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

Max F. Czapanskiy1,2,3, Jarrod A. Santora2,4,✉, Kimberly S. Dietrich1,2, Megan A. Cimino1,3, Elliott L. Hazen3, Christian S. Reiss5, and Richard R. Veit6

May 31, 2024

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.

1 Institute of Marine Sciences, University of California Santa Cruz  
2 Fisheries Ecology Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration  
3 Ecosystem Science Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration  
4 Department of Applied Math, University of California Santa Cruz  
5 Ecosystem Science Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration  
6 City University of New York, College of Staten Island, Biology Department

✉ Correspondence: [Jarrod A. Santora <jarrod.santora@noaa.gov>](mailto:jarrod.santora@noaa.gov)

Keywords: Biogeography; Krill; Marine mammal; Polar regions; Sea ice; Seabird; Zooplankton

# 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

## 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. 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 ± 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 ± 1.6%; thin ice and first-year ice sites had coverage of 55.6 ± 3.2 and 57.0 ± 3.2% (mean ± SE) (Table S1).

## 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 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 indicator 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 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 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.

## 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 variables, 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 (r2 = 0.061 and 0.054, respectively; Table 3; see Table S3 for the coefficient, r2, 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* concentrations. 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 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).

# 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). 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 associations 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. 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.

The winter seabird assemblage that we documented seems to suggest a shift of southerly species northwards to the edge of the marginal ice zone (snow and Antarctic petrels broadly, and Adélie penguins in the eastern region) as well as ubiquitous species, such as kelp gulls and southern giant petrels. 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.

# Figures

make\_fig\_top6map(read\_obj("topsix\_clim\_class", rast = TRUE))

|  |
| --- |
| Figure 1: 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). |

# Acknowledgements

# References

Ainley DG, Dugger KM, Toniolo V, Gaffney I (2007) [Cetacean Occurrence Patterns in the Amundsen and Southern Bellingshausen Sea Sector, Southern Ocean](https://doi.org/10.1111/j.1748-7692.2007.00109.x). Marine Mammal Science 23:287–305.

Ainley DG, Fraser WR, Sullivan CW, Torres JJ, Hopkins TL, Smith WO (1986) [Antarctic Mesopelagic Micronekton: Evidence from Seabirds That Pack Ice Affects Community Structure](https://doi.org/10.1126/science.232.4752.847). Science 232:847–849.

Ainley DG, Ribic CA, Fraser WR (1992) Does Prey Preference Affect Habitat Choice in Antarctic Seabirds? Marine Ecology Progress Series 90:207–221.

Ainley DG, Ribic CA, Spear LB (1993) [Species-Habitat Relationships Among Antarctic Seabirds: A Function of Physical or Biological Factors?](https://doi.org/10.2307/1369419) The Condor 95:806–816.

Ainley DG, Woehler EJ, Lescroël A (2017) [Birds and Antarctic sea ice](https://doi.org/10.1002/9781118778371.ch24). In: *Sea Ice*, 1st ed. Thomas DN (ed) Wiley, p 570–582

Bathmann UV, Makarov RR, Spiridonov VA, Rohardt G (1993) [Winter Distribution and Overwintering Strategies of the Antarctic Copepod Species *Calanoides* *Acutus*, *Rhincalanus* *Gigas* and *Calanus* *Propinquus* (Crustacea, Calanoida) in the Weddell Sea](https://doi.org/10.1007/BF00238360). Polar Biology 13.

Bester MN, Bornemann H, McIntyre T (2017) [Antarctic marine mammals and sea ice](https://doi.org/10.1002/9781118778371.ch22). In: *Sea Ice*, 1st ed. Thomas DN (ed) Wiley, p 534–555

Bestley S, Ropert-Coudert Y, Bengtson Nash S, Brooks CM, Cotté C, Dewar M, Friedlaender AS, Jackson JA, Labrousse S, Lowther AD, McMahon CR, Phillips RA, Pistorius P, Puskic PS, Reis AODA, Reisinger RR, Santos M, Tarszisz E, Tixier P, Trathan PN, Wege M, Wienecke B (2020) [Marine Ecosystem Assessment for the Southern Ocean: Birds and Marine Mammals in a Changing Climate](https://doi.org/10.3389/fevo.2020.566936). Frontiers in Ecology and Evolution 8:566936.

