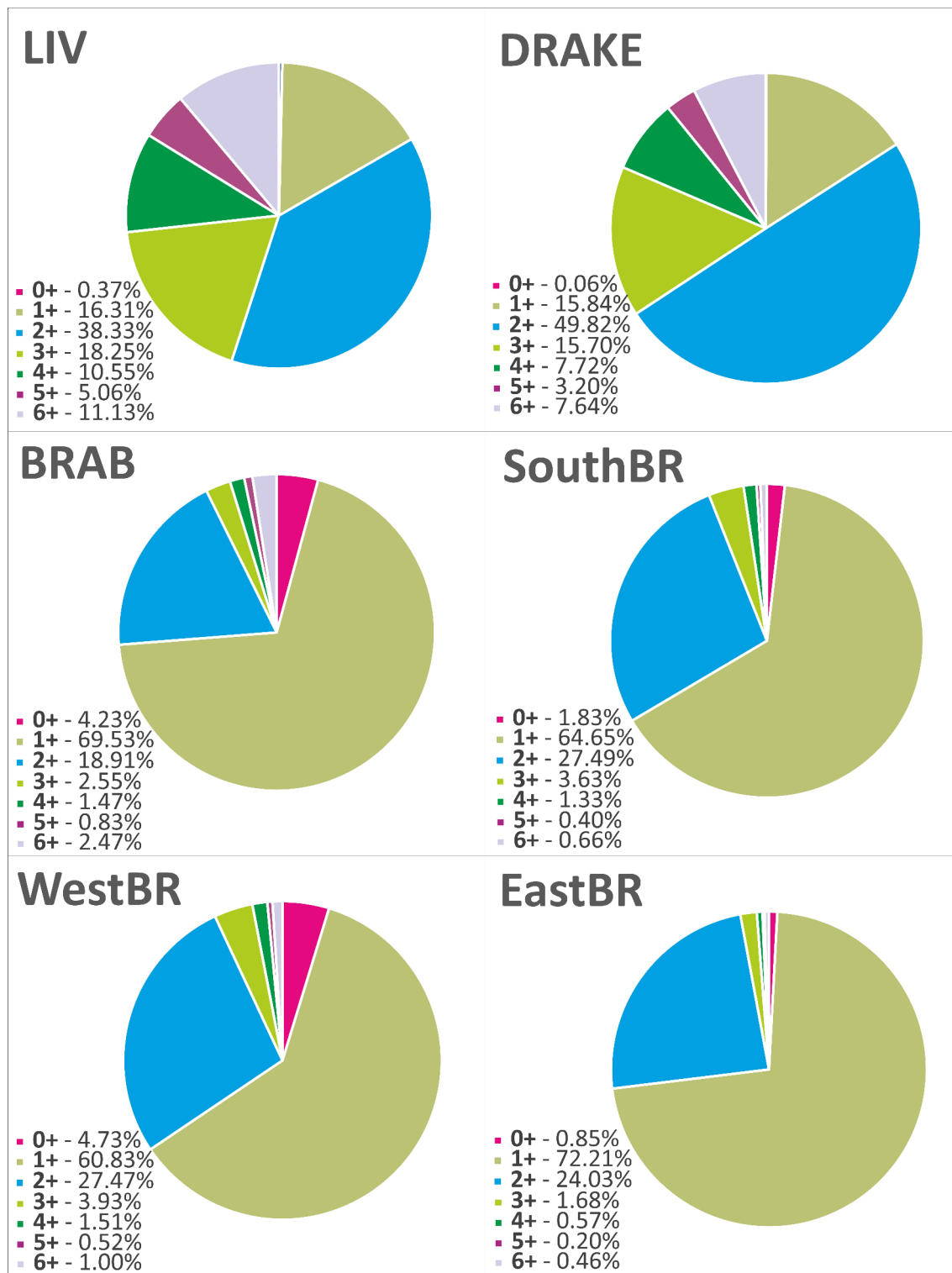




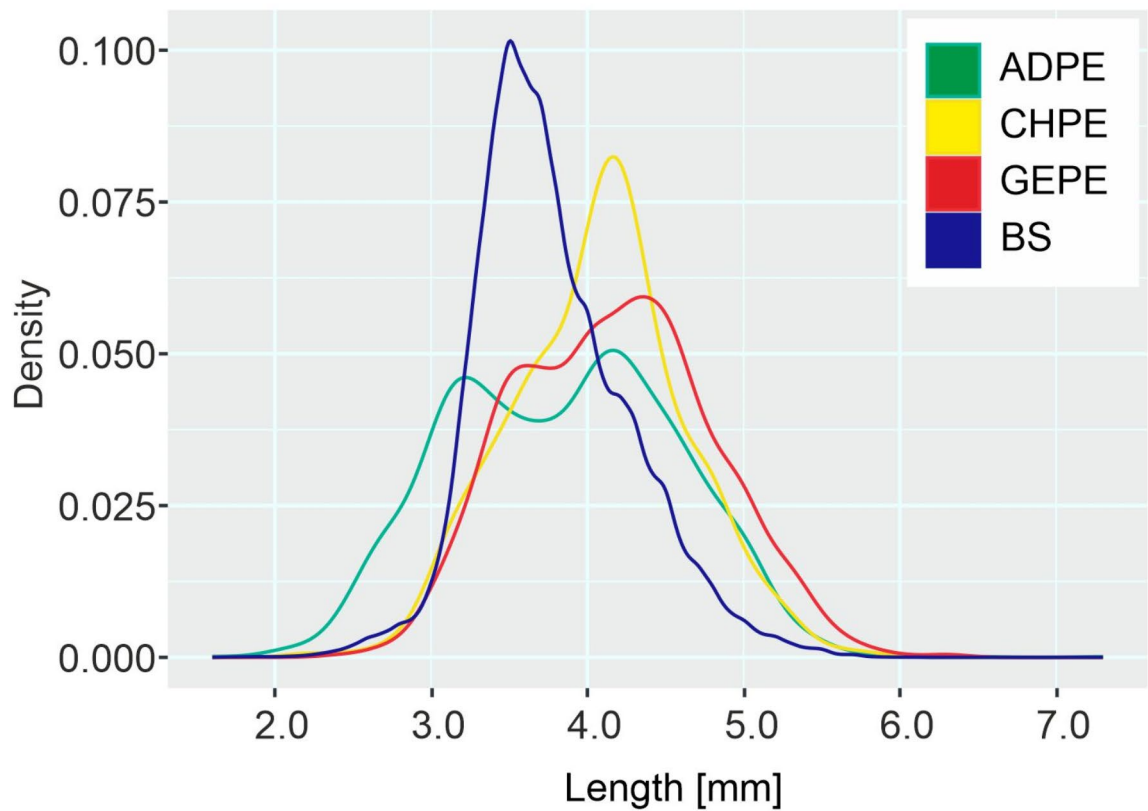
**Fig. 6.** Age structure of the Antarctic krill *Euphausia superba* in commercial catches from different months between December 2011 and March 2013 in the CCAMLR subarea 48.1.

