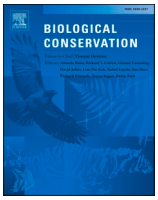
Biological Conservation 272 (2022) 109630

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon



Predator-derived bioregions in the Southern Ocean: Characteristics, drivers and representation in marine protected areas

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ARTICLE INFO

Keywords:
Biogeography
Conservation
Management
MPA
Antarctica
Subantarctic

ABSTRACT

Multiple initiatives have called for large-scale representative networks of marine protected areas (MPAs). MPAs should be ecologically representative to be effective, but in large, remote regions this can be difficult to quantify and assess. We present a novel bioregionalization for the Southern Ocean, which uses the modelled circumpolar habitat importance of 17 marine bird and mammal species. The habitat-use of these predators indicates biodiversity patterns that require representation in Southern Ocean conservation and management planning. In the predator habitat importance predictions, we identified 17 statistical clusters, falling into four larger groups. We characterized and contrasted these clusters based on their predator, prey and oceanographic characteristics. Under the existing Southern Ocean MPA network, some clusters fall short of 10 % representation, yet others meet or exceed these targets. Implementation of currently proposed MPAs can in some cases contribute to meeting even 30 % spatial coverage conservation targets. However, the effectiveness of mixed-use versus no-take MPAs should be taken into consideration, since some clusters are not adequately represented by no-take MPAs. These results, combined with previous studies in the Southern Ocean, can help inform the continued design, implementation, and evaluation of a representative system of MPAs for Southern Ocean conservation and management.

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https://doi.org/10.1016/j.biocon.2022.109630
Received 27 August 2021; Received in revised form 23 April 2022; Accepted 7 June 2022
Available online 17 June 2022

1. Introduction

Human pressures have changed marine systems globally (Halpern et al., 2015), and in response, marine protected areas (MPAs) have become an increasingly popular tool for biodiversity conservation and management (Butchart et al., 2012; Tundi Agardy, 1994). Over nearly 20 years, multiple international initiatives have called for adopting representative networks of MPAs. For example, the 2002 World Summit on Sustainable Development called on participating States to designate a global network of representative MPAs by 2012. In 2003, and again in 2014, the International Union for the Conservation of Nature World Parks Congress called specifically for protected areas to encompass 20–30 % of all marine habitats. In 2010, the Convention on Biological Diversity, under the Aichi Biodiversity Targets, proposed 10 % of the global oceans be designated as ecologically representative MPAs. Most recently in 2015, the United Nations Sustainable Development Goal 14 reiterates Aichi, calling for 10 % of coastal and marine areas to be protected by 2020 (Gjerde et al., 2016). While global coverage of marine protected areas (MPAs) increased from 2.9 to 7.5 % from 2010 to 2019 (Maxwell et al., 2020), it still falls short of the 10 % Aichi target, and in fact higher targets of at least 30 % may be necessary (O'Leary et al., 2016; Roberts et al., 2020). Further, MPAs are most effective when extractive activities such as fishing are not permitted (Edgar et al., 2014), but such 'fully protected' MPAs together with 'highly protected' MPAs, where only light extractive activities are allowed, cover only 2.7 % of oceans (www.mpatlas.org). Additionally, protected areas should be ecologically representative to effectively conserve biodiversity, yet this goal has not been achieved when assessed at a global level (Klein et al., 2015; Maxwell et al., 2020; Visconti et al., 2019).

That protected areas should be ecologically representative has been interpreted in various ways, including the coverage of species (e.g., Klein et al., 2015), their niches (e.g., Hanson et al., 2020) or ecoregions (e.g., Brooks et al., 2020a). The delineation of areas into ecoregions or bioregions (used henceforth) as "a biological and physical partitioning of geographic space based on the spatial distribution of multiple species, communities, ecosystems, or other biological characteristics" (Woolley et al., 2020) has been a long-standing goal of biogeographers (Kreft and Jetz, 2010; Reygondeau and Dunn, 2019); increasingly, bioregionalization is also an important component of ocean conservation and management (Lourie and Vincent, 2004; Woolley et al., 2020).

Delineation of biogeographic regions in the ocean is challenging, often relying on physical or biological surrogates to infer the distribution of more complex assemblages (Woolley et al., 2020). Achieving this has become more feasible with the development of satellite remote-sensing and the availability of large-scale species occurrence datasets (e.g., Costello et al., 2017; Longhurst, 2010; Lourie and Vincent, 2004; Reygondeau and Dunn, 2019; Woolley et al., 2020) but even so, regionalization must often make use of numerical models (e.g., Sonnewald et al., 2020) or predicted species or community distributions (e.g., Koubbi et al., 2011). A core goal of biogeography is to link any regionalization to their current or past physical and biological drivers, across various scales (Kreft and Jetz, 2010). From a conservation perspective, these links are critical to ensure that representativity, as assessed through bioregions, captures the biodiversity patterns or features used to construct the regionalization, and the underlying processes (Spalding et al., 2007; Woolley et al., 2020).

1.1. The Southern Ocean

The extended Southern Ocean (south of 40° S, see Section 2.1) is characterized by unique environments and fauna, the latter often adapted to extreme environmental conditions (De Broyer et al., 2014). It contains the highest percentage of wilderness (88.5 %), among all ocean realms (Jones et al., 2018) and influences global climate (Rintoul, 2018). Nonetheless, Southern Ocean ecosystems are increasingly under pressure from climate change and human use. Thus, the Southern Ocean constitutes a region of global importance for conservation (Chown et al., 2017; Xavier et al., 2016a). The Southern Ocean is subject to a unique multilateral governance system under the Antarctic Treaty System. Under the Convention on the Conservation of Antarctic Marine Living Resources (hereafter, Convention), the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) is tasked with conserving and managing marine living resources in the Convention Area in the Southern Ocean – around 10 % of the earth's oceans. The Convention mandates an ecosystem approach, with decisions based on the best available science. In line with this approach, CCAMLR has committed to implement a representative system of MPAs in the Southern Ocean and has thus far adopted two MPAs, with three more currently under consideration (Brooks et al., 2020a). Many Subantarctic islands overlapping with CCAMLR's boundaries fall under national jurisdiction and several of these nations have also implemented MPAs as a conservation tool (e.g., Lombard et al., 2007; Trathan et al., 2014; Brooks et al., 2019).