Burns JM, Costa DP, Fedak MA, Hindell MA, Bradshaw CJA, Gales NJ, McDonald B, Trumble SJ, Crocker DE (2004) [Winter Habitat Use and Foraging Behavior of Crabeater Seals Along the Western Antarctic Peninsula](https://doi.org/10.1016/j.dsr2.2004.07.021). Deep Sea Research Part II: Topical Studies in Oceanography 51:2279–2303.

Clarke A, Murphy EJ, Meredith MP, King JC, Peck LS, Barnes DKA, Smith RC (2007) [Climate Change and the Marine Ecosystem of the Western Antarctic Peninsula](https://doi.org/10.1098/rstb.2006.1958). Philosophical Transactions of the Royal Society B: Biological Sciences 362:149–166.

Corso AD, Steinberg DK, Stammerjohn SE, Hilton EJ (2022) [Climate Drives Long-Term Change in Antarctic Silverfish Along the Western Antarctic Peninsula](https://doi.org/10.1038/s42003-022-03042-3). Communications Biology 5:1–10.

Costa RR, Mendes CRB, Ferreira A, Tavano VM, Dotto TS, Secchi ER (2021) [Large Diatom Bloom Off the Antarctic Peninsula During Cool Conditions Associated with the 2015/2016 El Niño](https://doi.org/10.1038/s43247-021-00322-4). Communications Earth & Environment 2:252.

Croxall JP, Wood AG (2002) [The Importance of the Patagonian Shelf for Top Predator Species Breeding at South Georgia](https://doi.org/10.1002/aqc.480). Aquatic Conservation: Marine and Freshwater Ecosystems 12:101–118.

Dakos V, Bascompte J (2014) [Critical Slowing down as Early Warning for the Onset of Collapse in Mutualistic Communities](https://doi.org/10.1073/pnas.1406326111). Proceedings of the National Academy of Sciences 111:17546–17551.

Daneri GA, Carlini AR, Hernandez CM, Harrington A (2005) [The Diet of Antarctic Fur Seals, *Arctocephalus* *Gazella*, at King George Island, During the Summer–Autumn Period](https://doi.org/10.1007/s00300-004-0693-2). Polar Biology 28:329–333.

Delord K, Kato A, Tarroux A, Orgeret F, Cotté C, Ropert-Coudert Y, Cherel Y, Descamps S (2020) [Antarctic Petrels “on the Ice Rocks”: Wintering Strategy of an Antarctic Seabird](https://doi.org/10.1098/rsos.191429). Royal Society Open Science 7:191429.

Delord K, Pinet P, Pinaud D, Barbraud C, De Grissac S, Lewden A, Cherel Y, Weimerskirch H (2016) [Species-Specific Foraging Strategies and Segregation Mechanisms of Sympatric Antarctic Fulmarine Petrels Throughout the Annual Cycle](https://doi.org/10.1111/ibi.12365). Ibis 158:569–586.

Descalzo M, Daneri GA, Harrington A, Negrete J, Negri A, Corbalán A, Barrera-Oro E (2023) [The Relevance of Fish in the Summer Diet of the Antarctic Fur Seal (*Arctocephalus* *Gazella*) at Hope Bay, Antarctic Peninsula and Stranger Point, South Shetland Islands](https://doi.org/10.1007/s00300-023-03159-z). Polar Biology 46:809–818.

Dietrich KS, Santora JA, Reiss CS (2021) Winter and Summer Biogeography of Macrozooplankton Community Structure in the Northern Antarctic Peninsula Ecosystem. Progress in Oceanography 196:102610.

Dominello T, Širović A (2016) [Seasonality of Antarctic Minke Whale (*Balaenoptera* *Bonaerensis*) Calls Off the Western Antarctic Peninsula](https://doi.org/10.1111/mms.12302). Marine Mammal Science 32:826–838.

Ducklow HW, Cimino MA, Dunton KH, Fraser WR, Hopcroft RR, Ji R, Miller AJ, Ohman MD, Sosik HM (2022) [Marine Pelagic Ecosystem Responses to Climate Variability and Change](https://doi.org/10.1093/biosci/biac050). BioScience 72:827–850.

