



Sea-ice and macrozooplankton distribution as determinants of top predator community structure in Antarctic winter

Max F. Czapanskiy^{1,2,3}, Jarrod A. Santora^{2,4,*}, Kimberly S. Dietrich^{1,2}, Megan A. Cimino^{1,3}, Elliott L. Hazen³, Christian S. Reiss⁵, Richard R. Veit⁶

¹Institute of Marine Sciences, University of California Santa Cruz, Santa Cruz, California 95060, USA

²Fisheries Ecology Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Santa Cruz, California 95060, USA

³Ecosystem Science Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Monterey, California 93940, USA

⁴Department of Applied Math, University of California Santa Cruz, Santa Cruz, California 95060, USA

⁵Ecosystem Science Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, La Jolla, California 92037, USA

⁶City University of New York, College of Staten Island, Biology Department, Staten Island, New York 10314, USA

ABSTRACT: The Antarctic Peninsula marine ecosystem is highly productive, with large populations of commercially and ecologically important species including Antarctic krill *Euphausia superba*, Adélie penguins *Pygoscelis adeliae*, and crabeater seals *Lobodon carcinophagus*. The ecology of the peninsula is rapidly changing due to accelerating climate change and fishing pressure. Systematic ecosystem surveys have focused on austral spring and summer, leaving an information gap on winter ecosystem dynamics. Using data from 5 consecutive ecosystem surveys, we quantified the composition and distribution of winter predator communities and investigated the physical and biological influences on community structure. Seabirds and marine mammals clustered into 3 communities: an ice-associated community represented by Adélie penguins and crabeater seals; a diverse marginal ice zone community dominated by fur seals and several species of seabirds including 3 petrels, kelp gulls *Larus dominicanus*, and Antarctic terns *Sterna vittata*; and an open water community consisting of southern fulmars *Fulmarus glacialis* and 4 species of petrels. These communities were distributed along an environmental gradient ranging from ice-covered, cold, saline water to ice-free, warmer, and fresher water with greater chlorophyll concentrations. Predator communities were also associated with different communities of macrozooplankton: ice-associated predators with an extremely diverse assemblage of typically mesopelagic zooplankton; marginal ice zone predators with a community of large-bodied euphausiids (*E. superba*, *E. crystallophias*); and open water predators with a community of small-bodied euphausiids (*Thysanoessa macrura*). Our synthesis of integrated winter predator and macrozooplankton communities relative to sea-ice concentration provides reference points for future ecosystem assessments within this rapidly changing region.

KEY WORDS: Seabird · Marine mammal · Polar regions · Biogeography · Sea ice · Zooplankton · Krill

1. INTRODUCTION

The marine ecosystem surrounding the Antarctic Peninsula is highly productive and rapidly changing

(Clarke et al. 2007, Montes-Hugo et al. 2009). Integrated assessments and syntheses across trophic levels will help us better understand variability of the ecosystem and potential impacts of climate

*Corresponding author: jarrod.santora@noaa.gov

change, such as effects of phenological shifts and carry-over effects between seasons. Variability in the spring biomass and distribution of Antarctic phytoplankton, abundance and diversity of zooplankton, and population dynamics of upper trophic level species (e.g. reproductive success and recruitment) are controlled, in part, by physical and biogeochemical processes during the preceding winter (Hinke & Trivelpiece 2011, Saba et al. 2014, Meyer et al. 2017). However, systematic ecosystem surveys have focused on austral spring and summer due to more favorable weather. Thus, there is a paucity of information on winter ecosystem dynamics (i.e. diversity and distribution of communities). Since climate-related effects will likely accelerate and percolate through the ecosystem, it is important to document what these effects are, including anthropogenic stressors.

The effects of climate change and fisheries pressure near the northern Antarctic Peninsula are increasing faster in winter than in other seasons. Atmospheric temperatures around the Antarctic Peninsula increased faster than anywhere else in the southern hemisphere over the last 50 yr, with the most rapid warming occurring during austral winter (Jones et al. 2019, Ducklow et al. 2022). Warmer winters, combined with stronger winds, have reduced the duration of sea-ice coverage in the region by an average of >90 d yr^{-1} (Ducklow et al. 2013), leading to reduced biodiversity and biomass at the base of the food web, including phytoplankton, microzooplankton, and larval fish (Lin et al. 2021, Corso et al. 2022). Further, recent record low winter sea-ice coverage in the Antarctic Peninsula suggests that the rate of warming and overall resilience of the marine ecosystem may have been underestimated (Purich & Doddridge 2023). These winter ecosystem changes have negatively impacted predator populations, including those of penguins (Trivelpiece et al. 2011) and fur seals (Krause et al. 2022, Forcada et al. 2023) that had been recovering. Concurrently, the annual commercial catch of Antarctic krill *Euphausia superba* increased 4-fold from 2010 to 2020 (Kawaguchi & Nicol 2020). As winter sea-ice extent and concentration decrease, the winter fishery activities have expanded farther south and have become more spatially concentrated (Nicol & Foster 2016). This spatial shift has resulted in greater overlap between fisheries and predators at local scales (Hinke et al. 2017). The increasing overlap between commercial fisheries, and foraging seals and penguins, brings into question whether negative impact on predators will increase or decrease (Watters et al. 2020). Effective

ecosystem-based management of the Antarctic Peninsula is thus hindered by limited data on winter-time community structure and foraging interactions among species (Bestley et al. 2020).

The winter communities of seabirds and marine mammals in the northern Antarctic Peninsula is a mix of overwintering and seasonal members (Santora 2014). These species include a variety of ice-obligate, ice-avoidant, and intermediate species. Ice-obligate (pagophilic) species consist primarily of swimmers, such as crabeater seals *Lobodon carcinophaga*, Adélie penguins *Pygoscelis adeliae*, and leopard seals *Hydrurga leptonyx*. Most of these either follow the ice edge north as it advances in winter (Thiebot et al. 2019) or remain in the pack ice (Burns et al. 2004) all year. Pagophilic predators exploit prey resources associated with pack ice and rely on ice floes to haul out for rest, avoid predators, and reproduce (Southwell et al. 2003, Ainley et al. 2017, Bester et al. 2017). The ice-avoidant (open water) species include several fulmarine petrels, such as southern fulmars *Fulmarus glacialis*, cape petrels *Daption capense*, and blue petrels *Halobaena caerulea*. This guild is abundant in the region during the austral summer (Santora & Veit 2013, Warwick-Evans et al. 2021), but many individuals migrate farther north in winter (Delord et al. 2016). These seabirds have broader wing morphology adapted for efficient flight in strong, consistent winds (Ainley et al. 1993). In contrast, intermediate between these 2 guilds, snow petrels *Pagodroma nivea* and Antarctic petrels *Thalassoica antarctica* have narrower wings and forage in areas of marginal ice coverage (Santora 2014). During winter, they are largely confined to the marginal ice zone (Delord et al. 2016, 2020).