Multiple scientific efforts have informed CCAMLR's science-based process for designing a representative system of MPAs. Douglass et al. (2014) produced a benthic bioregionalization of the Southern Ocean based on biological data (species distribution, endemism and existing bioregion definitions) and nine abiotic data layers representing environmental drivers and dispersal barriers. Based on ocean depth, sea surface temperature, and the proportion of time a given cell was covered by sea ice, Raymond (2014) produced a pelagic regionalization for the Southern Ocean, consisting of 20 statistically-identified clusters. Recently, Brooks et al. (2020a) assessed these benthic and pelagic regions' representation in the designated and proposed network of MPAs in the CCAMLR Convention Area. While 11.98 % of the CCAMLR Area falls within MPAs (with 4.61 % highly protected, hereafter 'no-take'), most of the benthic bioregions and roughly half of the pelagic bioregions fell short of a 10 % representation threshold in the current MPA network (Brooks et al., 2020a).

The logistical challenges of conducting fieldwork in the Southern Ocean have necessitated predictive modelling to examine circumpolar biodiversity patterns (e.g., Fabri-Ruiz et al., 2020; Freer et al., 2019; Hindell et al., 2020; Pinkerton et al., 2010; Xavier et al., 2016b). For instance, Hindell et al. (2020) used electronic tracking data from 17 bird and mammal species to identify 'Areas of Ecological Significance' in the extended Southern Ocean. Their rationale was that predator spatial use patterns, modelled from animal tracking datasets, represent broader ecological relationships. Areas with congruent high habitat importance for different predator species should indicate places where biophysical features promote not only high abundance but also high diversity of prey species. Extending this idea, predator spatial patterns across species can be used to determine statistical bioregions (sensu Woolley et al., 2020). Different predator species use different prey and environments; as such, predator bioregions can act as surrogates for broader biogeographic patterns. We therefore implement this approach, using predator-derived habitat importance predictions for the whole Southern Ocean (Hindell et al., 2020) to identify clusters indicative of bioregions.

Specifically, we first identify and map statistical clusters in the habitat importance predictions of 17 Southern Ocean bird and mammal species. Second, we characterize and contrast the clusters based on their predator species characteristics, prey species characteristics (using published habitat maps for cephalopods, myctophids and euphausiids) and oceanographic characteristics. Finally, we assess the representation of the clusters in the network of current and proposed MPAs in the Southern Ocean.

2. Methods

2.1. Study area

Our study area is the circumpolar region south of 40° S. Broadly this corresponds with the Subantarctic, Subantarctic Water Ring, Austral

Polar and Antarctic biogeochemical provinces (nested within the Antarctic Westerly Winds and Antarctic Polar biomes) of Longhurst (2010), and the Southern Ocean zoogeographical ocean realm of Costello et al. (2017).

2.2. Computation

All analyses were conducted in R (R Core Team, 2021). Code is available in the Github repository https://github.com/ryanreisinger/soPredatorRegions.

2.3. Predator habitat importance

As input for our analyses, we used published maps of predicted habitat importance for 17 marine bird and mammal species in the Southern Ocean (Hindell et al., 2020) (Fig. 1b). Hindell et al. (2020) used electronic tracking data to model these species' habitat-use in response to a set of 19 biophysical environmental covariates. Combining these models with information on the relative abundance distribution of each species and models of habitat accessibility, they predicted habitat importance for each species across the Southern Ocean.

2.4. Clusters

To identify statistical clusters in the predator habitat importance data, we ran a *k*-medoid cluster analysis on the Manhattan distances calculated among species habitat importance scores in each cell, using the CLARA (CLustering LARge Applications) method implemented in the *cluster* package (Maechler et al., 2021). To choose the number of clusters (*k*), we calculated a measure of the clustering performance – the average silhouette width – for values of *k* from 2 to 40 (Rousseeuw, 1987). To visualize the relationship among the clusters, we applied hierarchical clustering (*hclust* function in R) based on Gower's distance calculated with the *vegdist* function in package *vegan* (Oksanen et al., 2020).

2.5. Environmental drivers

To visualize the clusters in two dimensions, we performed nonmetric multidimensional scaling (nMDS) of species habitat importance values of cells, based on Gower distance among them (*metaMDS* function in package *vegan*). Because the full dataset was too large to compute nMDS, we used a subset of 500 randomly selected cells from each cluster. Next, we explored the relationship of these clusters to the set of 19 environmental covariates used by Hindell et al. (2020) to model the predator species' habitat-use. The covariates include remotely sensed, measured in situ, or model-estimated parameters representing biophysical features that influence the movement, distribution, and density of marine predators. Many of these parameters are commonly used in ocean biogeochemical regionalization (e.g., ocean depth, sea surface temperature). Data sources and details of how the covariates were compiled are given in Hindell et al. (2020) and Supplementary Table S1. We assessed each environmental covariate's influence by fitting vectors (one for each covariate; function *envfit* in the *vegan* package) to the two nMDS axes and plotting these on the ordination. The vectors show the maximum increasing gradient direction for each covariate, and each vector's length is proportional to the correlation between the covariate and the ordination.

2.6. Representation of clusters in MPA networks

To assess the representation of clusters in current and proposed MPAs, we used data from the Marine Protection Atlas (Marine Conservation Institute, 2020; United Nations Environment Programme World Conservation Monitoring Centre and International Union for the Conservation of Nature, 2020). Designated MPAs are those that have formal recognition and legislation (Fig. 1c). Among these, we distinguished fully no-take MPAs, where the whole MPA is designated as an area where extractive activities such as fishing are not permitted, and mixed-use MPAs, where extractive activities are permitted in part or all of the MPA. Proposed MPAs are those where the intent to create an MPA has been made public (https://mpatlas.org/glossary), and often the proposed boundaries are still under evaluation (Fig. 1c). In proposed MPAs, we did not distinguish fully no-take from mixed-use MPAs since this information is often not yet available.