Ducklow HW, Fraser WR, Meredith MP, Stammerjohn SE, Doney SC, Martinson DG, Sailley SF, Schofield OM, Steinberg DK, Venables HJ, others (2013) West Antarctic Peninsula: An Ice-Dependent Coastal Marine Ecosystem in Transition. Oceanography 26:190–203.

Dufrêne M, Legendre P (1997) Species Assemblages and Indicator Species: The Need for a Flexible Asymmetrical Approach. Ecological monographs 67:345–366.

Eayrs C, Li X, Raphael MN, Holland DM (2021) [Rapid Decline in Antarctic Sea Ice in Recent Years Hints at Future Change](https://doi.org/10.1038/s41561-021-00768-3). Nature Geoscience 14:460–464.

Esposito C, Bichet O, Petit M (2021) [First Sightings of Antarctic Minke Whale (Balaenoptera Bonaerensis) Mother–Calf Pairs in French Polynesia](https://doi.org/10.1578/AM.47.2.2021.175). Aquatic Mammals 47:175–180.

Evans PGH (1982) [Associations Between Seabirds and Cetaceans: A Review](https://doi.org/10.1111/j.1365-2907.1982.tb00015.x). Mammal Review 12:187–206.

Filun D, Thomisch K, Boebel O, Brey T, Širović A, Spiesecke S, Van Opzeeland I (2020) [Frozen Verses: Antarctic Minke Whales (*Balaenoptera* *Bonaerensis*) Call Predominantly During Austral Winter](https://doi.org/10.1098/rsos.192112). Royal Society Open Science 7:192112.

Flores H, Hunt BPV, Kruse S, Pakhomov EA, Siegel V, Van Franeker JA, Strass V, Van De Putte AP, Meesters EHWG, Bathmann U (2014) [Seasonal Changes in the Vertical Distribution and Community Structure of Antarctic Macrozooplankton and Micronekton](https://doi.org/10.1016/j.dsr.2013.11.001). Deep Sea Research Part I: Oceanographic Research Papers 84:127–141.

Forcada J, Hoffman JI, Gimenez O, Staniland IJ, Bucktrout P, Wood AG (2023) [Ninety Years of Change, from Commercial Extinction to Recovery, Range Expansion and Decline for Antarctic Fur Seals at South Georgia](https://doi.org/10.1111/gcb.16947). Global Change Biology:gcb.16947.

Fraser WR, Ainley DG (1986) [Ice Edges and Seabird Occurrence in Antarctica](https://doi.org/10.2307/1310216). BioScience 36:258–263.

Harrison NM, Whitehouse MJ, Heinemann D, Prince PA, Hunt GL Jr., Veit RR (1991) [Observations of Multispecies Seabird Flocks Around South Georgia](https://doi.org/10.1093/auk/108.4.801). The Auk 108:801–810.

Herr H, Kelly N, Dorschel B, Huntemann M, Kock K-H, Lehnert LS, Siebert U, Viquerat S, Williams R, Scheidat M (2019) [Aerial Surveys for Antarctic Minke Whales (*Balaenoptera* *Bonaerensis*) Reveal Sea Ice Dependent Distribution Patterns](https://doi.org/10.1002/ece3.5149). Ecology and Evolution 9:5664–5682.

Hinke JT, Cossio AM, Goebel ME, Reiss CS, Trivelpiece WZ, Watters GM (2017) [Identifying Risk: Concurrent Overlap of the Antarctic Krill Fishery with Krill-Dependent Predators in the Scotia Sea](https://doi.org/10.1371/journal.pone.0170132). PLOS ONE 12:e0170132.

Hinke JT, Trivelpiece WZ (2011) [Daily Activity and Minimum Food Requirements During Winter for Gentoo Penguins (*Pygoscelis* *Papua*) in the South Shetland Islands, Antarctica](https://doi.org/10.1007/s00300-011-1018-x). Polar Biology 34:1579–1590.

Hoffman W, Heinemann D, Wiens JA (1981) [The Ecology of Seabird Feeding Flocks in Alaska](https://doi.org/10.1093/auk/98.3.437). The Auk 98:437–456.