At fine spatial scales (<10 km), the structure of the top predator community of the Antarctic Peninsula in winter is driven by both physical (sea-ice coverage) and biological (prey abundance and distribution) factors (Fraser & Ainley 1986, Reiss et al. 2017). The mesoscale (10s to 100s km) distribution of macrozooplankton communities is more geographically consistent in winter than summer, independent of ice conditions (Dietrich et al. 2021), whereas the fine-scale distribution of seabird communities dynamically responds to ice coverage in all seasons (Ainley et al. 1993). Five winter communities of macrozooplankton have previously been identified in this region (Dietrich et al. 2021). Two of these communities contain smaller euphausiids (*Thysanoessa macrura*, *Euphausia frigida*, *E. triacantha*) and amphipods (*Primno*, *Themisto*) and occupy the region offshore of the shelf, north and west of

the South Shetland Islands. Within the Bransfield Strait, a community dominated by large euphausiids (*E. superba*, *E. crystallorophias*) occurs in the western part of the strait, while a highly diverse assemblage including chaetognaths, *Calanoides acutus*, and siphonophores occurs in the eastern strait. A fifth macrozooplankton community is ubiquitous within this region and contains pelagic tunicates (*Salpa thompsoni*) and gastropods (*Clione limacina*). If the distribution of prey communities influences structure of predator communities, then we would expect associations between the open water seabird guild and the off-shelf macrozooplankton communities (called 2a and 2b by Dietrich et al. 2021), as well as the pagophilic penguin/pinniped predator community with the Bransfield Strait macrozooplankton communities (called 3a and 3b by Dietrich et al. 2021). Conversely, if the physical factors influencing predator community distribution at the fine-scale also drive mesoscale patterns, then predator communities would be associated directly with ice coverage (and perhaps hydrology) rather than macrozooplankton communities.

Here, we investigated the ecological determinants of top predator community structure in the Antarctic Peninsula during winter (August to September) using data from 5 consecutive ecosystem surveys in 2012–2016. The study period coincided with several high and low sea-ice years, and captured natural variability in the extent and distribution of the winter marginal ice zone habitat within the northern Antarctic Peninsula marine ecosystem (Santora 2014, Reiss et al. 2017, Dietrich et al. 2021). Antarctic sea ice reached a record high in 2014, before the current regime of rapid declines (Parkinson 2019), and an extreme El Niño event in 2015/2016 had substantial impacts on phytoplankton and zooplankton communities (Costa et al. 2021, Walsh & Reiss 2023). We clustered top predator observations into distinct communities following the methods used for macrozooplankton communities from the same surveys (Dietrich et al. 2021). We quantified associations between the top predator communities and (1) physical environmental factors and (2) macrozooplankton communities to test the hypothesis that community structure at lower trophic levels, combined with sea-ice extent, determines community structure at higher trophic levels. Our winter ecosystem observations have potential implications for future climate and fishery impact assessments that emphasize relationships between the physical environment, macrozooplankton distribution, and top predator community structure.

2. MATERIALS AND METHODS

2.1. Survey area data

2.1.1. Survey design

We surveyed the South Shetland Island and Elephant Island regions during the austral winters (August to September) of 2012–2016 as part of the US Antarctic Marine Living Resources (AMLR) program aboard the RV Ice Breaker (RVIB) 'Nathaniel B. Palmer' (Fig. 1). The main objectives of the survey were to map hydrographic conditions, study the distribution and abundance of fish, krill, and other zooplankton through acoustic methods and net hauls, and describe the spatial distribution of seabirds and marine mammals. We followed methods consistent with the long-term austral summer surveys conducted by the US AMLR program (Reiss et al. 2017). We sampled between 33 and 108 stations per year, dependent on ice conditions. Stations were spaced approximately 25–30 km apart, and the full survey area covered an area of approximately 120 000 km².

2.1.2. Visual surveys

Sighting surveys for seabirds and marine mammals were conducted from the bridge of the ship, following established methodologies described in a previous study (Santora 2014). Two observers collected observations simultaneously during daylight hours. One observer recorded seabirds, while the other scanned for marine mammals in the water and on the ice using binoculars. Observers used 10 × 50 binoculars and image-stabilized 20 × 60 binoculars. The pilot house/bridge of the RVIB 'Nathaniel B. Palmer' is 54 ft (~16.5 m) above sea level. Observations only stopped when the ship could not move forward through the sea ice, and no observations were made during station sampling.

During each survey, we continuously monitored and classified sea-ice conditions according to the international sea-ice protocol (ASPeCt) (Worby & Allison 1999, Santora 2014, Reiss et al. 2017). This involved estimating the percentage of ice cover on a scale of 0 to 10, where 0 is open water and 10 is complete ice coverage (fully consolidated). We also identified different types of ice, including first-year, multi-year, and thin gray ice. An automatic logger recorded the ice conditions every 10 s, updated by the observer as conditions changed.

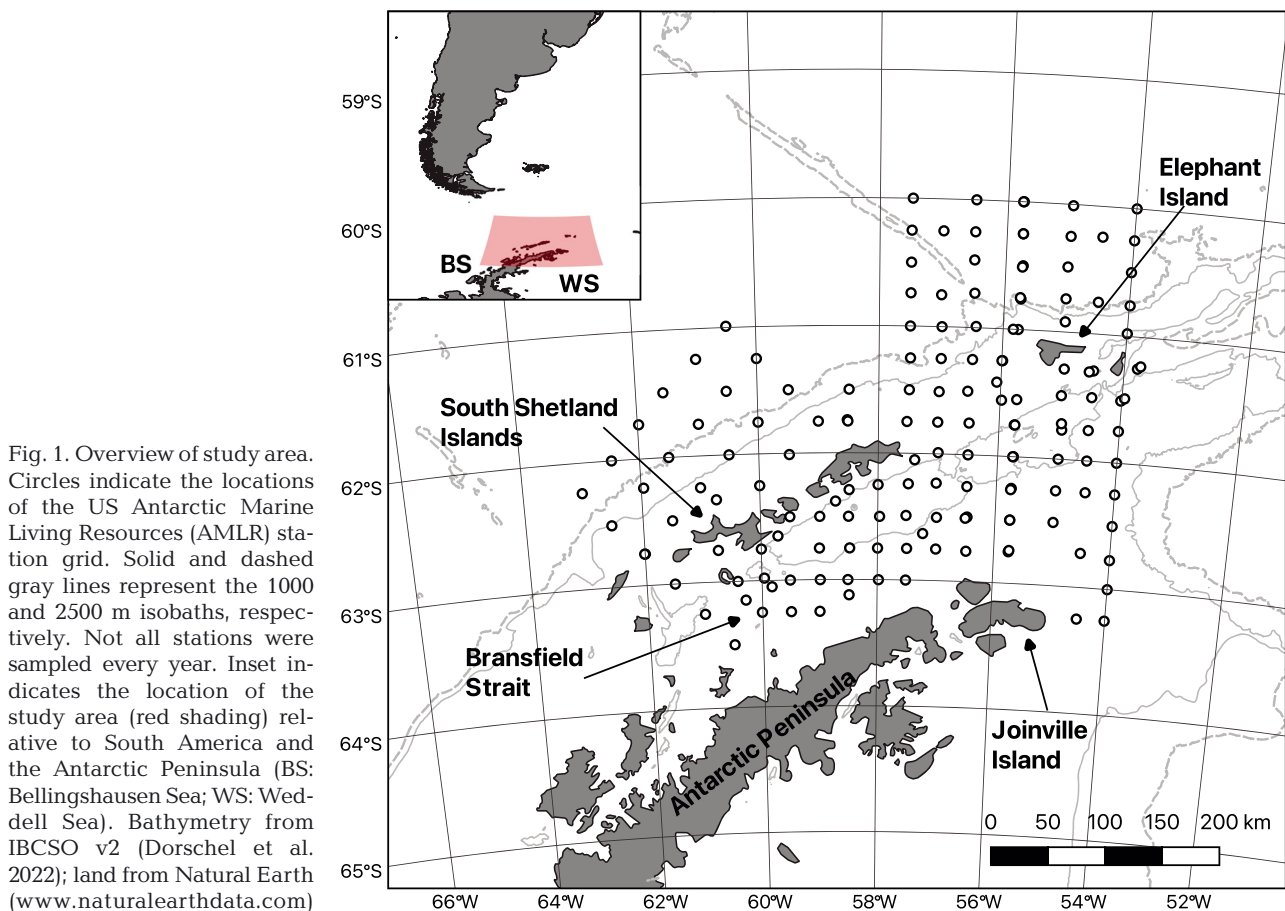


Fig. 1. Overview of study area. Circles indicate the locations of the US Antarctic Marine Living Resources (AMLR) station grid. Solid and dashed gray lines represent the 1000 and 2500 m isobaths, respectively. Not all stations were sampled every year. Inset indicates the location of the study area (red shading) relative to South America and the Antarctic Peninsula (BS: Bellingshausen Sea; WS: Weddell Sea). Bathymetry from IBCSO v2 (Dorschel et al. 2022); land from Natural Earth (www.naturalearthdata.com)

2.1.3. Hydrology

We measured hydrology at each survey station. Conductivity and temperature in the water column were measured using a Sea-Bird Inc. SBE-9/11+ CTD profiler (Table 1). We used Niskin sampling bottles to collect water samples for measuring chlorophyll *a* (chl *a*) and phaeopigment concentrations (Table 1). For full details, see Dietrich et al. (2021).