2.7. Prey information

We obtained published habitat suitability predictions for 29 prey species in three major mid-trophic level groups that are common prey of Southern Ocean predators: cephalopods (15 species; Xavier et al., 2016b), myctophids (10 species; Freer et al., 2019) and euphausiids (4 species; Cuzin-Roudy et al., 2014). Cephalopods and myctophids correspond with 'mesopelagic' prey, while euphausiids correspond with 'zooplankton'. To assess the relationship between predicted habitat suitability for these mid-trophic level species and the clusters we identified in the predator data, we trained a random forest model to classify the 17 clusters based on the habitat suitability values for the 29 prey species (Supplement). We also tested whether there were significant differences among prey habitat importance scores in the clusters using a PERMANOVA test (Anderson, 2001) (Supplement).

3. Results

Among average silhouette width for values of *k* from 2 to 40, we selected $k = 17$ clusters, a compromise between a very low ($k = 2$) and much higher ($k = 33$) number of clusters that both had higher silhouette values (Supplementary Fig. S1).

The hierarchical clustering dendrogram revealed four groups of clusters corresponding with higher level divisions among the 17 clusters (Fig. 2). Considering the clustering and species information together (Fig. 2), the first five clusters (from the left) can be described as Antarctic, characterized by four clusters (13–17) with high scores for Antarctic species (e.g., Antarctic petrel *Thalassoica antarctica*, Adélie penguin *Pygoscelis adeliae*, emperor penguin *Aptenodytes forsteri*, Weddell seal *Leptonychotes weddellii*, crabeater seal *Lobodon carcinophaga*) and one cluster (14) located mainly in the Indian and Pacific sectors with low scores for 14 species, but high scores for crabeater seal, humpback whale *Megaptera novaeangliae*, and emperor penguin. Geographically, these clusters, denoted as the Antarctic group, lie within the zone of maximum sea ice extent. Cluster 15 is restricted mainly to the Western Antarctic Peninsula and Weddell Sea (Fig. 1a).

The remaining three groups of clusters are all associated with the Antarctic Circumpolar Current fronts (Fig. 1a).

Two clusters - 09 and 10 - lie in the south Atlantic associated with islands in the Scotia Arc (Fig. 1a), hence denoted as the Scotia Arc group. These clusters have high habitat importance scores across many top predators, mainly Subantarctic-breeding species (Fig. 2), that are driven by the large population sizes for many species breeding at South Georgia.

The next group of clusters, 01–04 and 08, lie mostly outside of Areas of Ecological Significance defined by Hindell et al. (2020), and are characterized by lower values for several species, but slightly higher values for species capable of travelling far (Fig. 2). We thus refer to this as the Distant Subantarctic group. This group includes two large clusters in the Pacific and Indian sectors (Fig. 1a).

The next group (05–07, 11, 12) includes Subantarctic island clusters arcing from the east Atlantic eastward through the Indian to the west Pacific (Fig. 1a), characterized by high values for Subantarctic-breeding species (Fig. 2). We refer to these clusters as the Subantarctic group.

In the ordination of species habitat importance values (Fig. 3a), the Antarctic clusters (13–17) are separated by increasing sea ice concentration and standard deviation of sea ice concentration.