size of krill in the penguin diet with the size of krill in commercial catches from December 2011–March 2012 and December 2012–March 2013. The results showed that the differences between the size of krill in the diets of the studied penguins and the size of krill recorded in commercial catches in the Bransfield Strait were not statistically significant, but the krill caught by commercial vessels were generally smaller than those consumed in the diets of the studied *Pygoscelis* penguins. However, notably, during the present study, the size range of krill in the catches was most similar to the size range of krill in the diet of Adélie penguins. Juárez et al.<sup>25</sup> studied krill in the diets of Adélie and gentoo penguins at Stranger Point (King George Island) from 2011 to 2013, but their diet sampling period was slightly shorter and took place in January and February. The results obtained by those authors revealed that the krill in the diets of both species were very similar in size to the krill recorded in commercial catches; for Adélie penguins, 40.75 mm (2011), 33.43 mm (2012), and 38.13 mm (2013) (38.4 mm – our data) were recorded; and for gentoo penguins, 44.74 mm (2011), 43.73 mm (2012), 40.84 mm (2013) (41.7 mm – our data) were recorded. The conclusions of these authors were different from those resulting from this work because, in our opinion, penguins are clearly looking for larger krill than those that dominate in the environment. However, the results from analyses of penguin diets and commercial fishing indicate that Adélie penguins are likely to be at risk from intensified commercial fishing because their krill size preferences match most appropriately with the size range of the krill caught. Chinstrap and gentoo penguins appear to be more selective and choose larger krill, even if the smaller krill are dominant in a given area. Because the area of the Bransfield Strait is an area where smaller/younger krill occur, fishing there will certainly have a negative impact not only on Adélie penguin populations, but also on their congeners. Current management of krill resources in the Southern Ocean does not consider interannual changes in krill abundances resulting from, for example, differences in the winter sea ice cover, and Krüger et al.<sup>55</sup> reported that very high krill catches during years of low ice resulted in lower reproductive success of penguins in that region and that fisheries with a climatic fluctuations may have a synergistic effect. Considering that they are also affected by additional stress factors in the form of climate change and, as a result, the progressive reduction in sea ice, the disappearance of colonies in the northern areas of the South Shetland Islands is already being observed<sup>56</sup>; however, new colonies of chinstrap penguins are simultaneously being observed, for example, in the areas of Deception Island and Low Island, as well as along the Danco Coast and David Coast<sup>6</sup>. Most likely, gentoo penguins also tend to inhabit more southern areas, especially since the larger krill preferred by this species are present there. Large gentoo colonies also occur in the Danco Coast area<sup>42</sup>, and since 1994, new colonies have formed around Anvers Island, Cape Renard and farther south<sup>5</sup>. Gentoo penguins from Cape Shirreff migrate into the southwestern Bransfield Strait during the winter<sup>36,40</sup>, which seems to be because the largest krill are observed there. In this study, Antarctic krill larger than 41 mm.

were recorded in May and July in the southern parts of the strait. Research by Kawaguchi et al.<sup>56</sup> on the growth of krill has shown that the growth rate of krill varies depending on its stage of development as well as the season. These authors have shown that in December the growth of 30 mm long krill in the Indian Ocean



**Fig. 7.** Age structure of krill fished between December 2011 and March 2013 in the CCAMLR subarea 48.1 divided into sectors: *LIV* Livingston Island, *BRAB* Brabant Island, *DRAKE* Southern parts of the Drake Passage, *EastBS* Eastern parts of the Bransfield Strait, *WestBS* Western parts of the Bransfield Strait, *SouthBS* Southern part of the Bransfield Strait.



Anova  $p < 0.05$

TukeyHSD	diff	lwr	upr	p
BS - ADPE	-0.619695	-0.911153	-0.328238	0.0000003
BS - CHPE	-2.898714	-3.517139	-2.280289	0.0000000
BS - GEPE	-3.9119889	-4.281797	-3.542180	0.0000000

**Fig. 8.** Size range of the Antarctic krill *Euphausia superba* recorded in the Bransfield Strait (BS) from December 2011–March 2012 and December 2012–March 2013 and in the diets of penguins of the genus *Pygoscelis* breeding on King George Island during the Antarctic summers of 2011/2012 and 2012/2013 (ADPE – *Pygoscelis adeliae*, CHPE – *P. antarcticus*, GEPE – *P. papua*); the results of ANOVA and Tukey’s test comparing krill length.

sector of the Southern Ocean was the highest in December and reached 0.279 mm/d, which means that 10 mm of growth requires approximately 35 days. In the case of 40 mm long krill, the growth is slower, and 10 mm of growth requires more than 75 days.

