Tracking of marine predators to protect Southern Ocean ecosystems

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Southern Ocean ecosystems are under pressure from resource exploitation and climate change[1,2]. Mitigation requires identification and protection of Areas of Ecological Significance (AES), which have eluded identification at the ocean-basin scale. For this globally significant region, we identify AES using assemblage-level tracking of marine predators and assess current threats and protection levels. Integration of >4000 tracks from 17 bird and mammal species reveal AES around sub-Antarctic islands in the Atlantic and Indian Oceans and over the Antarctic continental shelf. Fishing pressure is disproportionately concentrated inside AES, and climate change over the next century is predicted to impose pressure on these areas, particularly around the Antarctic continent. Currently, 7.1% of the ocean south of 40˚S is under formal protection, including 29% of the total AES area. The establishment and regular revision of networks of protection encompassing AES is needed to provide long-term mitigation of growing pressures on Southern Ocean ecosystems.

The Southern Ocean, defined here as the circumpolar waters south of 40°S, is home to a unique fauna and plays an important role in biogeochemical cycles and the global climate system[1]. Past industrial sealing, whaling and demersal fishing caused significant perturbations from which some Southern Ocean ecosystems are only now starting to recover[3]. Squid and toothfish harvesting continue[4,5] and interest in the expansion of Antarctic krill fisheries is growing[6]. These target species are important prey for upper trophic organisms with krill a key component of the Southern Ocean food web, raising substantial concerns about impacts on Southern Ocean ecosystems[2]. Anthropogenic greenhouse gas emissions are simultaneously causing large changes to the Southern Ocean[7]. Strong interest has therefore developed in long-term conservation of the Southern Ocean, but management authorities face the considerable challenge of implementing conservation goals within existing management frameworks[2].

A first step in meeting this challenge is to identify regions that should be considered for protection, for example because of their high biodiversity, biological productivity, or particular importance for life-history stages of species[8,9]. The distribution and demography of marine predators provides a viable basis for this[10], particularly in the vast and remote Southern Ocean where integrated ecosystem measures are difficult to obtain at management-relevant, ocean-basin scales[11]. Indeed, on-shore measures of Southern Ocean marine predators have been used as regional indicators of ecosystem status for several decades[12]. Spatial aggregations of predators at sea identify not only areas that are important to the predator species themselves, which depend on lower trophic levels[13], but also areas of broader ecosystem importance such as regions of elevated productivity and biomass at lower trophic levels[14]. Combining information across predator species with diverse diets and life histories is essential for an ecosystem-wide approach that is less susceptible to factors affecting individual species[12]. Recognition of the value of tracking data for broad-scale conservation decision-making is growing[15].

Using predator tracking data to identify Areas of Ecological Significance

In the Southern Ocean, many predator species with differing diets and movement patterns have been tracked[16]. We synthesised tracking data from 4060 individuals of 17 species (Fig. 1a) to provide a circumpolar assessment of regions of ecological importance in the Southern Ocean. We identified regions preferred by multiple predator species as indicators of high levels of lower trophic biomass and biodiversity, and refer to these as Areas of Ecological Significance[17] (AES). Our definition of AES is not the same as Ecologically and Biologically Significant Marine Areas (EBSAs), or Key Biodiversity Areas (KBAs). However, it is consistent with several of the criteria used for defining EBSAs or KBAs, particularly biological productivity and diversity[8], and so provides a similar qualitative, integrated assessment of biodiversity patterns.

We assembled tracking data from 17 species of seabirds (12 species) and marine mammals (5 species), collected between 1991 and 2016[16]. We used habitat selection models (Methods and Supplement, Extended Data 1–3) of individual predator species and then combined their spatial predictions to identify regions important to our full suite of species (Fig. 1b). This enabled us to account for incomplete tracking coverage (i.e., colonies from which no animals were tracked) and predict habitat importance for each species across the entire Southern Ocean. Combined, these provided an integrated and spatially explicit assessment of areas of high biodiversity and biomass at multiple trophic levels. Sea surface temperature (SST) and wind strength were most often the best predictors of habitat selectivity in these species-specific models (Extended Data 4). SST has been linked to global patterns of marine biodiversity[18]; in the Southern Ocean it acts as an indicator of water masses with different ecological properties[19]. Wind exerts several influences including driving ocean currents and mixing, transport of iron, sea-ice dynamics, and determining primary production[20] and has been linked, for example, to the global distribution of albatrosses and petrels[21]. The importance of other predictor variables differed among species (Extended Data 4). The relationship between habitat selectivity and environmental predictors differed across species showing how species used their environments in different ways (Extended Data 5).