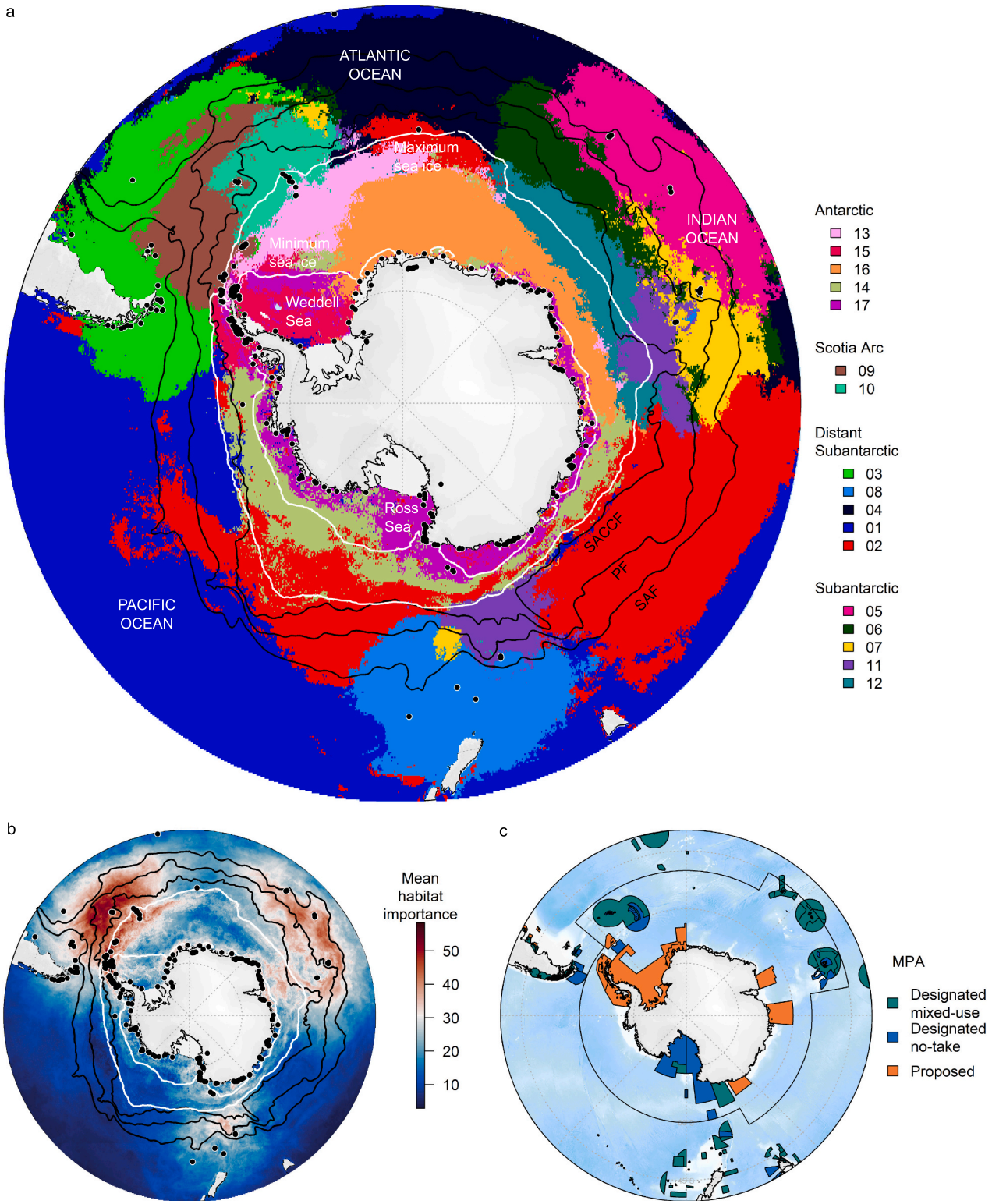

Fig. 1. 17 clusters (a) resulting from clustering of habitat importance scores of 17 marine predator species (mean scores shown in b). The clusters are aggregated into four higher-level regions: Antarctic, Scotia Arc, Distant Subantarctic and Subantarctic (see Fig. 2). Shown in c are designated mixed-use (green), designated no-take (blue) and proposed (orange) Marine Protected Areas (MPAs).
Black points in a and b indicate colony locations of the 17 marine predator species. Black lines in a and b indicate oceanographic fronts, from north to south, the Subantarctic Front (SAF), the Polar Front (PF), and the Southern Antarctic Circumpolar Current Front (SACCF), from Park and Durand (2019). The white lines (a and b) indicate median sea ice extent from 1981 to 2010 in September (maximum sea ice) and March (minimum sea ice) (Fetterer et al., 2017). The black line in c indicates the boundary of the Convention on the Conservation of Antarctic Marine Living Resources Area. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

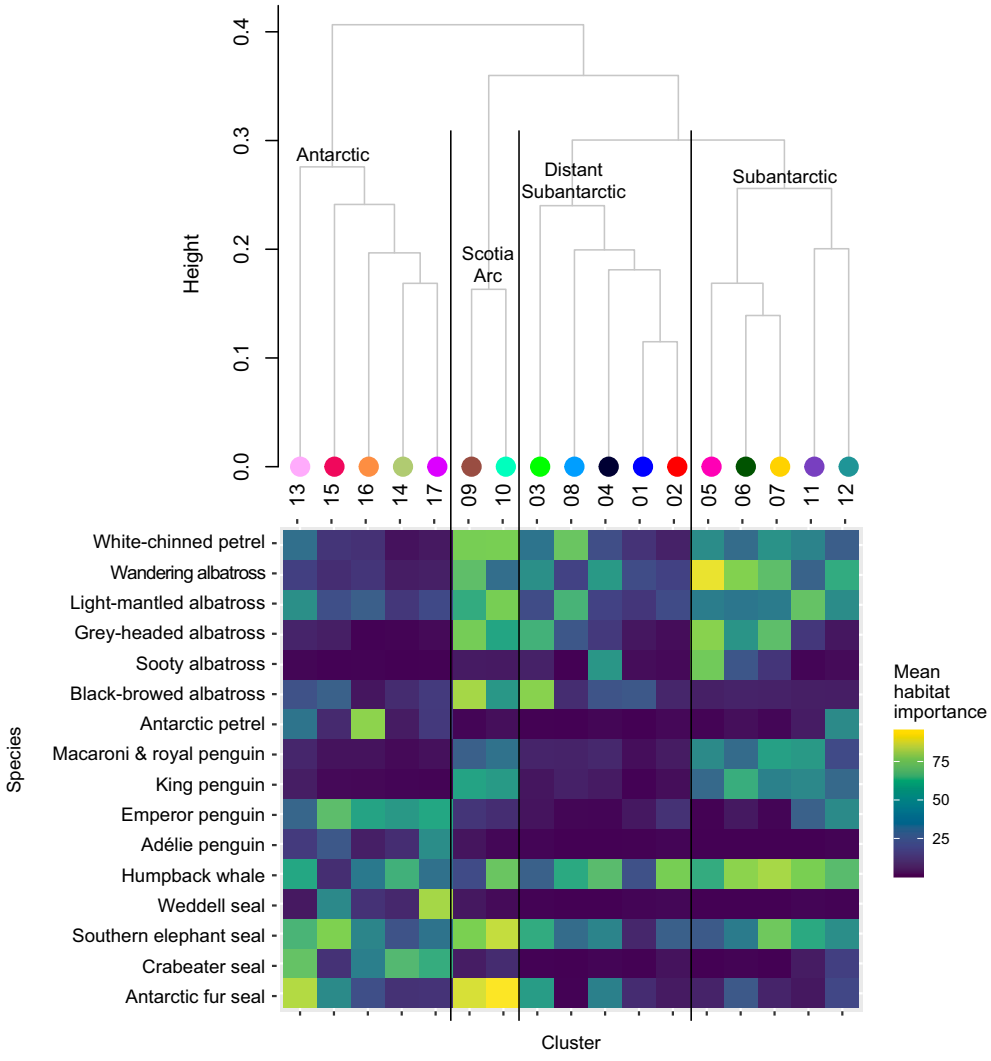

Fig. 2. Relationship among clusters and species composition. Heatmap showing habitat importance values per species (vertical axis) in each of the 17 predator clusters (horizontal axis). For each species, in each cluster, the mean habitat importance was calculated as the mean value of all grid cells. The dendrogram above the heatmap represents the hierarchical clustering of Gower's distance among the 17 predator clusters. Colors of the nodes match the map in Fig. 1a. The 17 clusters are aggregated into higher-level regions, indicated by black vertical lines and labels on the dendrogram: Antarctic, Scotia Arc, Distant Subantarctic and Subantarctic. Species habitat importance scores per cluster are shown in Supplementary Fig. S2.