**Krill availability in the CCAMLR subarea 48.1**

During the study period, greater krill catches were recorded in the Bransfield Strait than in the other analyzed areas within CCAMLR subarea 48.1. This is probably one of the main reasons, in addition to the smaller and

	Mean length [cm]	STD	Min.	Max.	Q25	Q50	Q75
BS – Bransfield Strait	3.78	0.49	1.70	6.10	3.44	3.70	4.10
ADPE – <i>Pygoscelis adeliae</i>	3.84	0.73	1.60	7.30	3.20	3.90	4.40
CHPE – <i>Pygoscelis antarcticus</i>	4.17	0.55	2.20	5.80	3.70	4.10	4.40
GEPE – <i>Pygoscelis papua</i>	4.17	0.62	2.40	6.30	3.70	4.20	4.60

**Table 3.** Basic statistics on the average size of krill observed in catches from December 2011 to March 2012 and from December 2012 to March 2013 in the Bransfield Strait (BS) and in the diet of *Pygoscelis* penguins (ADPE – *Pygoscelis adeliae*, CHPE – *P. antarcticus*, GEPE – *P. papua*) in the summer of 2011/2012 and 2012/2012.

later occurrence of sea ice, driving the increasing fishing intensity in the Bransfield Strait, as demonstrated previously by Santa Cruz et al.<sup>18</sup>. Those authors revealed that 48–57% of all current catches over a 2–6 month period are concentrated in this area. Reiss et al.<sup>57</sup> also indicated that fishing seasons will gradually lengthen, which is directly related to milder climatic conditions, and currently, fishing takes place even in August. This could have potentially long-term consequences for predators in this area, including the already dramatically declining Adélie penguin populations. Spatially, fishing is mostly concentrated in areas where scientific research indicates the highest abundance and biomass of krill. During the analyses conducted in this study, the highest krill biomass was observed in the eastern and western parts of the Bransfield Strait, as well as in the Livingston Island area. Warwick-Evans et al.<sup>54</sup> also indicated, on the basis of modeling studies, that the areas with the highest Antarctic krill densities vary seasonally, but the highest values are recorded on the eastern and western sides of the strait, as well as the areas of Livingston Island and the Drake Passage. This finding clearly suggests the possibility of increasing and prolonged fishing activity overlapping with the areas with the highest krill abundance. This should be considered by CCAMLR, which is responsible for both regulating fishing activity and protecting predators that depend on krill in the area.

Conclusions

1. In the entire Bransfield Strait, young Antarctic krill are caught at one and two years of age and presumed to have not initiated reproduction processes.
2. In the light of the environmental changes taking place, especially in the West Antarctic region, dedicated CCAMLR working groups should conduct a detailed analysis of the population structure of the caught Antarctic krill, as well as the spatiotemporal intensity of commercial fishing in the Bransfield Strait area.
3. The results of the diet investigation of *Pygoscelis* penguins do not reflect the structure of the environmental krill population available in their feeding area. All *Pygoscelis* penguin species studied preferred larger krill than those dominant in the environment.
4. In the following years potential areas where new colonies of the studied penguins might be observed in the southern part of the Bransfield Strait and the areas of the Brabant, Anvers and Livingston Islands were identified. In these regions of the WAP, large krill are recorded, corresponding to the food preferences of the species studied.

Data availability

The biomass and size data for the Antarctic krill *E. superba* in the CCAMLR subarea 48.1 are available from CCAMLR but restrictions apply to the availability of these data, which were used with permission for the current study, and so are not publicly available. However, the data are available from the authors upon reasonable request and with the permission of CCAMLR. The diet samples of *Pygoscelis* penguins are not publicly available but are available from the corresponding author upon reasonable request.

Received: 8 April 2024; Accepted: 11 September 2024

Published online: 15 September 2024

References

1. Atkinson, A., Siegel, V., Pakhomov, E. A., Jessopp, M. J. & Loeb, V. A re-appraisal of the total biomass and annual production of Antarctic krill. *Deep-Sea Res. I Oceanogr. Res. Pap.* **56** (5), 727–740 (2009).