2.2. Statistical analysis

We standardized our data to integrate visual surveys (line transects) with oceanographic sampling stations (discrete points). First, we aggregated all transect observations (relative abundance counts of seabirds and mammals, and ice conditions) into 1.85 km bins. We then associated each sampling station with all transect intervals conducted within 15 km and 3 d of the station to form 'sites'. We excluded intervals farther in space or time than 15 km and 3 d from a sample station from the community analysis. After

associating transect intervals and sample stations in sites, we aggregated the relative predator abundance and ice conditions of each site. We normalized relative predator abundance by sampling effort (ind. km^{-1}), then applied a pseudo-log transformation (i.e. $\log_{10}(x + 1)$) to minimize the influence of highly abundant taxa. The analysis of macrozooplankton in these surveys (Dietrich et al. 2021) excluded taxa observed at fewer than 5% of sample stations; the seabird and marine mammal assemblage is much less diverse than macrozooplankton, so we did not exclude any species. We aggregated ice conditions across intervals within a site as the most frequent ice type (open, thin, first-year, or multi-year sea ice) and mean percent coverage.

We assessed the community structure from relative abundance data using cluster and ordination analyses. First, we calculated a Bray-Curtis dissimilarity matrix using the R package 'vegan' (Oksanen et al. 2022) to estimate dissimilarities in species composition between sites. We then generated hierarchical clusters using Ward's minimum variance linkage method, implemented in the R package 'cluster'

Table 1. Environmental variables measured during survey. Hydrographic variables (upper mixed layer [UML] depth, temperature, salinity, chlorophyll *a* [chl *a*], and phaeopigment) were collected at sampling stations. Ice variables (type and coverage) were collected along transects and associated with the nearest station. Macrozooplankton communities were classified based on net tows collected at the sampling stations (see Dietrich et al. 2021)

Variable	Description	Collection location
UML depth (m)	Depth at which the density differed by 0.05 kg m ⁻³ from the average density of the upper 10 m of the water column (Mitchell & Holm-Hansen 1991)	Station
Temperature (°C)	Average UML temperature	Station
Salinity (PSU)	Average UML salinity	Station
Chl <i>a</i> (mg m ⁻²)	Average integrated chl <i>a</i> to 100 m from bottles	Station
Phaeopigment (mg m ⁻²)	Average integrated phaeopigment to 100 m from bottles	Station
Ice type	Factor with 4 levels: open, thin, first-year, multi-year	Transect
Ice coverage	Percent cover	Transect
Macrozooplankton community	Factor with 5 levels corresponding to the clusters identified by Dietrich et al. (2021): 1 (<i>Salpa</i> and <i>Clione</i>), 2a (small <i>Euphausia</i> , myctophid larvae, and amphipods), 2b (<i>Thysanoessa</i>), 3a (extremely diverse, including siphonophores, chaetognaths, copepods), and 3b (<i>E. superba</i> and <i>E. crystallorophias</i>)	Station

(Maechler et al. 2022), applied to the dissimilarity matrix. We determined the optimal number of clusters (*k*) to retain from the hierarchy using the gap statistic (Tibshirani et al. 2001). The gap statistic compares the within-cluster variation of different values of *k* to their expected values under a null reference distribution. The gap statistic, *f*, usually increases with *k*, but exhibits a shoulder at the optimal number of clusters. A recommended heuristic for finding the shoulder is selecting the smallest *k* such that the gap statistic for *k*, *f*(*k*), is greater than the gap statistic for *k* + 1 less the standard error, *s*:

$$f(k) > f(k+1) - s(k+1) \quad (1)$$

We described each predator cluster with a smaller number of indicator species. Using the R package 'labdsv', we calculated indicator values, *d*, which indicate the relative affinity of a species to a particular cluster (Dufrêne & Legendre 1997, Roberts 2019). The indicator value for species *i* in cluster *c*, *d*_{*ic*}, is the product of relative frequency, *f*_{*ic*}, and relative abundance, *a*_{*ic*}, where *f*_{*ic*} is the fraction of sites in *c* where *i* was present and *a*_{*ic*} is the ratio of per-site abundance of *i* in *c* to the overall per-site abundance of *i*. *d* ranges between 0 and 1, where values close to 1 indicate a species that was ubiquitous within the cluster and highly abundant relative to other clusters. Indicator values ≥ 0.25 were retained as significant indicators.

To explore the relationship between community structure and the environment, we reduced the dimensionality of the community data using non-metric multidimensional scaling (NMDS). For this purpose,

we used the same Bray-Curtis dissimilarity matrix from the cluster analysis. We determined the number of NMDS axes to retain by examining a scree plot, which plots overall stress of the fit against the number of axes, and assessed quality of fit using a Shepard diagram, which plots the dissimilarity distances in the reduced space against the original dissimilarity distances. We chose the smallest number of axes with stress < 0.2 and examined the correlation in the Shepard diagram for goodness of fit.

We used linear regression to quantify the relationship between the retained NMDS axes and the environmental, biological, and temporal variables. We performed this analysis with the 'envfit()' function in the 'vegan' package, which treats environmental variables as the response variables and NMDS ordination scores as the predictors. The environmental variables included physical conditions (hydrology and ice conditions), biology (macrozooplankton community), and temporal variables (Table 1). Temporal variables included time of day of the net tow, to account for diel patterns in macrozooplankton distribution, as well as year, to account for interannual variability. The regression coefficients obtained from the analysis represent the direction and magnitude of the maximal change in community structure associated with each environmental variable. We tested for significant associations between predator and macrozooplankton communities using a chi-squared test and assessed the statistical significance of individual predator–prey community associations via post hoc analysis of the Pearson residuals.