Among these Antarctic clusters, 13 and 15 lie closer to the x-axis center of the ordination, correlated with increasing vertical mixing and its standard deviation and chlorophyll-a concentration (Fig. 3a). However, Antarctic clusters 13 and 16 are distinguished from other Antarctic clusters by their higher standard deviation of sea ice concentration (Supplementary Fig. S3) since they are located mainly in a seasonal sea ice area (Fig. 3a). The Antarctic cluster 17 lies farthest out but is quite widely dispersed along the vertical axis (Fig. 3a), reflecting circumpolar variation in environmental covariates due to its nearly circum-Antarctic geographic distribution (Fig. 1a). Most of the clusters in the Subantarctic group (05–07 and 11) are more tightly clustered, and correlated with increasing wind speed, sea surface temperature and its gradient, ice accessibility, current, sea surface height standard deviation and eddy kinetic energy. Subantarctic cluster 12 is more isolated and dispersed; geographically it is associated with the maximum sea ice extent in the Indian sector (Fig. 1a). The Scotia Arc clusters (09 and 10) are less clustered, and lie somewhat intermediate to the Antarctic and Subantarctic clusters.

The Antarctic clusters had higher sea ice related variables. The other groups of clusters had higher wind, sea surface temperature and its gradient, current, eddy kinetic energy and sea surface height standard deviation. Among these latter cluster groups, some sea ice influence (higher standard deviation of sea ice concentration) distinguished the Scotia Arc clusters from the Subantarctic and Distant Subantarctic clusters (Supplementary Fig. S3).

Clusters in the Antarctic group have good coverage overall, currently exceeding the 10 % threshold and meeting the 30 % threshold if proposed MPAs are implemented (Fig. 4c). However, two clusters (Antarctic 15 and 16) currently fall short of 10 % coverage (Fig. 4b). Subantarctic clusters overall meet the 10 % goal but fall short of the higher 30 % goal; importantly, there are almost no proposed MPAs in this regional cluster and two of the five clusters do not meet the 10 % goal (Fig. 4b, c). Among the distant Subantarctic clusters, coverage is currently very low: no clusters meet even the 10 % goal (Fig. 4b). While the Antarctic clusters have relatively high coverage in no-take MPAs, the proportion of no-take MPAs in the other cluster groups is low, less than 5 % overall (Fig. 4b, c).

Supplementary Fig. S4 shows the predicted habitat importance of prey in each cluster and the ranked importance of each species in discriminating clusters, according to the random forest model. According to the PERMANOVA test, there were significant differences in prey habitat importance among clusters ($F = 748.91$, $df = 16$, $p = 0.001$).

The five Antarctic clusters (13–17) are distinguished from all other clusters by the low mean habitat importance of the first-ranked prey species - the myctophid *Electrona carlsbergi*. This contrasts with the second-ranked species, the cephalopod *Slosarczykovia circumantarctica*, that has widespread importance in various habitats (i.e., medium habitat importance in the Antarctic clusters, relatively high habitat importance in the Scotia clusters, and low to medium importance in other Subantarctic clusters). The next four species, all cephalopods and myctophids, have low habitat importance in the Antarctic cluster but