2. SC-CAMLR-XXIX Scientific Committee For The Conservation Of Antarctic Marine Living Resources, Report Of The Twenty-Ninth Meeting Of The Scientific Committee, CCAMLR. & Hobart Tasmania Australia, 1–426 (2010).

3. CCAMLR Fishery Report. in Area 48. CCAMLR Secretariat, Hobart, Tasmania, Australia, pp. 1–34 (2023).

4. Hill, S. L. et al. Is current management of the Antarctic krill fishery in the Atlantic sector of the Southern ocean precautionary? *CCAMLR Sci.* **23**, 31–51 (2016).

5. Herman, R. et al. Update on the global abundance and distribution of breeding Gentoo Penguins (*Pygoscelis papua*). *Polar Biol.* **43**, 1947–1956 (2020).

6. Strycker, N. et al. A global population assessment of the chinstrap penguin (*Pygoscelis antarctica*). *Sci. Rep.* **10** <https://doi.org/10.1038/s41598-020-76479-3> (2020).

7. Wilson, R. P. & Wilson, M. P. T. Foraging ecology of breeding *Spheniscus* penguins in *Penguin Biology* (ed. Davis, L. S., Darby, J. T.) 181–206 (Academic Press, 1990).

8. Oosthuizen, W. C. et al. The foraging behavior of nonbreeding Adélie Penguins in the Western Antarctic Peninsula during the breeding season. *Ecosphere* **13** (5), e4090. <https://doi.org/10.1002/ecs2.4090> (2022).