Hopkins TL, Torres JJ (1988) [The Zooplankton Community in the Vicinity of the Ice Edge, Western Weddell Sea, March 1986](https://doi.org/10.1007/BF00442033). Polar Biology 9:79–87.

Hunt GL, Heinemann D, Veit RR, Heywood RB, Everson I (1990) [The Distribution, Abundance and Community Structure of Marine Birds in Southern Drake Passage and Bransfield Strait, Antarctica](https://doi.org/10.1016/0278-4343(90)90021-D). Continental Shelf Research 10:243–257.

Jones ME, Bromwich DH, Nicolas JP, Carrasco J, Plavcová E, Zou X, Wang S-H (2019) [Sixty Years of Widespread Warming in the Southern Middle and High Latitudes (1957–2016)](https://doi.org/10.1175/JCLI-D-18-0565.1). Journal of Climate 32:6875–6898.

Kawaguchi S, Nicol S (2020) Krill Fishery. Fisheries and Aquaculture:137–158.

Krause DJ, Bonin CA, Goebel ME, Reiss CS, Watters GM (2022) [The Rapid Population Collapse of a Key Marine Predator in the Northern Antarctic Peninsula Endangers Genetic Diversity and Resilience to Climate Change](https://doi.org/10.3389/fmars.2021.796488). Frontiers in Marine Science 8:796488.

Lee JF, Friedlaender AS, Oliver MJ, DeLiberty TL (2017) [Behavior of Satellite-Tracked Antarctic Minke Whales (*Balaenoptera* *Bonaerensis*) in Relation to Environmental Factors Around the Western Antarctic Peninsula](https://doi.org/10.1186/s40317-017-0138-7). Animal Biotelemetry 5:23.

Levin PS, Fogarty MJ, Murawski SA, Fluharty D (2009) [Integrated Ecosystem Assessments: Developing the Scientific Basis for Ecosystem-Based Management of the Ocean](https://doi.org/10.1371/journal.pbio.1000014). PLoS Biology 7:e1000014.

Lin Y, Moreno C, Marchetti A, Ducklow H, Schofield O, Delage E, Meredith M, Li Z, Eveillard D, Chaffron S, Cassar N (2021) [Decline in Plankton Diversity and Carbon Flux with Reduced Sea Ice Extent Along the Western Antarctic Peninsula](https://doi.org/10.1038/s41467-021-25235-w). Nature Communications 12:4948.

Lorentsen S-H, Klages N, Røv N (1998) Diet and Prey Consumption of Antarctic Petrels *Thalassoica* *Antarctica* at Svarthamaren, Dronning Maud Land, and at Sea Outside the Colony. Polar Biology 19:414–420.

Maechler M, Rousseeuw P, Struyf A, Hubert M, Hornik K (2022) Cluster: Cluster analysis basics and extensions.

Massom RA, Stammerjohn SE (2010) [Antarctic Sea Ice Change and Variability – Physical and Ecological Implications](https://doi.org/10.1016/j.polar.2010.05.001). Polar Science 4:149–186.

Meyer B, Freier U, Grimm V, Groeneveld J, Hunt BPV, Kerwath S, King R, Klaas C, Pakhomov E, Meiners KM, Melbourne-Thomas J, Murphy EJ, Thorpe SE, Stammerjohn S, Wolf-Gladrow D, Auerswald L, Götz A, Halbach L, Jarman S, Kawaguchi S, Krumpen T, Nehrke G, Ricker R, Sumner M, Teschke M, Trebilco R, Yilmaz NI (2017) [The Winter Pack-Ice Zone Provides a Sheltered but Food-Poor Habitat for Larval Antarctic Krill](https://doi.org/10.1038/s41559-017-0368-3). Nature Ecology & Evolution 1:1853–1861.

Moffat C, Meredith M (2018) [Shelf–Ocean Exchange and Hydrography West of the Antarctic Peninsula: A Review](https://doi.org/10.1098/rsta.2017.0164). Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences 376:20170164.

Monier SA, Veit RR, Manne LL (2020) [Changes in Positive Associations Among Vertebrate Predators at South Georgia During Winter](https://doi.org/10.1007/s00300-020-02720-4). Polar Biology 43:1439–1451.