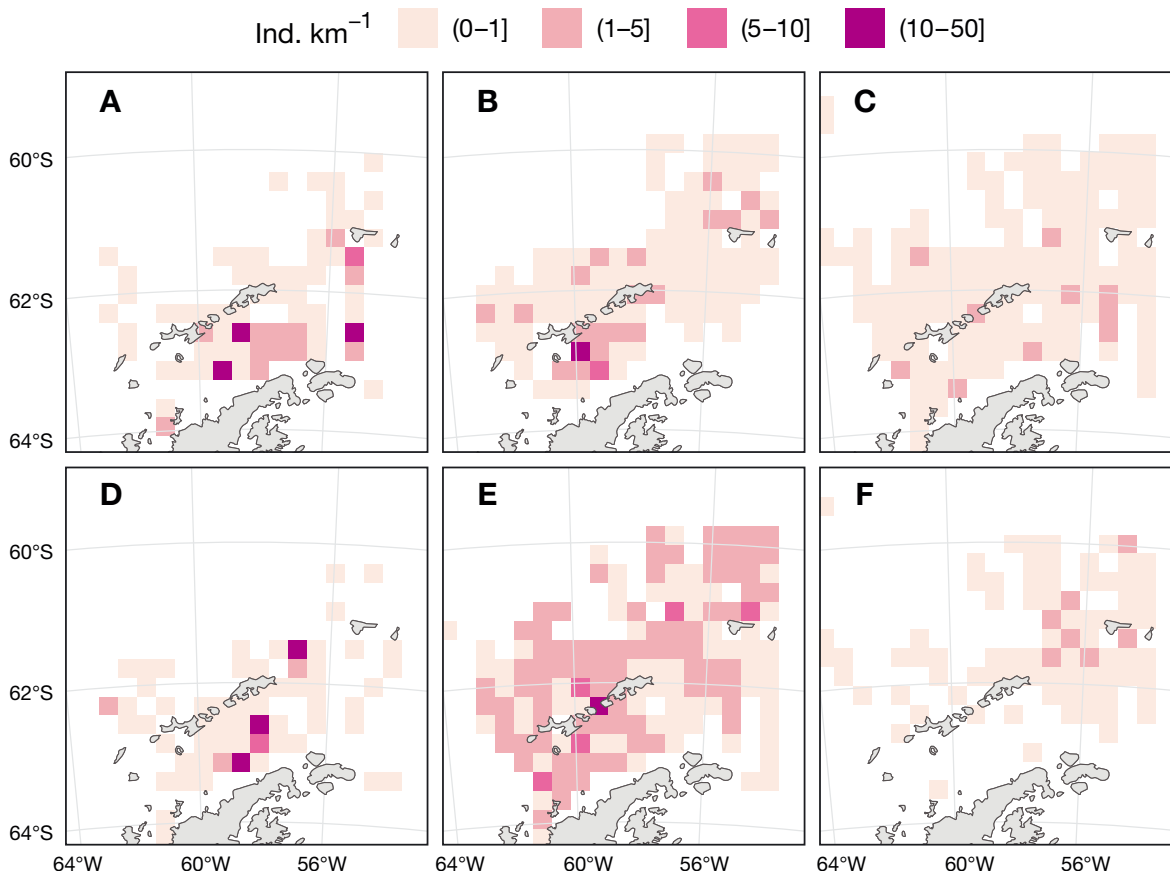


Fig. 2. Geographic distributions of the 6 most abundant species observed during the surveys, averaged across survey years: (A) Adélie penguin, (B) Antarctic fur seal, (C) Antarctic petrel, (D) crabeater seal, (E) snow petrel, (F) southern fulmar. Unlike the cluster analysis, these maps aggregate sightings from all visual surveys within the study area. The sightings associated with sites are a subset of these (i.e. sightings more than 15 km or 3 d from a sampling station are included here)

3. RESULTS

3.1. Visual surveys

During the 5 survey years, we sighted a total of 22 species of seabirds and marine mammals (Table 2). The most abundant species were snow petrels, Adélie penguins, and Antarctic fur seals. The most widespread species observed were snow petrels, Antarctic petrels, and southern giant petrels. The 6 most abundant species (total individuals observed in Table 2) averaged across years were widely distributed across the study region, although densities varied by species (Fig. 2). Distribution maps of all seabird (Fig. S1) and marine mammal species (Fig. S2) are provided in the Supplement at www.int-res.com/articles/suppl/m738p057_supp.pdf. We observed predators in proximity (15 km, 3 d) to 245 sampling stations, ranging from 19 stations in 2012 to 68 stations in 2014. Each station was associated with 30.2 ± 10.3 km (mean $\pm$ SD) of visual survey effort (Table S1).

With the exception of 2012, when sampling was most limited, ice conditions observed during visual surveys exhibited more interannual variability in type (multi-year ice, first-year ice, thin ice, open water) than percent coverage. In 2012, surveys were restricted to the northernmost part of the survey region, and open water was the most common type (93.3%). In the other survey years, the most common ice type was thin ice (2013, 2015, and 2016) or first-year ice (2014) (Table S1). Ice coverage was relatively consistent within ice types across years. Overall, sites categorized as open water had ice coverage of $6.4 \pm 1.6\%$; thin ice and first-year ice sites had coverage of 55.6 ± 3.2 and $57.0 \pm 3.2\%$ (mean $\pm$ SE) (Table S1).

3.2. Predator clusters

We retained 3 predator clusters from the hierarchical analysis, which we refer to as the 'pack ice', 'marginal ice', and 'open water' communities based on

Table 2. Predator species observed during surveys. Ind.: total individuals observed; Sites: number of sites where species was present; Freq: percentage of sites where species was present. Typical prey and foraging behavior are presented for context

Species	Ind.	Sites	Freq (%)	Typical prey	Foraging behavior	Reference
Snow petrel <i>Pagodroma nivea</i>	12314	233	59.1	Myctophids	Surface feeding (<5 m)	Spear & Ainley (1998), Delord et al. (2016)
Antarctic petrel <i>Thalassoica antarctica</i>	2351	209	53.0	Myctophids, krill, squid	Surface feeding (<5 m)	Spear & Ainley (1998), Delord et al. (2020)
Southern giant petrel <i>Macronectes giganteus</i>	620	177	44.9	Juvenile pinnipeds and seabirds, carrion	Scavenging, surface feeding (<5 m)	Hunter (1983)
Antarctic fur seal <i>Arctocephalus gazella</i>	5443	152	38.6	Krill, myctophids	Diving (~15–50 m)	Staniland et al. (2011)
Kelp gull <i>Larus dominicanus</i>	679	127	32.2	Limpets, krill	Surface feeding (<5 m)	Silva et al. (2001)
Southern fulmar <i>Fulmarus glacialisoides</i>	1089	108	27.4	Myctophids, krill, squid	Surface feeding (<5 m)	Ridoux & Offredo (1989), Spear & Ainley (1998)
Cape petrel <i>Daption capense</i>	544	84	21.3	Krill, myctophids	Surface feeding (<5 m)	Ridoux & Offredo (1989), Spear & Ainley (1998)
Adélie penguin <i>Pygoscelis adeliae</i>	8532	68	17.3	Krill	Diving (~15–50 m)	Cimino et al. (2016), Juárez et al. (2018)
Crabeater seal <i>Lobodon carcinophagus</i>	3112	58	14.7	Krill	Diving (~50–200 m)	Burns et al. (2004), Hückstädt et al. (2012)
Blue petrel <i>Halobaena caerulea</i>	655	53	13.5	Krill, myctophids, amphipods	Surface feeding (<5 m)	Prince (1980)
Leopard seal <i>Hydrurga leptonyx</i>	195	49	12.4	Seals, penguins, fish, krill	Diving (~50–100 m)	Walker et al. (1998), Casaux et al. (2009), Krause et al. (2015)
Antarctic tern <i>Sterna vittata</i>	157	37	9.4	Krill, myctophids	Surface feeding (<5 m)	Croxall & Prince (1980), Ainley et al. (1992)
Pale-faced sheathbill <i>Chionis albus</i>	31	25	6.3	Carrion	Scavenging	Favero (1996)
Minke whale <i>Balaenoptera bonaerensis</i>	43	17	4.3	Krill	Diving (~5–100 m)	Friedlaender et al. (2014)
Weddell seal <i>Leptonychotes weddellii</i>	19	16	4.1	Fish, squid	Diving (~100–350 m)	Testa (1994), Lake et al. (2003)
Gentoo penguin <i>Pygoscelis papua</i>	142	12	3.0	Krill, fish	Diving (~25–100 m)	Croxall & Prince (1980), Cimino et al. (2016)
Elephant seal <i>Mirounga leonina</i>	17	11	2.8	Myctophids, squid	Diving (~200–800 m)	Guinet et al. (2014), Daneri et al. (2015)
Killer whale <i>Orcinus orca</i>	48	5	1.3	Whales, seals, toothfish, penguins	Complex and diverse	Pitman & Ensor (2003)
Emperor penguin <i>Aptenodytes forsteri</i>	4	2	0.5	Krill, silverfish	Diving (~50–300 m)	Kirkwood & Robertson (1997), Rodary et al. (2000)
Southern bottlenose whale <i>Hyperoodon planifrons</i>	5	2	0.5	Squid	Diving (>500 m)	MacLeod et al. (2003)
Antarctic shag <i>Leucocarbo bransfieldensis</i>	89	1	0.3	Demersal fish	Diving (<50 m)	Casaux & Barrera-Oro (2006)
Ross seal <i>Ommatophoca rossii</i>	1	1	0.3	Myctophids, squid	Diving (~100–300 m)	Blix & Nordøy (2007), Southwell et al. (2012)