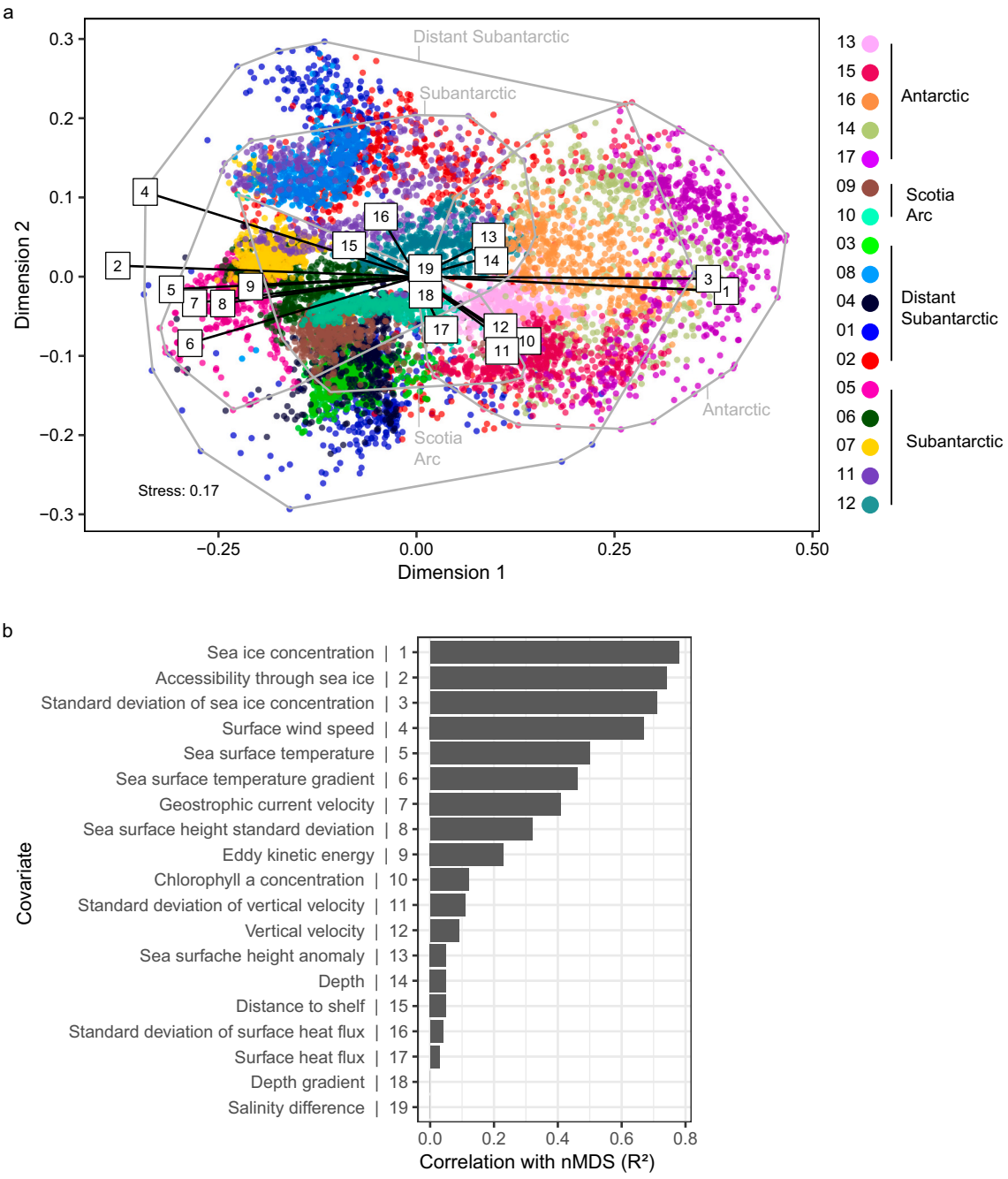

Fig. 3. Ordination of clustering and environmental correlates. a) Non-metric multidimensional scaling of distances among grid cells. Each point represents one of 500 samples from the full dataset, and the points are colored by their cluster membership. Overlaid vectors show the direction of the maximum increasing gradient for each of 19 environmental covariates. Numbered labels as in (b). Each vector's length is proportional to the correlation between the covariate and the ordination. Grey contours are convex hulls surrounding all points in each of the higher-level regions. b) Shows the correlation values (R^2, horizontal axis) of the covariates with the ordination in (a).

generally higher habitat importance in other clusters except Subantarctic 12, which is adjacent to the Antarctic. The euphausiid *Euphausia superba*, which is considered an Antarctic keystone species, is overall ranked 13th, but has high importance in the Antarctic clusters. Within the species analyzed, the cephalopod *Doryteuthis gahi* is the only species that is represented only by a low importance in cluster Distant Subantarctic 03, with very low importance elsewhere. Similarly, the euphausiid *E. crystallorophias* has a low to medium importance only in the Antarctic clusters, with very low importance elsewhere.

4. Discussion

We present a novel bioregionalization for the Southern Ocean, which uses the modelled habitat importance of 17 marine bird and mammal species. The habitat-use of these species indicates biodiversity patterns that should be considered when assessing the representativity of Southern Ocean marine conservation and management planning. Our results provide new insights into the ecological representation afforded by current and proposed management efforts. We assessed the representativity of all clusters because representation should encompass all ecosystem types. Furthermore, while certain clusters represent

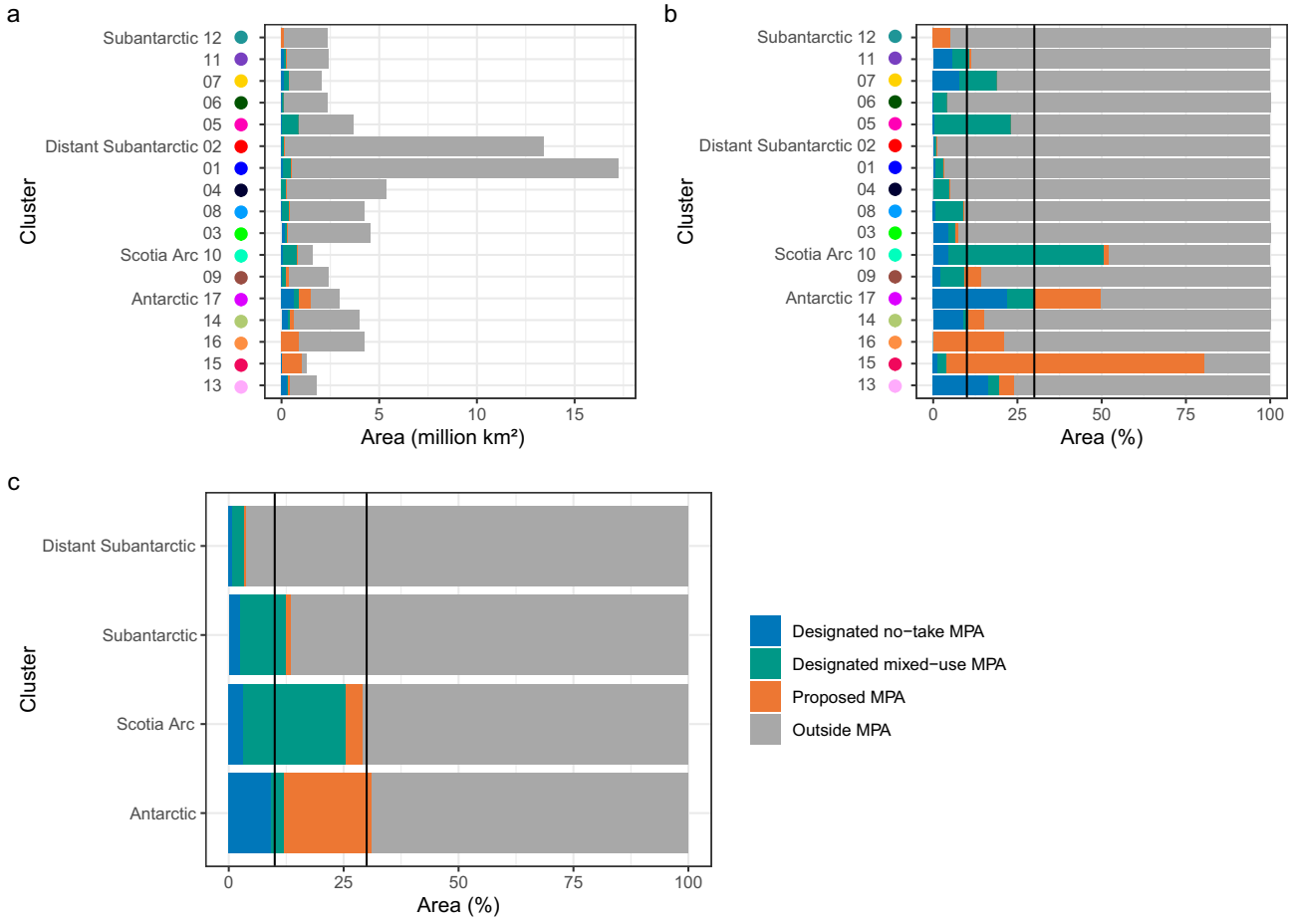

Fig. 4. MPA coverage. Coverage (horizontal axis) of the 17 predator clusters in designated Marine Protected Areas (MPAs; fully no-take in blue, mixed-use in green), proposed MPAs (orange) or outside MPAs (grey), by a) area and b) percentage area. c) shows the same as (b) but aggregated by higher-level regional clusters. In (b) and (c), vertical black lines are at 10 % coverage (the current global conservation target according to Aichi Target 11) and at 30 % coverage (a commonly proposed target). Maps of the MPAs and predator clusters are shown in Fig. 1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