Montes-Hugo M, Doney SC, Ducklow HW, Fraser W, Martinson D, Stammerjohn SE, Schofield O (2009) [Recent Changes in Phytoplankton Communities Associated with Rapid Regional Climate Change Along the Western Antarctic Peninsula](https://doi.org/10.1126/science.1164533). Science 323:1470–1473.

Nicol S, Foster J (2016) The Fishery for Antarctic Krill: Its Current Status and Management Regime. Biology and ecology of Antarctic krill:387–421.

Oksanen J, Simpson GL, Blanchet FG, Kindt R, Legendre P, Minchin PR, O’Hara RB, Solymos P, Stevens MHH, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Carvalho G, Chirico M, De Caceres M, Durand S, Evangelista HBA, FitzJohn R, Friendly M, Furneaux B, Hannigan G, Hill MO, Lahti L, McGlinn D, Ouellette M-H, Ribeiro Cunha E, Smith T, Stier A, Ter Braak CJF, Weedon J (2022) Vegan: Community ecology package.

Parkinson CL (2019) [A 40-y Record Reveals Gradual Antarctic Sea Ice Increases Followed by Decreases at Rates Far Exceeding the Rates Seen in the Arctic](https://doi.org/10.1073/pnas.1906556116). Proceedings of the National Academy of Sciences 116:14414–14423.

Polito MJ, Goebel ME (2010) [Investigating the Use of Stable Isotope Analysis of Milk to Infer Seasonal Trends in the Diets and Foraging Habitats of Female Antarctic Fur Seals](https://doi.org/10.1016/j.jembe.2010.08.015). Journal of Experimental Marine Biology and Ecology 395:1–9.

Purich A, Doddridge EW (2023) [Record Low Antarctic Sea Ice Coverage Indicates a New Sea Ice State](https://doi.org/10.1038/s43247-023-00961-9). Communications Earth & Environment 4:314.

Reiss CS, Cossio A, Santora JA, Dietrich KS, Murray A, Mitchell BG, Walsh J, Weiss EL, Gimpel C, Jones CD, Watters GM (2017) [Overwinter Habitat Selection by Antarctic Krill Under Varying Sea-Ice Conditions: Implications for Top Predators and Fishery Management](https://doi.org/10.3354/meps12099). Marine Ecology Progress Series 568:1–16.

Ribic CA, Ainley DG, Glenn Ford R, Fraser WR, Tynan CT, Woehler EJ (2011) [Water Masses, Ocean Fronts, and the Structure of Antarctic Seabird Communities: Putting the Eastern Bellingshausen Sea in Perspective](https://doi.org/10.1016/j.dsr2.2009.09.017). Deep Sea Research Part II: Topical Studies in Oceanography 58:1695–1709.

Ridoux V, Offredo C (1989) The Diets of Five Summer Breeding Seabirds in Adélie Land, Antarctica. Polar Biology 9:137–145.

Risch D, Norris T, Curnock M, Friedlaender A (2019) [Common and Antarctic Minke Whales: Conservation Status and Future Research Directions](https://doi.org/10.3389/fmars.2019.00247). Frontiers in Marine Science 6:247.

Roberts DW (2019) Labdsv: Ordination and multivariate analysis for ecology.

Saba GK, Fraser WR, Saba VS, Iannuzzi RA, Coleman KE, Doney SC, Ducklow HW, Martinson DG, Miles TN, Patterson-Fraser DL, Stammerjohn SE, Steinberg DK, Schofield OM (2014) [Winter and Spring Controls on the Summer Food Web of the Coastal West Antarctic Peninsula](https://doi.org/10.1038/ncomms5318). Nature Communications 5:4318.

Santora JA (2014) [Environmental Determinants of Top Predator Distribution Within the Dynamic Winter Pack Ice Zone of the Northern Antarctic Peninsula](https://doi.org/10.1007/s00300-014-1502-1). Polar Biology 37:1083–1097.

Santora JA, Veit RR (2013) [Spatio-Temporal Persistence of Top Predator Hotspots Near the Antarctic Peninsula](https://doi.org/10.3354/meps10350). Marine Ecology Progress Series 487:287–304.