Table 3. Indicator species for each predator cluster. Indicator values are the product of relative frequency and relative abundance, ranging from 0 to 1. Only species with indicator values ≥ 0.25 are shown for each cluster. See Section 2 for details

Predator cluster	Indicator species	Indicator value
Marginal ice	Antarctic fur seal	0.84
	Snow petrel	0.48
	Kelp gull	0.37
	Southern giant petrel	0.36
	Antarctic tern	0.32
	Antarctic petrel	0.29
Open water	Southern fulmar	0.42
	Antarctic petrel	0.41
	Snow petrel	0.34
	Cape petrel	0.28
	Southern giant petrel	0.25
Pack ice	Adélie penguin	0.37
	Crabeater seal	0.30

their indicator species (Table 3) and relationships to sea-ice coverage (Fig. 3). See Fig. S3 for the gap statistic curve, which we used to identify the optimal number of clusters.

The marginal ice community had the greatest number of indicator species (6) and the highest indi-

cator values (Antarctic fur seals: 0.84; snow petrels: 0.48). The highest indicator value in the open water cluster belonged to southern fulmars (0.42), closely followed by 4 other species of petrels. The marginal ice and open water clusters shared 3 indicator species: snow petrel, Antarctic petrel, and southern giant petrel. The pack ice cluster had only 2 indicator species: Adélie penguins (0.37) and crabeater seals (0.30).

Predator densities varied among clusters (Table S2). Snow petrels and Adélie penguins had the greatest overall density across clusters (1.665 and 1.153 ind. km^{-1} , respectively), though their densities were greatest in the marginal ice zone (3.116 and 4.036 ind. km^{-1} , respectively). Other abundant predators in the marginal ice zone included Antarctic fur seals (2.892 ind. km^{-1}), crabeater seals (0.437 ind. km^{-1}), Antarctic petrels (0.258 ind. km^{-1}), and kelp gulls (0.158 ind. km^{-1}). Antarctic fur seals and snow petrels were ubiquitous in the marginal ice cluster (observed at 100.0 and 96.3% of sites, respectively). Despite their high densities, Adélie penguins were only observed at 42.6% of sites in the marginal ice cluster (compared to 67.9% of pack ice sites).

Crabeater seals and Adélie penguins were the most abundant predators in the pack ice cluster (1.380

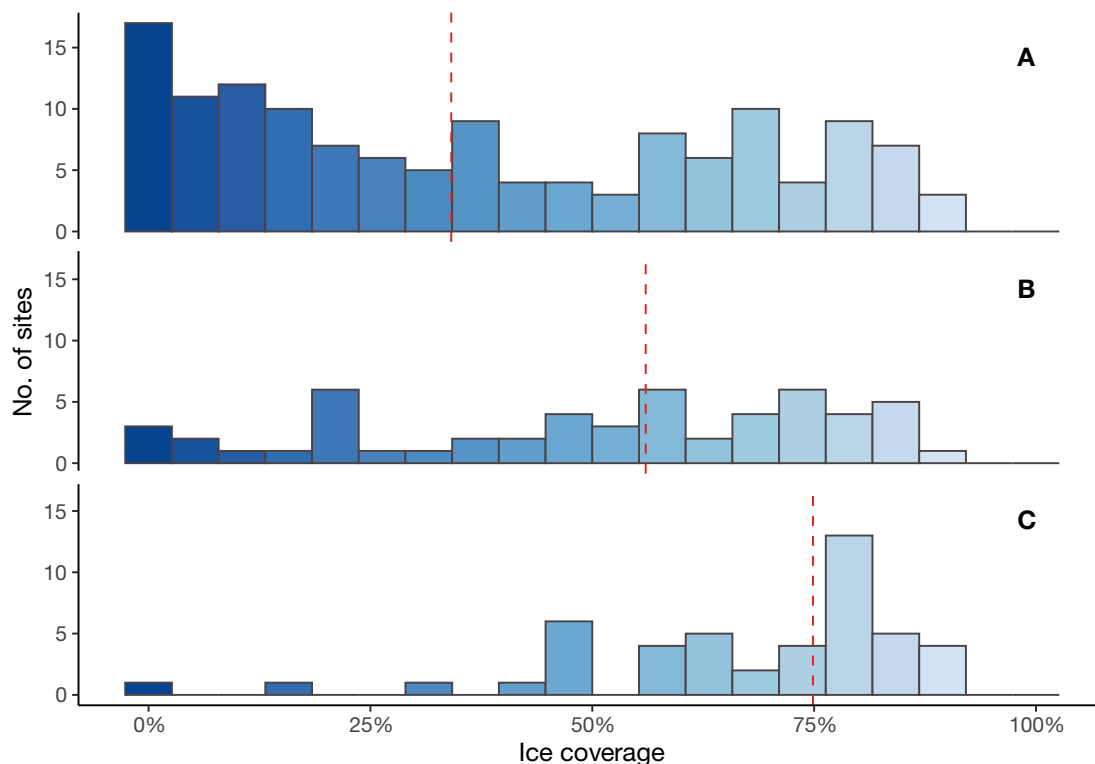


Fig. 3. Distribution of sea-ice coverage among sites, by predator cluster: (A) open water, (B) marginal ice, (C) pack ice. Dashed red line: median ice coverage

and 0.948 ind. km⁻¹), followed by snow petrels (0.463 ind. km⁻¹), Antarctic petrels (0.177 ind. km⁻¹), Antarctic fur seals (0.121 ind. km⁻¹), and kelp gulls (0.108 ind. km⁻¹). Whereas 5 species were observed at 70% or more of the marginal ice sites, only snow petrels (92.5%) were observed at 70% or more of the pack ice sites. Predator densities were lower in the open water cluster. The most abundant predators, snow petrels (1.554 ind. km⁻¹) and Antarctic petrels (0.404 ind. km⁻¹), were also the most prevalent (95.7 and 92.8% of sites, respectively). Antarctic fulmars (0.240 ind. km⁻¹, 59.4% of sites) and blue petrels (0.125 ind. km⁻¹, 32.6% of sites) were observed in greater densities and at higher frequencies in the open water cluster than other clusters. Cape petrels were observed with greater frequency in the open water cluster (47.8% of sites) than the marginal ice (20.4%) and pack ice (13.2%), but their densities were greater in the marginal ice (0.116 ind. km⁻¹) than the open water (0.084 ind. km⁻¹) cluster.

