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

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Abstract

The Antarctic Peninsula marine ecosystem is highly productive, with large populations of commercially and ecologically important species including Antarctic krill (*Euphausia superba*), Adelié 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 glacialoides*) and 4 species of petrels. These communities were distributed along an environmental gradient ranging from ice-covered, cold, saline waters 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 community (*E. superba* , *E. crystallorophias*); 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.

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# 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 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.

Winter-time climate change near the northern Antarctic Peninsula and fisheries pressure are increasing faster 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 glacialoides*, 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, Delord et al. 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*, *E. 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.

# Materials and Methods

## Survey area data

### 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 120000 km2.

### Visual surveys

Sighting surveys for seabirds and marine mammals were conducted from the bridge of the ship, following established methodologies described in previous studies (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 though 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 & Veit 2013, 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.

### 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).

## 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. log10(*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’ (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* [Equation 1](#eq-gap-stat).

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*, *dic*, is the product of relative frequency, *fic*, and relative abundance, *aic*, where *fic* is the fraction of sites in *c* where *i* was present and *aic* 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.

# Results

# Note the path that we need to use to access our data files when rendering this document  
my\_data <- read.csv(here::here('analysis/data/raw\_data/my\_csv\_file.csv'))

plot(rnorm(10))

|  |
| --- |
| Figure 1: A plot of random numbers |

[Figure 1](#fig-demo-plot) shows how we can have a caption and cross-reference for a plot. Note that figure label and cross-references must both be prefixed with fig-

Here is an example of inline code 3.14 in the middle of a sentence.

# Discussion

# Conclusion

# Acknowledgements

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