community types of high importance for several predator species, others nevertheless have importance for individual species, particularly wide-ranging ones (see Fig. 2 and Supplementary Fig. S2). We show that under existing MPAs, some predator clusters fall short of 10 % representation, yet others meet or exceed these targets. Further, implementation of currently proposed MPAs can in some cases contribute to meeting even more ambitious (30 % spatial coverage) conservation targets. However, the effectiveness of mixed-use versus no-take MPAs should be taken into consideration (Sala et al., 2018), since some clusters are not adequately represented by no-take MPAs.

Marine birds and mammals are mobile and may occupy high trophic levels, as such they are considered sentinel species that potentially reflect the state of their environment (Hazen et al., 2019). In a conservation context, predators have also been used as umbrella and flagship species (Hooker and Gerber, 2004). The umbrella species (or umbrella group) concept assumes that the distribution of the species or groups in question is indicative of those of other species (Zacharias and Roff, 2001). Several studies (e.g., Hindell et al., 2011, 2020; Raymond et al., 2014; Reisinger et al., 2018) have used the rationale that areas of high habitat importance for multiple marine predator species can be considered 'Areas of Ecological Significance', which can be identified using habitat predictions for multiple species. We extend this rationale to show how information on the habitat importance of multiple predator species can be used not only to identify important areas, but to identify distinct bioregions, which could be considered in spatial conservation and management plans. Our approach blends the concepts of using predators as surrogate species (indicators and umbrellas), with a bioregionalization approach. At the same time, the charisma of many marine predator species means that they can be flagship species (Zacharias and Roff, 2001) used to gather support for spatial conservation (e.g., Handley et al., 2021).

Because we used habitat importance predictions for a suite of marine predators with different diets and distributions, their range of preferred habitats encompasses areas that are different in terms of their prey composition and oceanographic characteristics. Indeed, prey assemblages were significantly different among clusters. For example, for cephalopods, these differences are attributed to their preferred habitats, with some species being associated with Antarctic (e.g., *Psychroteuthis glacialis*), Subantarctic (e.g., *Histioteuthis eltaninae*) or even warmer waters (e.g., *H. atlantica*) while other species have a widespread distribution and are not limited by water masses (e.g., *Slosarczykovia circumantarctica, Moroteuthopsis longimana, Galiteuthis glacialis*) (Xavier et al., 2016b). Moreover, the cephalopod *Doryteuthis gahi* was only represented and of low importance in the Distant Subantarctic cluster, as this species is mostly distributed on the coasts of South America (particularly on the Patagonian Shelf) (Jereb and Roper, 2010). However, although of only low importance in our analysis, it may be of higher importance in South American assemblages of marine predators.

The clustering analysis similarly captured differences in the biogeography of myctophid species. Species known to have distributions largely restricted to conditions south of the Polar Front, including *Electrona antarctica* and *Gymnoscopelus opisthopterus*, had high habitat

importance within the Antarctic regional cluster, while species classed as having Subantarctic distribution patterns (e.g., *Protomyctophum tenisoni* and *Gymnoscopelus fraseri*) were absent from it (Duhamel et al., 2014). Other species had affinities to multiple clusters possibly reflecting their broad, circumpolar range or ontogenetic shifts in habitat preferences (Duhamel et al., 2014; Freer et al., 2020; Saunders et al., 2017). It is notable that *E. carlsbergi* and *Krefftichthys anderssoni*, dominant prey species of the king penguin *Aptenodytes patagonicus* (e.g., Cherel and Ridoux, 1992), had highest affinities within the Scotia Arc and Subantarctic clusters, matching those of this specialized predator.

Model predictions currently provide the only practicable way of having spatially congruent predator and prey information for the whole Southern Ocean, but nevertheless bring some potential pitfalls. When using modelled predictions to infer the relationships between predator clusters and prey, the distributions of both predators and prey are modelled functions of environmental covariates. This can introduce some artificial dependency that is not purely a result of each group's response to the factors determining its distribution (inasmuch as these can be modelled) and the availability of relevant covariates may be limited. However, in this case prey predictions were made using different models, including different environmental covariates (Cuzin-Roudy et al., 2014; Freer et al., 2019; Xavier et al., 2016b), which has the effect of limiting any such dependency. We examined prey assemblages in each predator cluster, but future work should examine biodiversity of other taxa to determine to what extent marine predators are good indicators of biodiversity patterns. There is theoretical and empirical support that marine predators are suitable indicators for pelagic ecosystems, but this is probably not true for other ecosystems, such as benthic ecosystems, let alone interactions between such domains. This underlines the fact that a pelagic bioregionalization is only one of many information layers that should be considered when assessing MPA networks.

Since the predator distributions are predictions modelled in response to environmental covariates, it follows that the predictions will necessarily capture environmental factors. Hence there is a risk that using such predictions to identify bioregions is conceptually circular, as Vilhena and Antonelli (2015) warn for terrestrial systems. Nonetheless, this approach is necessitated by the difficulty of wide scale, representative surveys in oceanic regions (Woolley et al., 2020) such as the Southern Ocean. Predator clusters could act as an initial assay used to identify key biophysical oceanographic drivers or regions, which could themselves then be used for later regionalization applications.