The open water community was observed most frequently (56.3% of sites), followed by the marginal ice (22.0%) and pack ice (21.6%) communities (Table 4), with variability between years related to the spatial distribution of sea ice (Fig. 4). Geographically, in general, the open water community occupied the northern offshore regions and the gap between

Table 4. Relative frequency of predator communities by year. No.: number of sites assigned to each cluster; Freq.: relative frequency of that cluster

Year	Predator cluster					
	Open water		Marginal ice		Pack ice	
	No.	Freq. (%)	No.	Freq. (%)	No.	Freq. (%)
2012	14	73.68	3	15.79	2	10.53
2013	25	53.19	11	23.40	11	23.40
2014	39	57.35	14	20.59	15	22.06
2015	39	65.00	8	13.33	13	21.67
2016	21	41.18	18	35.29	12	23.53
Total	138	56.33	54	22.04	53	21.63

Elephant Island and the rest of the Shetland Islands (Fig. 5). We found predators characteristic of the marginal ice community in the western Bransfield Strait and north of Elephant Island. The pack ice community primarily occupied the eastern Bransfield Strait.

3.3. Environmental determinants of community structure

We retained 3 NMDS axes for investigating the relationships between the environment and community structure of predators (stress = 0.135). Two vari-

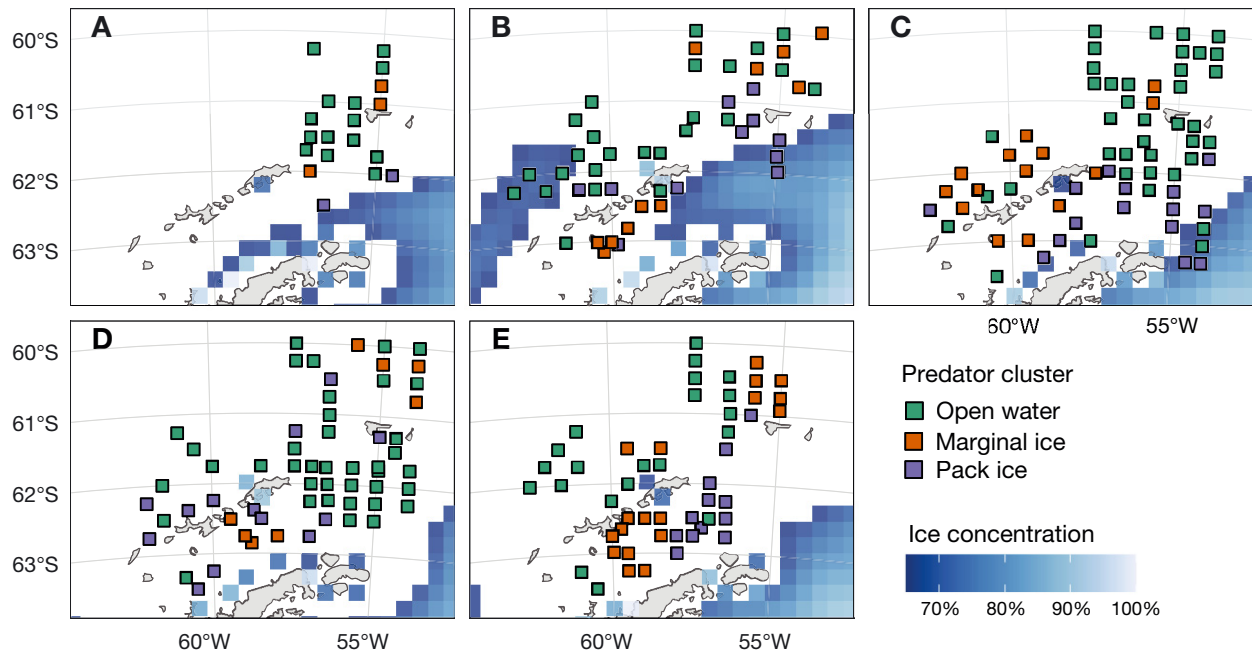


Fig. 4. Geographic distribution of predator communities in each survey year (A–E: 2012–2016, respectively). Areas of extensive sea-ice coverage are indicated by blue gradient, where satellite-derived mean sea-ice coverage in the month of August in each year exceeded 65%

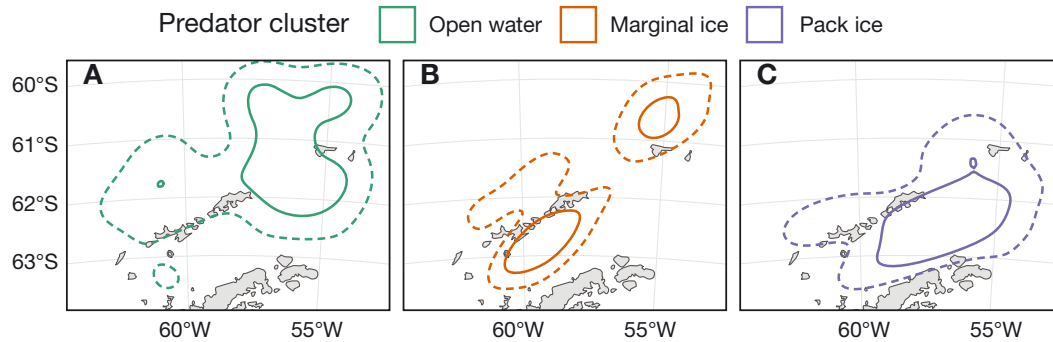


Fig. 5. Geographic distribution of predator communities across survey years (2012–2016). Solid and dashed lines indicate the 50 and 95% contours of the kernel density estimate for each cluster, pooling sites from all years

ables, sampling year and ice coverage, were significantly correlated with the ordination scores ($p = 0.002$ and 0.013 , respectively), although the effect size was small ($r^2 = 0.061$ and 0.054 , respectively; Table 3; see Table S3 for the coefficient, r^2 , and p -values of the environmental fit regression). The pack ice cluster occupied a wide range of values on NMDS axis 1, overlapping with the other 2 clusters (Fig. 6). The marginal ice and open water clusters were well separated by NMDS axis 2.

The predator clusters differed in temperature, salinity, and chl a , but not by mixed layer depth or phaeopigment (Table 5). Relative to the open water community, the pack ice community was associated with colder, more saline water with lower chl a concentra-

tions. The marginal ice community occupied intermediate habitats.

The predator clusters were significantly associated with macrozooplankton clusters (χ^2 test, $p < 0.001$). Five pairwise associations of predators with prey were significant after applying Bonferroni correction (Table 6). The pack ice community was positively associated with macrozooplankton community 3a (an extremely diverse assemblage associated with cold, high-salinity water) and negatively associated with cluster 2b (*Thysanoessa macrura*). The marginal ice community was positively associated with macrozooplankton community 3b (large krill, including *Euphausia superba*). The open water predator community was positively associated with cluster 2b and