9. Ainley, D. G. & Wilson, R. P. Fish-birds at home in their oceanic habitats in: The Aquatic World of Penguins. Fascinating Life Sciences (eds Ainley, D. G. & Wilson, R. P.) (Springer, 2023).
10. Lowther, A. D., Trathan, P., Tarrux, A., Lydersen, C. & Kovacs, K. M. The relationship between coastal weather and foraging behaviour of chinstrap penguins, *Pygoscelis antarctica*. *ICES J. Mar. Sci.* **75** (6), 1940–1948 (2018).
11. Warwick-Evans, V. et al. Using habitat models for chinstrap penguins *Pygoscelis antarctica* to advise krill fisheries management during the penguin breeding season. *Divers. Distrib.* **24**, 1756–1771 (2018).
12. Phillips, J. A. et al. Foraging conditions for breeding penguins improve with distance from colony and progression of the breeding season at the South Orkney Islands. *Mov. Ecol.* **9** <https://doi.org/10.1186/s40462-021-00261-x> (2021).
13. Clucas, G. V., Warwick-Evans, V., Hart, T. & Trathan, P. N. Using habitat models for chinstrap penguins, *Pygoscelis antarctica*, to inform marine spatial management around the South Sandwich Islands during the penguin breeding season. *Deep-Sea Res. II: Top. Stud. Oceanogr.* **199** <https://doi.org/10.1016/j.dsr2.2022.105093> (2022).
14. Dunn, M. J., Silk, J. R. D. & Trathan, P. N. Post-breeding dispersal of Adélie penguins (*Pygoscelis adeliae*) nesting at Signy Island, South Orkney Islands. *Polar Biol.* **34**, 205–214 (2011).
15. Hinke, J. T., Santos, M. M., Korczak-Abshire, M., Milinevsky, G. & Watters, G. M. Individual variation in migratory movements of chinstrap Penguins leads to widespread occupancy of ice-free winter habitats over the continental shelf and deep ocean basins of the Southern Ocean. *PLoS ONE* **14**, e0226207 (2019).
16. Krafft, B. A. et al. Standing stock of Antarctic krill (*Euphausia superba* Dana, 1850) (Euphausiacea) in the Southwest Atlantic sector of the Southern Ocean, 2018–19. *J. Crustac Biol.* **41** (3), 1–17 (2021).
17. Kawaguchi, S. & Nicol, S. Learning about Antarctic krill from the fishery. *Ant. Sci.* **19**, 219–230 (2007).
18. Santa Cruz, F., Ernst, B., Arata, J. A. & Parada, C. Spatial and temporal dynamics of the Antarctic krill fishery in fishing hotspots in the Bransfield Strait and South Shetland Islands. *Fish. Res.* **208**, 157–166. <https://doi.org/10.1016/j.fishres.2018.07.020> (2018).
19. Constable, A. J., de la Mare, W. K., Agnew, D. J., Everson, I. & Miller, D. Managing fisheries to conserve the Antarctic marine ecosystem: Practical implementation of the convention on the conservation of Antarctic marine living resources (CCAMLR). *ICES J. Mar. Sci.* **57**, 778–791 (2000).
20. Nicol, S., Foster, J. & Kawaguchi, S. The fishery for Antarctic krill—Recent developments. *Fish. Fish.* **13**, 30–40 (2012).
21. Wawrzyniak-Borejko, J., Panasiuk, A., Hinke, J. T. & Korczak-Abshire, M. Are the diets of sympatric pygoscelid penguins more similar than previously thought? *Polar Biol.* **45**, 1559–1569 (2022).
22. La Mesa, M., Riginella, E., Mazzoldi, C. & Ashford, J. Reproductive resilience of ice-dependent Antarctic silverfish in a rapidly changing system along the Western Antarctic Peninsula. *Mar. Ecol.* **36**, 235–245 (2015).
23. Corso, A. D., Steinberg, D. K., Stammerjohn, S. E. & Hilton, E. J. Climate drives long-term change in Antarctic silverfish along the Western Antarctic Peninsula. *Commun. Biol.* **5**, 104. <https://doi.org/10.1111/maec.12140> (2022).
24. Watters, G. M., Hinke, J. T. & Reiss, C. S. Long-term observations from Antarctica demonstrate that mismatched scales of Fisheries management and predator-prey interaction lead to erroneous conclusions about precaution. *Sci. Rep.* **10** (1), 1–9 (2020).
25. Juárez, M. A. et al. Size structure of Antarctic krill inferred from samples of pygoscelid penguin diets and those collected by the commercial krill fishery. *Mar. Biol.* **168**, 22; (2021). <https://doi.org/10.1007/s00227-021-03831-0>
26. Fraser, W. R. & Hofmann, E. E. A predator's perspective on causal links between climate change, physical forcing and ecosystem response. *Mar. Ecol. Prog. Ser.* **265**, 1–15 (2003).
27. Wilson, R. P. An improved stomach pump for penguins and other seabirds. *J. Field Ornithol.* **55**, 109–112 (1984).
28. Panasiuk, A., Wawrzyniak-Borejko, J., Musiał, A. & Korczak-Abshire, M. *Pygoscelis* penguin diets on King George Island, South Shetland Islands, with a special focus on the krill *Euphausia superba*. *Ant. Sci.* **32** (1), 21–28 (2020).