Distribution of Areas of Ecological Significance

Regions with the highest overall habitat importance scores were identified as Areas of Ecological Significance (AES; calculated as the upper decile of those scores). These were located over the Antarctic continental shelf (89% of AES pixels south of 60°S were over or within 200 km of the shelf) and in two northerly aggregations: one encompassing much of the Scotia Sea and surrounding waters, and the second covering the chain of sub-Antarctic islands from the Prince Edward Islands through to parts of the Kerguelen Plateau (Fig. 1c). Regions of lower importance were identified in the southern Pacific and Indian Oceans. The distribution of AES is associated with the availability of suitable breeding/resting habitat, as well as regional oceanography and sea-ice dynamics that affect biological production (Fig. 1c). The AES were based on a combination of island-breeding and wholly pelagic species, and therefore reflect broad-scale patterns of importance. These patterns are supported by: (i) broad-scale patterns of primary production — Southern Ocean land masses provide iron fertilization that stimulates downstream production in this otherwise iron-limited ecosystem[22]; (ii) historical whaling catches north of 60°S, which show that fewer whales were taken in the southern Indian or Pacific Oceans, and that the region identified as an AES in the south Atlantic corresponds with high whale catches[23]; and (iii) recent and historical estimates of Antarctic krill distribution, with high concentrations in the south Atlantic and lower concentrations in the south Pacific and southern Indian Ocean[24]. The AES in the south Atlantic corresponds to the area of elevated krill biomass, whereas the AES in the Indian Ocean partially corresponds to a region dominated by myctophid fish and other euphausiids[25].

Exposure of Areas of Ecological Significance to potential stressors in the Southern Ocean

The Southern Ocean is subject to several stressors that influence its ecosystems, including expanding resource extraction and rapid climate change[26]. We note that both temperature and wind, which were important parameters in many of our species-specific habitat models, are changing and projected to continue to do so[27].

Fishing has both direct effects, through incidental bycatch, and indirect effects through resource competition[28]. Many demersal finfish were exploited during the latter part of the 20th century, leading to the decimation of some stocks in the Antarctic and sub-Antarctic[5]. Finfish fishing in the Antarctic is now regulated and focused on toothfish species caught with longlines. Fisheries for Antarctic krill began in the 1960s and are now concentrated in the south Atlantic sector, most notably at the Antarctic Peninsula and South Shetland Islands, the South Orkney Islands and South Georgia[6]. Krill is managed with a low, precautionary catch limit, taking account of the key role it plays in the Antarctic food web. By global standards, fishing pressure in the Southern Ocean is low[29], but indications are that pressure on its marine resources will grow[2,5,6]. Fishing effort (Fig. 2a) was significantly different inside and outside of the AES (Fig. 2b), with a disproportionate amount of moderate-to-high effort (≥100 total hours of fishing) occurring inside AES. Of cells with moderate-to-high fishing effort, 37.9% were AES, despite AES only representing 10% of the study area. Areas of conspicuous fishing effort around southern South America, New Zealand, and Australia should be treated with caution, since our study does not include temperate predator species likely to figure prominently in these ecosystems (Fig. 2a). Nonetheless, relatively high intensity fishing areas directly relevant to the Southern Ocean occurred around the Falkland Islands/Islas Malvinas, where squid and some finfish are targeted, South Georgia (ice fish, krill and toothfish), at the West Antarctic Peninsula (krill), and over the Kerguelen (toothfish and ice fish) and Campbell (squid and finfish) plateaux[4–6]. Relatively important fisheries for toothfish also occur within the Ross Sea[30].

The physical attributes of the Southern Ocean are changing. Sea-ice is a critical component of high-latitude ecosystems, playing central roles in oceanographic, biogeochemical, and ecological processes. The biological consequences of sea-ice changes in the Southern Ocean include changes in breeding site availability or access, prey availability, and changes to ecosystem structure and function[31]. The pattern of change in sea-ice in the Antarctic displays considerable regional and temporal variation. In the West Antarctic Peninsula, sea-ice extent has declined markedly in recent decades, but has increased in other areas[32]. Most climate projections indicate that overall sea-ice will decline over the next century[27]. Given the broad influence of both SST and wind on ecosystems, these components can also influence aspects of an animal's biology, including breeding phenology, foraging success, survival and reproductive performance[26]. However, when we contrasted the rates of change of sea-ice duration, SST and wind patterns inside and outside of the AES there were only slight differences, and considerable regional variation (Extended Data 6). The subtle nature of the differences in environmental change inside AES versus outside them does not negate the fact that the study area, overall, is undergoing marked changes in physical environmental processes, and that ecologically important areas are not being spared from these changes.