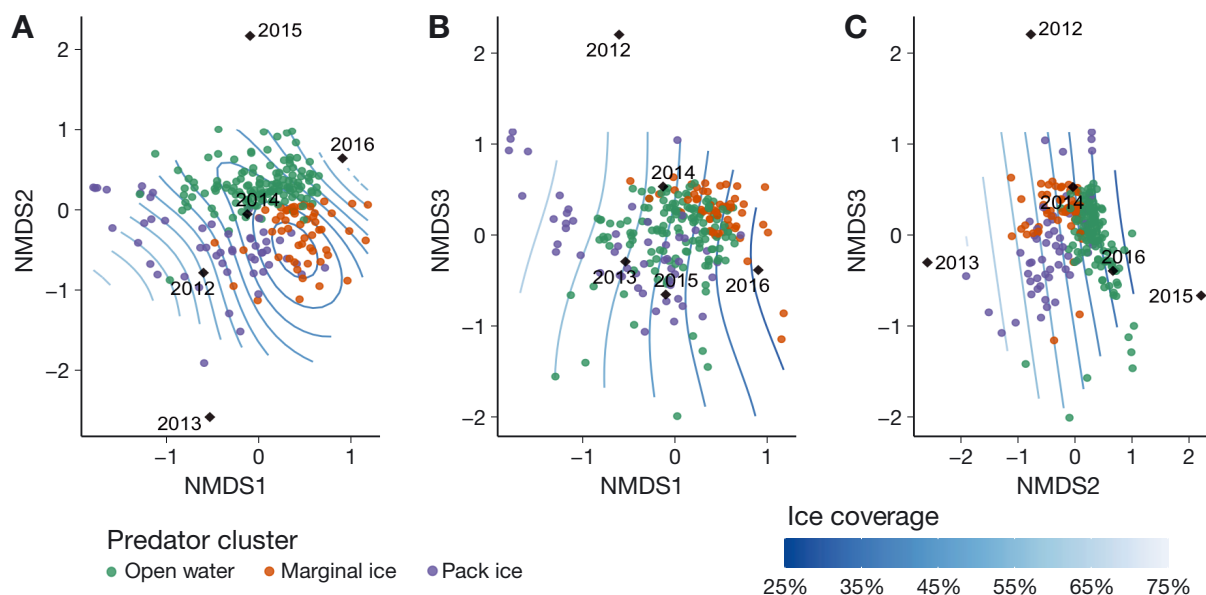


Fig. 6. Distribution of sites and environmental loadings in non-metric multidimensional scaling (NMDS) ordination: (A) first and second NMDS axes, (B) first and third NMDS axes, (C) second and third NMDS axes. Black diamonds indicate centroids of survey years, and contours represent the fitted surface of sea-ice coverage. Sites are color-coded by predator cluster assignment

Table 5. Summary of environmental conditions associated with predator clusters. See Table 1 for descriptions of environmental variables. Environmental variables that differed significantly ($p < 0.05$) between clusters are indicated with an asterisk (Kruskal-Wallis test with Bonferroni correction)

Variable	Predator cluster								
	Open water			Marginal ice			Pack ice		
	Mean	Q1	Q3	Mean	Q1	Q3	Mean	Q1	Q3
UML depth (m)	99.5	64.8	118	120	73.0	139	126	72.0	174
Temperature ($^{\circ}\text{C}$) [*]	−1.73	−1.82	−1.69	−1.73	−1.81	−1.69	−1.80	−1.84	−1.76
Salinity (PSU) [*]	34.1	33.9	34.2	34.2	34.1	34.3	34.3	34.1	34.4
Chl <i>a</i> (mg m^{-2}) [*]	13.4	8.63	16.4	13.0	7.98	16.9	9.39	5.76	13.1
Phaeopigment (mg m^{-2})	3.73	2.24	4.96	3.30	1.67	4.14	2.96	1.13	3.72

Table 6. Contingency table of predator and macrozooplankton clusters. Macrozooplankton cluster names (1, 2a, 2b, 3a, 3b) from Dietrich et al. (2021). Significant differences ($p < 0.05$) are indicated in **bold** with asterisks (post hoc analysis of the Pearson residuals)

Predator cluster	1		2a		2b		3a		3b	
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
Open water	55	58.6	41	33.8	33*	22.5*	7	11.8	2*	11.3*
Marginal ice	23	22.9	12	13.2	6	8.8	1	4.6	12*	4.4*
Pack ice	26	22.5	7	13	1*	8.7*	13*	4.5*	6	4.3

negatively associated with 3b. Macrozooplankton cluster 1 (a ubiquitous cluster indicated by *Salpa* and *Clione*) was not significantly associated with any predator cluster. Macrozooplankton cluster 2a (indicated by important prey species such as *E. frigida*, *E. triacantha*, myctophid larvae, and *Themisto gaudichaudii*) was also not significantly associated with any predator cluster, although it was associated most often with the open water predator cluster (Table 6).

4. DISCUSSION

We analyzed the composition and distribution of predator communities around the northern Antarctic Peninsula in winter to investigate associations among marine predators, their prey, and the physical environment. We identified 3 communities of predators, and hypothesized that the spatial organization of these communities is related to the distribution of macrozooplankton communities and a gradient in sea-ice coverage. The pagophilic community (e.g. Adélie penguins, crabeater seals) consisted of species with diets dominated by Antarctic krill (Table 2) that rely on the pack ice throughout the annual cycle (Ainley et al. 2017, Bester et al. 2017). Predators in the marginal ice zone (e.g. Antarctic fur seals, snow petrels) and in open water (e.g. southern fulmars, other petrels) communities also consume Antarctic

krill, but their diets are more diverse, with a greater reliance on fish, especially myctophids such as *Electrona antarctica* (Table 2) (Ridoux & Offredo 1989, Ainley et al. 1992, Lorentsen et al. 1998, Ferretti et al. 2001). Despite the diet overlap between these 2 communities, they tend to segregate spatially according to ice coverage due to differing foraging strategies. Marginal ice zone predators use ambush and pursuit plunging behavior to exploit prey among ice floes, which open water predators have not been observed to do (Ainley et al. 1993).

The spatial associations between ecological communities and sea-ice conditions largely supported our hypothesis that spatial associations between predator and macrozooplankton communities would fall along a sea-ice coverage gradient. Open water predators associated with an offshore zooplankton community, as predicted. Two different ice-associated predator communities emerged from our analysis: one that favors marginal sea-ice conditions and the western Bransfield Strait, and another that prefers greater sea-ice coverage and the eastern Bransfield Strait. The significant association between marginal ice predators and the *Euphausia superba*/*E. crystallorophias* zooplankton community reflects a direct trophic connection between krill predators and their prey. However, the mechanism driving the association between pack ice predators and a diverse zooplankton community indicated by chaetognaths, *Calanoides*

acutus, siphonophores, and many other taxa (called 3a by Dietrich et al. 2021) is less clear. Many of the indicator taxa for zooplankton community 3a occupy the mesopelagic in open water and marginal ice conditions, but their relative abundances in the epipelagic and surface waters increase when sea-ice coverage is greater (Ainley et al. 1986, Hopkins & Torres 1988, Bathmann et al. 1993, Flores et al. 2014). Thus, the association between pack ice predators and this macrozooplankton community is likely not a direct trophic relationship, but rather one that reflects shared habitat selection for greater sea-ice coverage.