29. Makarov, R. R. & Denys, C. J. Stages of sexual maturity of *Euphausia superba* Dana. *BIOMASS Handb.* **11**, 1–13 (1980).
30. Groeneveld, J. et al. How biological clocks and changing environmental conditions determine local population growth and species distribution in Antarctic krill (*Euphausia superba*): A conceptual model. *Ecol. Model.* **303**, 78–86 (2015).
31. Candy, S. G. & Kawaguchi, S. Modelling growth of Antarctic krill. II. Novel approach to describing the growth trajectory. *Mar. Ecol. Prog. Ser.* **306**, 17–30 (2006).
32. Johnston, N. M. et al. Status, change, and futures of zooplankton in the Southern Ocean. *Front. Ecol. Evol.* **9** <https://doi.org/10.3389/fevo.2021.624692> (2021).
33. Krause, D. J., Bonin, K. A., Goebel, M. E., Reiss, C. S. & Watters, G. M. The rapid population collapse of a key marine predator in the Northern Antarctic Peninsula endangers genetic diversity and resilience to climate change. *Front. Mar. Sci.* **8** <https://doi.org/10.3389/fmars.2021.796488> (2022).
34. Salmerón, N. et al. Contrasting environmental conditions precluded lower availability of Antarctic krill affecting breeding chinstrap penguins in the Antarctic Peninsula. *Sci. Rep.* **13** <https://doi.org/10.1038/s41598-023-32352-7> (2023).
35. Morley, S. A. et al. Global drivers on Southern ocean ecosystems: Changing physical environments and anthropogenic pressures in an earth system. *Front. Mar. Sci.* **7** <https://doi.org/10.3389/fmars.2020.547188> (2020).
36. Hinke, J. T. et al. Identifying risk: Concurrent overlap of the Antarctic krill fishery with krill-dependent predators in the Scotia sea. *PLoS ONE* **12** (1), e0170132. <https://doi.org/10.1371/journal.pone.0170132> (2017).
37. Trathan, P. N. et al. The ecosystem approach to management of the Antarctic krill fishery—the ‘devils are in the detail’ at small spatial and temporal scales. *J. Mar. Syst.* **225**, 103598. <https://doi.org/10.1016/j.jmarsys.2021.103598> (2022).
38. Croxall, J. P., Prince, P. A. & Ricketts, C. Relationships between prey life-cycles and the extent, nature and timing of seal and seabird predation in the Scotia Sea (ed. Siegfried, W. R., Condy, P., Laws, R. M.). *Proceedings of the fourth SCAR symposium on Antarctic biology*, (Springer, 1985).
39. Trivelpiece, W., Trivelpiece, S. & Volkman, N. Ecological segregation of Adélie, Gentoo, and Chinstrap Penguins at King George Island, Antarctica. *Eco* **68**, 351–361 (1987).
40. Korczak-Abshire, M., Hinke, J. T., Milinevsky, G., Juárez, M. A. & Watters, G. M. Coastal regions of the northern Antarctic Peninsula are key for gentoo populations. *Biol. Lett.* **17**, 20200708. <https://doi.org/10.5061/dryad.5x69p8d20> (2021).
41. Lynch, H. J., Naveen, R., Trathan, P. N. & Fagan, W. F. Spatially integrated assessment reveals widespread changes in penguin populations on the Antarctic Peninsula. *Ecology* **93**, 1367–1377 (2012).
42. Wethington, M., Flynn, C., Borowicz, A. & Lynch, H. J. Adélie penguins north and east of the ‘Adélie gap’ continue to thrive in the face of dramatic declines elsewhere in the Antarctic Peninsula region. *Sci. Rep.* **13**, 2525. <https://doi.org/10.1038/s41598-023-29465-4> (2023).
43. Ainley, D. G., Ribic, C. A. & Spear, L. B. Species-habitat relationships among Antarctic seabirds: A function of physical or biological factors? *Condor* **95** (4), 806–816 (1993).
44. Czepanskiy, M. F. et al. Se-ice and microzooplankton distribution as determinants of top predator community structure in Antarctic winter. *Mar. Ecol. Prog. Ser.* **738**, 57–73 (2024).
45. Siegel, V. A concept of seasonal variation of krill (*Euphausia superba*) distribution and abundance west of the Antarctic Peninsula in Antarctic ocean and resources Variability (ed. Sahrhage, D.) 219–230 (Springer, 1988).
46. Siegel, V. & Loeb, V. Recruitment of Antarctic krill *Euphausia superba* and possible causes for its variability. *Mar. Ecol. Prog. Ser.* **123**, 45–56 (1995).
47. Siegel, V. & Loeb, V. Length and age at maturity of Antarctic krill. *Ant. Sci.* **6** (4), 479–482 (1994).
48. Siegel, V., Reiss, C. S., Dietrich, K. S., Haraldsson, M. & Rohardt, G. Distribution and abundance of Antarctic krill (*Euphausia superba*) along the Antarctic Peninsula. *Deep-Sea Res. I* **77**, 63–74 (2013).
49. Sangrá, P. et al. The Bransfield current system. *Deep-Sea Res.* **158**, 390–402 (2011).