The predator clusters we identified captured broad environmental distinctions, particularly between Antarctic and Subantarctic regions, as well as more subtle distinctions in oceanographic characteristics. Existing regionalizations (e.g., Costello et al., 2017; Longhurst, 2010; Raymond, 2014) are typically zonal (latitudinal) in the Antarctic and Subantarctic, due to zonal gradients in major environmental characteristics, such as sea surface temperature, wind and the presence of sea ice, that fundamentally affect marine ecosystems (Longhurst, 2010). Particularly, the oceanographic fronts associated with the Antarctic Circumpolar Current (Fig. 1) are among the Southern Ocean's most significant features (Park and Durand, 2019). This large-scale zonal arrangement is reflected in the biogeographic patterns of Southern Ocean marine predators (Ropert-Coudert et al., 2014). All but one species in our study rely on land or ice substrates during their life cycles, and their movements are to an extent constrained by the availability of these substrates, especially for breeding. Thus, two broad species suites, comprising Antarctic, often ice-breeding, species, versus land-breeding species are among the drivers of the clusters (Fig. 3). The specific locomotion modes (e.g., swimming versus flying) and life histories (income versus capital breeders, duration and frequency of offspring care) of species further influence the movement range of each species. The predator clusters we identified thus have a strong zonal component, as expected, but also meridional (longitudinal) components related to distance from islands and oceanographic differences among ocean basins that influence abundance among breeding locations. For example, the Scotia clusters (09 and 10) include large population centers at South Georgia, distinguishing them from the other Subantarctic clusters, while clusters distant from land and ice are characterized by species with high mobility (e.g., Distant Subantarctic 04: humpback whale, wandering albatross *Diomedea exulans*, sooty albatross *Phoebetria fusca*). This particularly appears to drive the distinction between groups of clusters with high versus low mean habitat importance: the latter are usually far from any Subantarctic breeding sites or the Antarctic continent.

Across the suite of existing MPAs, only two predator clusters are well represented in no-take areas (Antarctic 17 encompassed in the Ross Sea region MPA; Antarctic 13 encompassed in the South Georgia and South Sandwich Islands MPA), while an additional six predator clusters are encompassed in mixed-use MPAs (encompassed in the suite of Subantarctic MPAs). If current MPA proposals are adopted and implemented via CCAMLR, additional predator clusters will be encompassed at the 10 % threshold (e.g., Antarctic clusters 16 and 15 encompassed in the Weddell Sea and part of the East Antarctic MPA proposals). However, even with existing and proposed MPAs, some predator clusters fall short of the 10 % threshold (e.g., Distant Subantarctic 04 and 08, Subantarctic 06,). Additional MPAs could work to encompass these clusters with high mean habitat importance and would also help in providing connectivity across the CCAMLR region between existing Subantarctic MPAs. Further, national governments with jurisdiction over Subantarctic waters might increase the area encompassed by their MPAs and/or the level of protection.

However, some underrepresented areas (Distant Subantarctic 04 and 08) fall outside of CCAMLR and national waters, into Areas Beyond National Jurisdiction. In these areas fishing activities are governed by regional fisheries management organizations (RFMO). While RFMOs have yet to designate MPAs in international waters, they have at times set up fisheries closures or areas off limits to bottom fishing (e.g., to protect vulnerable marine ecosystems) (Wagner et al., 2020). In the North Atlantic, the OSPAR Convention provides a mechanism to designate MPAs which rely on a memorandum of understanding with the regional fisheries management organizations in the region (O'Leary et al., 2012). Perhaps most promising for protecting Areas Beyond National Jurisdiction are ongoing negotiations for a new legally binding instrument specifically focused on governing biodiversity (Gjerde et al., 2019). Under this new legal instrument, multilateral MPAs designed to protect biodiversity in Areas Beyond National Jurisdiction will be possible. However, the Areas Beyond National Jurisdiction negotiations are ongoing without a clear end date, nor a specific path forward for designating MPAs (as well as management, research and more importantly monitoring).

CCAMLR and governments involved in managing the Southern Ocean have been leaders in adopting international MPAs. Yet, progress towards Southern Ocean protected areas has taken time. Adopting, implementing, and expanding MPAs in national waters is a complex process that can be rapid (e.g., South Georgia and the South Sandwich Islands (Trathan et al., 2014)), or take many years (e.g., Heard & McDonald Islands; Brooks et al., 2019). Designating MPAs through multilateral agreements – like CCAMLR, which requires unanimous agreement for all policy decisions – is much more difficult. The Ross Sea region MPA, for instance, required 10 years of scientific planning and five years of multilateral negotiations at CCAMLR (Brooks et al., 2020b). Further, the Southern Ocean is vast and remote, which presents costly and logistically-demanding challenges to complete research, monitoring, management and enforcement – all essential ingredients for an MPA to effectively conserve biodiversity (Gill et al., 2017; Wilhelm et al., 2014). Nevertheless, implementing MPAs grounded in best science is the first step. The work presented here, combined with previous studies in the Southern Ocean (e.g., Brooks et al., 2020a; Douglass et al., 2014; Hindell et al., 2020; Raymond, 2014), and beyond (Visalli et al., 2020) provide the best available science, which can continue to inform

the design and evaluation of a truly representative system of MPAs. Our results emphasize the importance of designating current MPA proposals in the Antarctic (such as the East Antarctic MPA) to meet CCAMLR's stated goals of a system of MPAs representative of Southern Ocean biodiversity and aligned with international conservation targets. The integrative value of predator habitat-use information lends support to these proposals, highlighting gaps in protection. Further this work lends support for existing MPAs (e.g., in the Ross Sea) and can be used towards evaluating efficacy (e.g., the Ross Sea MPA comes up for review in 2027 with many predator species being used as indicators to evaluate change). Work to conceptualize and adopt MPAs across the Southern Ocean is maturing, bringing with it the evidential support needed to implement CCAMLR's mandate of conservation. It will be important to maintain focus on this mandate in the face of growing economic interests (Rintoul et al., 2018).

Funding

Funding was provided by the French Foundation for Research on Biodiversity (FRB; www.fondationbiodiversite.fr) in the context of the CESAB project 'RAATD' and by WWF. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

CRediT authorship contribution statement

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We are grateful to Jean-Olivier Irisson for providing the euphausiid predictions and to Beth Pike for providing data from the Marine Protection Atlas.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2022.109630.

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