Two non-indicator species, cape petrels and Antarctic minke whales *Balaenoptera bonaerensis*, are abundant in the northern Antarctic Peninsula during summer, yet neither emerged as an indicator species in our analysis. Cape petrels are one of the most common breeding seabirds around the Antarctic Peninsula and form dense hotspots in spring and summer (Hunt et al. 1990, Santora & Veit 2013, Warwick-Evans et al. 2021). However, in winter, the bulk of the population shifts to lower latitudes as far north as the Patagonian Shelf (Croxall & Wood 2002, Delord et al. 2016). Consistent with what is known about their habitat associations, cape petrels were more abundant in the open water community than in either of the other 2 predator communities. Nonetheless, their overall abundance was sufficiently low that they did not meet the threshold for indicator species. Previous surveys of the winter seabird assemblages around the Antarctic Peninsula observed greater abundances of cape, blue, and Kerguelen petrels in the offshore areas west and north of our study area (Whitehouse & Veit 1994, Ribic et al. 2011). Like cape petrels, Antarctic minke whales are thought to be abundant predators in the northern Antarctic Peninsula during summer; however, their preference for dense sea-ice coverage presents a substantial challenge for abundance estimation (Herr et al. 2019, Risch et al. 2019). Although part of the population migrates to lower latitudes in winter (Lee et al. 2017, Esposito et al. 2021), Antarctic minke whales are acoustically detectable at higher latitudes year-round (Dominello & Širović 2016, Filun et al. 2020). The characteristic 'bio-duck' minke call is frequently detected during austral winter east of our study region in the Weddell Sea (Filun et al. 2020) and further south along the western Antarctic Peninsula (Dominello & Širović 2016). Therefore, it is possible that Antarctic minke whales were more abundant in our study region than our data indicate, distributed in areas inaccessible to research vessels. Given the limited sample sizes and biases in our data, we cannot determine the predator community associ-

ations of Antarctic minke whales. Our analysis included 43 Antarctic minke whales: 30 individuals at 7 marginal ice sites, 8 individuals at 5 open water sites, and 5 individuals at 5 pack ice sites. This pattern of relative abundance may indicate that Antarctic minke whales are members of the marginal ice predator community (which was also associated with the prey of these species, large-bodied krill). Alternatively, Ainley et al. (2007) suggested that Antarctic minke whales are pagophilic members of the pack ice predator community, and their apparent association with marginal ice communities is the result of sampling bias due to habitat inaccessibility.

Relative to the summer seabird assemblage, the winter seabird assemblage shared some ubiquitous species (e.g. kelp gulls and southern giant petrels) but also included more southerly species that shifted northwards to the edge of the marginal ice zone (snow and Antarctic petrels broadly, and Adélie penguins in the eastern region). These latter species opportunistically forage and scavenge within the marginal ice zone. Positive associations between these ice-dependent seabirds and pinnipeds likely represent a stable foraging community and reflect concentrations of krill and other macrozooplankton within the marginal ice zone. Therefore, increases in sea-ice concentrations towards maximum coverage (no open water present) would likely shift the entire predator community further to the north, as access to open water would be limited to the south.

Our data represent a baseline of biophysical conditions during a period of relatively high sea-ice coverage compared to recent declines (Eayrs et al. 2021). Our 5 yr winter synthesis of sea ice, hydrography, macrozooplankton, and top predators is unlikely to be replicated in the near future, due to increased costs of shipboard research, reduced availability of research vessels, and prioritized sampling during the Antarctic summer. The spatial averages of community composition (i.e. predator clusters; Fig. 5) may be considered essential foraging habitats for overwintering predators. The open water assemblage occupies the most temporally variable ocean habitat that we sampled, which changes based on currents and latitudinal position of the marginal ice zone. The marginal ice habitat was considerably smaller, with 2 important concentrations: southwest part of the Bransfield Strait, and open water to the north of Elephant Island. Antarctic krill are consistently concentrated in the southern region over multiple years (Reiss et al. 2017), and stable sea-ice concentrations are more likely to occur there due to coastal ocean processes (coastal currents, formation of eddies) and shifts in ice from higher latitudes (Moffat & Meredith 2018).

We found consistently high concentrations of crabeater seals and fur seals within both marginal ice zone habitats (Figs. 2 & 4), and the presence of sea ice likely contributes by supporting haul-out habitat for seal thermoregulation and rest between foraging bouts. There were more concentrations of fur seals compared to crabeater seals within the marginal ice zone north of Elephant Island. We did not always encounter high concentrations of krill in this region, which might explain the reduction in crabeater seals, or that fur seals were targeting other forage taxa, perhaps myctophids (Daneri et al. 2005, Polito & Goebel 2010, Descalzo et al. 2023), that our net hauls were inadequate at catching.

Comparatively, the marginal ice zone habitat north of Elephant Island is likely more hydrographically dynamic and less stable or predictable as suitable foraging habitat for ice-obligate species, compared to the southern Bransfield Strait. Within the southern Drake Passage, the southern Antarctic Circumpolar Current and its associated frontal boundary likely influences the rate at which sea ice can form and accumulate within the Elephant Island area (Stammerjohn et al. 2008). Winds and ocean currents play a significant role in how sea ice forms, and ocean atmospheric conditions further to the south are more stable for facilitating sea-ice growth (Massom & Stammerjohn 2010). The pack ice community where we repeatedly encountered dense first- and multi-year ice floes was restricted to the eastern Bransfield Strait and reflects ocean conditions from the higher-latitude Weddell Sea, and where we observed some of the largest concentrations of Adélie penguins and crabeater seals. During winter, this essential foraging habitat likely reflects the only available habitat within this region, as areas to the south are mostly completely ice covered with little access to open water for diving predators. Therefore, declines in sea ice within this area would likely have significant impacts on the ecology and overwintering survival of these ice-dependent predators.

Species interactions play a key role in the community organization of marine predators (Stachowicz 2001, Veit & Harrison 2017). Identifying habitat utilization and ecological associations of individual species is crucial for establishing a robust baseline for their needs and formulating conservation strategies. However, examining habitat associations within species assemblages may provide further insights into how members of a community interact with each other (Hoffman et al. 1981, Levin et al. 2009). Further, if the presence or abundance of one species is critical to the stability and resilience of the community to

environmental change, then the changes in the abundance structure of that community need to be assessed (Stachowicz 2001, Dakos & Bascompte 2014). For example, we found a predator community within the marginal ice zone that contained flying (gulls, terns, and petrels) and diving (fur seals) predators. If the aerial predators rely on diving predators to drive prey nearer to the surface (Harrison et al. 1991, Veit & Harrison 2017), then changes in sea-ice habitat used by fur seals for haul out and rest would have additional indirect effects on the winter feeding ecology of flying seabirds within this region (Evans 1982, Veit et al. 1993, Monier et al. 2020). Our analysis of species assemblages within 3 distinct communities (i.e. open water, marginal ice, and pack ice) may provide a simplified approach to examining future changes in the entire predator community, as opposed to multiple assessments of individual species' responses to climate change. Therefore, we recommend that future studies aiming to link climate change projections, including changes in winter sea-ice concentration, assess how the 3 communities may shift or contract/expand geographically under different scenarios. Importantly, the geographic extent, environmental conditions, and macrozooplankton species associations underlying the 3 communities (Tables 4–6) are provided and can be used to develop predator community habitat models allowing for prediction in years outside of the intensive sampling period. Suggested geographic community analyses may include quantifying the habitat size and range (e.g. horizontal area and extent) of each community relative to various climate change scenarios. This community synthesis should provide helpful data for assessing climate change impacts, as well as winter-related conservation and ecosystem management needs.

There is concern that expansion of the Antarctic krill fishery into austral autumn and winter may impact the overwintering ecology of seabirds and marine mammals (Hinke et al. 2017, Watters et al. 2020, Trathan et al. 2022). Potential impacts include bycatch through fishing gear interactions, entanglement, and ship strikes, and possibly depletion of key prey patches that predators are reliant upon. Given the spatial consistency of Antarctic krill concentrations in southern Bransfield Strait during winter (Reiss et al. 2017, Dietrich et al. 2021) and the dense concentrations of pinnipeds and seabirds present within the marginal sea-ice zone, increased fishing activity within this location has potential negative consequences to the predator community. Further, as global warming exacerbates long-term reductions

in winter sea-ice concentration and extent, lower sea-ice years may allow for greater seasonal expansion of the krill fishery, thereby reducing important prey resources and creating potentially more conflicts with predators that are unable to shift their distributions.

Data availability. All data underlying this study are deposited in the US Antarctic Program Data Center (<https://doi.org/10.15784/601795>). Code required to reproduce the analysis is deposited in Zenodo (<https://doi.org/10.5281/zenodo.11397472>).

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