50. Veny, M., Aguiar-González, B., Marrero-Díaz, Á. & Rodríguez-Santana, Á. Seasonal circulation and volume transport of the bransfield current. *Progr Oceanogr.* **204**, 102795. <https://doi.org/10.1016/j.pocean.2022.102795> (2022).
51. Gallagher, K. L., Dinniman, M. S. & Lynch, H. J. Quantifying Antarctic krill connectivity across the West Antarctic Peninsula and its role in large-scale *Pygoscelis* penguin population dynamics. *Sci. Rep.* **13**, 12072. <https://doi.org/10.1038/s41598-023-39105-6> (2023).
52. Moffat, C. & Meredith, M. Shelf–ocean exchange and hydrography west of the Antarctic Peninsula: A review. *Phil Trans. R Soc.* **376**, 20170164. <https://doi.org/10.1098/rsta.2017.0164> (2018).
53. Zhou, M., Niiler, P. P. & Hu, J. H. Surface currents in the Bransfield and Gerlache Straits, Antarctica. *Deep-Sea Res. I Oceanogr. Res. Pap.* **49** (2), 267–280 (2002).
54. Warwick-Evans, V., Fielding, S., Reiss, C. S., Watters, G. M. & Trathan, P. N. Estimating the average distribution of Antarctic krill *Euphausia superba* at the northern Antarctic Peninsula during austral summer and winter. *Polar Biol.* **45**, 857–871 (2022).
55. Krüger, L., Huerta, M. F., Santa Cruz, F. & Cárdenas, C. A. Antarctic krill fishery effects over penguin populations under adverse climate conditions: Implications for the management of fishing practices. *Ambio* **50**, 560–571 (2021).
56. Kawaguchi, S., Candy, S. G., King, R., Naganobu, M. & Nicol, S. Modelling growth of Antarctic krill. I. Growth trends with sex, length, season, and region. *Mar. Ecol. Prog Ser.* **306**, 1–15 (2006).
57. Reiss, C. S. et al. Overwinter habitat selection by Antarctic krill under varying sea-ice conditions: Implications for top predators and fishery management. *Mar. Ecol. Prog Ser.* **568**, 1–16 (2017).