Southwell C, Kerry K, Ensor P, Woehler EJ, Rogers T (2003) [The Timing of Pupping by Pack-Ice Seals in East Antarctica](https://doi.org/10.1007/s00300-003-0534-8). Polar Biology 26:648–652.

Stachowicz JJ (2001) [Mutualism, Facilitation, and the Structure of Ecological Communities](https://doi.org/10.1641/0006-3568(2001)051[0235:MFATSO]2.0.CO;2). BioScience 51:235.

Stammerjohn SE, Martinson DG, Smith RC, Iannuzzi RA (2008) [Sea Ice in the Western Antarctic Peninsula Region: Spatio-temporal Variability from Ecological and Climate Change Perspectives](https://doi.org/10.1016/j.dsr2.2008.04.026). Deep Sea Research Part II: Topical Studies in Oceanography 55:2041–2058.

Thiebot J-B, Ropert-Coudert Y, Raclot T, Poupart T, Kato A, Takahashi A (2019) [Adélie Penguins’ Extensive Seasonal Migration Supports Dynamic Marine Protected Area Planning in Antarctica](https://doi.org/10.1016/j.marpol.2019.103692). Marine Policy 109:103692.

Tibshirani R, Walther G, Hastie T (2001) [Estimating the Number of Clusters in a Data Set via the Gap Statistic](https://doi.org/10.1111/1467-9868.00293). Journal of the Royal Statistical Society: Series B (Statistical Methodology) 63:411–423.

Trathan PN, Warwick-Evans V, Young EF, Friedlaender A, Kim JH, Kokubun N (2022) [The Ecosystem Approach to Management of the Antarctic Krill Fishery - the “Devils Are in the Detail” at Small Spatial and Temporal Scales](https://doi.org/10.1016/j.jmarsys.2021.103598). Journal of Marine Systems 225:103598.

Trivelpiece WZ, Hinke JT, Miller AK, Reiss CS, Trivelpiece SG, Watters GM (2011) Variability in Krill Biomass Links Harvesting and Climate Warming to Penguin Population Changes in Antarctica. Proceedings of the National Academy of Sciences 108:7625–7628.

Veit RR, Harrison NM (2017) [Positive Interactions Among Foraging Seabirds, Marine Mammals and Fishes and Implications for Their Conservation](https://doi.org/10.3389/fevo.2017.00121). Frontiers in Ecology and Evolution 5:121.

Veit RR, Silverman ED, Everson I (1993) [Aggregation Patterns of Pelagic Predators and Their Principal Prey, Antarctic Krill, Near South Georgia](https://doi.org/10.2307/5204). Journal of Animal Ecology 62:551–564.

Walsh J, Reiss C (2023) [Extreme El Niño Southern Oscillation Conditions Have Contrasting Effects on the Body Condition of Five Euphausiid Species Around the Northern Antarctic Peninsula During Winter](https://doi.org/10.1007/s00300-023-03129-5). Polar Biology 46:319–338.

Warwick-Evans V, A Santora J, Waggitt JJ, Trathan PN (2021) [Multi-Scale Assessment of Distribution and Density of Procellariiform Seabirds Within the Northern Antarctic Peninsula Marine Ecosystem](https://doi.org/10.1093/icesjms/fsab020). ICES Journal of Marine Science 78:1324–1339.

Watters GM, Hinke JT, Reiss CS (2020) [Long-Term Observations from Antarctica Demonstrate That Mismatched Scales of Fisheries Management and Predator-Prey Interaction Lead to Erroneous Conclusions about Precaution](https://doi.org/10.1038/s41598-020-59223-9). Scientific Reports 10:2314.

Whitehouse MJ, Veit RR (1994) [Distribution and Abundance of Seabirds and Fur Seals Near the Antarctic Peninsula During the Austral Winter, 1986](https://doi.org/10.1007/BF00238448). Polar Biology 14:325–330.

Worby A, Allison I (1999) Part I, Observational technique and results. In: *A technique for making ship-based observations of Antarctic sea ice thickness and characteristics*. Research report (Antarctic CRC), Antarctic CRC, Hobart, Tas.