Assessment of current and proposed spatial management

Management of marine systems is complex, especially in areas beyond national jurisdiction[33] where international effort is required, particularly for species that move between national and international waters[34]. Relevant management includes traditional process-oriented tools, such as individual species protection, stock assessments, decision rules and catch limits, as well as spatial tools such as marine protected areas (MPAs)[35], but also altered fishing practices for mitigating bycatch[36]. In the high-latitude Southern Ocean, the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) employs an ecosystem-based management framework intended to ensure that there are no long-term effects from fisheries on marine ecosystems[37]. This includes setting precautionary, spatially explicit catch quotas and a call for the establishment of a network of MPAs, the design considerations of which can include the potential to provide climate change refugia and the inclusion of reference areas to help separate the effects of fishing from climate related environmental change. Both approaches will benefit from better understanding of the locations of AES. Outside the CCAMLR framework, MPAs have also been established by sovereign management authorities around some sub-Antarctic islands (Fig. 3a). Several other MPAs are currently under development, including within CCAMLR and by national authorities (Fig. 3a). However, the level of protection afforded by any individual MPA depends upon its governance structure and the type and level of permitted activities (e.g., fishing)[9,38]

An appropriately designed protected-area network can help buffer the effects of climate change and reduce the effect of stressors such as bycatch or competition from fisheries[39]. We therefore quantified the coverage and placement of individual MPAs with reference to identified AES. Overall, 7.1% of the ocean south of 40°S is currently protected by MPAs, and this would increase to 11.2% if all currently proposed MPAs were implemented (Fig. 3b). This already meets, in a regional setting, the 10% global Aichi Target 11 for 2020. The Southern Ocean's level of protection is high by global standards, as only 3.6% of the world's oceans fall within MPAs, increasing to 7.3% with the addition of planned and announced MPAs[38]. However, protection needs to be targeted at areas of high conservation value, including those important for the persistence of biodiversity[9]. Existing MPAs cover 27% of the AES identified (Fig. 3b). Southern Ocean MPAs are predominantly in sub-Antarctic regions, and here they show high levels of congruence with AES (Fig. 3a). Of note is the Davis Bank region, south of the Falkland Islands/Islas Malvinas, where there are high levels of fishing inside AES (Fig. 1, 2a, b). This area is now part of a recently implemented MPA by Argentina (Fig. 3a). Adoption of proposed MPAs for the Antarctic continental margins would raise MPA coverage of AES to 39% (Fig. 3b), including areas in East Antarctica, the Weddell Sea, and the Antarctic Peninsula. The largest total AES (4.0 million km^2, 56% of AES) are under CCAMLR jurisdiction (Fig. 3a,c), followed by 1.9 million km^2 (27% of AES) in national waters (EEZs) and only 1.2 million km^2 (16% of AES) are outside the CCAMLR Convention Area and national waters (Fig. 3c). Implementation of MPA proposals would benefit Southern Ocean ecosystems, especially those in the Antarctic Peninsula, East Antarctic and Weddell Sea.

Likely effects of future climate change

We estimated the likely effects of future climate change on the distribution of AES under two Representative Concentration Pathway (RCP) simulations: a medium-forcing scenario (RCP4.5) and a more extreme, high-forcing scenario (RCP8.5)[40]. For each scenario, eight global climate models, considered to be most suitable for Southern Ocean studies by reliably reproducing extant sea-ice conditions, were used to predict locations of AES-like habitat in 2100. Here we discuss only the RCP8.5 results, since current CO_2 emissions are in line with this scenario[41]. Results for the moderate RCP4.5 scenario are presented in Extended Data 7. There was an overall reduction in AES-like area (-3.3%), partitioned into an increase in sub-Antarctic AES-like cells (+5.7%), but outweighed by a decrease in Antarctic AES-like cells (-10.2%).