## Acknowledgements

The authors would like to acknowledge CCAMLR for providing data on the green weight and size of the Antarctic krill in the CCAMLR subarea 48.1 and the Antarctic Ecosystem Research Division, Southwest Fisheries Science Center, National Marine Fisheries Service National Oceanic and Atmospheric Administration (USA) for providing *Pygoscelis* penguin diet samples and research data on the Llano Point breeding site. The penguin population data used in the present study were collected at the Henryk Arctowski Polish Antarctic Station. We would also like to express our gratitude to Justyna Wawrzyniek-Borejko for her contribution to the study of the diet of *Pygoscelis* penguins. Finally, we thank the anonymous reviewers for their very helpful suggestions and comments, which allowed us to improve the manuscript.

## Author contributions

AP – conceptualization, investigation, formal analysis, visualization, writing original draft; GGG – formal analysis, methodology, visualization; writing—review & editing; MKA – formal analysis, methodology, writing—review & editing.

## Declarations

## Competing interests

The authors declare no competing interests.

## Ethical accord statement

All methods were performed in accordance with the relevant guidelines and regulations.

## Additional information

**Correspondence** and requests for materials should be addressed to A.P.

**Reprints and permissions information** is available at [www.nature.com/reprints](http://www.nature.com/reprints).

**Publisher's note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

**Open Access** This article is licensed under a Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License, which permits any non-commercial use, sharing, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if you modified the licensed material. You do not have permission under this licence to share adapted material derived from this article or parts of it. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by-nc-nd/4.0/>.

© The Author(s) 2024