In the sub-Antarctic, AES-like areas generally moved south (Fig. 4a), resulting in an overall growth in sub-Antarctic AES area (Fig. 4b). This general southward migration of important habitat is consistent with projections for individual predator species (e.g., [42]) as well as for other species including krill and salps[43,44]. The advantages for predators from the overall increase in area of sub-Antarctic AES may be offset by increased cost of travel to more distant foraging grounds, at least for diving central place foragers (penguins and fur seals), while volant species (albatrosses and petrels) or those unconstrained by terrestrial breeding sites (whales) may benefit from increased sub-Antarctic foraging opportunities (e.g., [45]). Changes in the future distribution of AES-like areas along the Antarctic margin are more spatially heterogeneous, with areas of AES loss interspersed with areas of AES gain or retention (Fig. 4a). However, there will be a net loss (-10.2%) of AES-like cells in the CCAMLR Convention area (Fig. 4b). The heterogeneity of this pattern is due in part to the dynamic nature of the high-latitude Antarctic marine environment and the uncertainty across a number of climate-model variables in this region. This uncertainty is due to the variability in skill of models in reproducing current climate and the large envelope of projected responses from those models. Our projections are based on unchanged future availability (i.e., colony locations and sizes) and species-environment relationships. However, as species adapt to future pressures and changes to available breeding habitat, populations are likely to change both their preferred colony locations and habitat usage. Sub-Antarctic-breeding species have limited availability of alternative breeding sites, but colony sizes might change. Ice-breeding species may be able to relocate, whilst land-breeding species that require ice-free terrain may be able to occupy previously vacant areas, or some may move to regions that become ice-free due to changing local conditions (e.g., [46]). Our projected loss of AES-like habitat on the Antarctic margin suggests that these populations will be under pressure as the climate continues to change, and therefore continued monitoring of these species, and on-going assessment of the effectiveness of management actions (e.g. MPAs), will be important. Monitoring of colonies will need to detect local colonisations, particularly when populations are small[47]. As part of the designation of MPAs within CCAMLR, research and monitoring plans are necessary and required; *inter alia*, these plans should consider changes to species-environment relationships and other dynamic processes within and adjacent to the protected area, given the pressures of ongoing climate change.

There was a mixed response across the eight climate models, with changes in the number of AES-like cells included in current MPAs ranging from -8.7% to +8.4% (Fig 4b). When the proposed MPAs are included (current + proposed), all climate models indicated a decrease (between -16.9% to -0.9%) in the number of AES-like cells within MPAs. This suggests that proposed MPAs are in areas projected to become less-similar to existing AES by 2100. Any protection afforded by MPAs in such areas could provide better medium-term opportunities for populations to adapt as they will not have to cope with both climate change and other stressors during that period.

Conclusion

Our work provides strong evidence in support of the ecological importance of existing and proposed Southern Ocean MPAs. By integrating tracking data from a suite of predators we identified regions likely to have high biodiversity and biomass of the prey (and concomitant ecosystems) of the animals that were tracked. Our AES are clearly candidates for protection; as such, the implementation of the proposed MPAs within the CCAMLR region would greatly increase the protection of important Southern Ocean habitat. Several MPA proposals have failed to reach consensus within the CCAMLR process and, even when adopted result in MPAs with varying degrees of protection. Many sources of input are needed to establish MPAs, but the AES described here will play a key role in making the scientific case in this multi-faceted process[2,48], by providing ecosystem-level analysis of areas most warranting protection. MPA design should also consider future conditions. Pressures on AES due to climate change will affect all parts of the Southern Ocean, but their effects are likely to be strongest along the Antarctic margin. Species responses to these pressures are currently difficult to predict, highlighting the importance of continued monitoring as part of ongoing management actions. Because only 16% of all Southern Ocean AES lie outside the CCAMLR Convention Area or national waters, the responsibilities for these future actions fall mostly to CCAMLR members and those nations with sovereign territory in the sub-Antarctic. Adaptive management approaches to conservation measures (including MPAs) will be necessary to deal with these future changes in a timely way. The Southern Ocean can be an exemplar of how science, policy and management can interact to meet the challenges of a changing planet. In the Southern Ocean, these challenges will be considerable, including increased fishing pressure as the global demand for marine resources grows[49]. Our results highlight where future science-informed policy efforts might best be directed, including both adaptive spatial protection and improved robust fisheries management. Similar synthetic approaches should capitalise on the increasing amount of tracking data being collected through large-scale initiatives (e.g., [50]) to indicate regions in need of protection globally.

REFERENCES [main text]

1. Stark, J. S., Raymond, T., Deppeler, S. L. & Morrison, A. K. *Antarctic Seas*. *World Seas: an Environmental Evaluation* (Elsevier Ltd., 2019). doi:10.1016/b978-0-12-805068-2.00002-4.
2. Chown, S. L. & Brooks, C. M. The State and Future of Antarctic Environments in a Global Context. *Annu. Rev. Environ. Resour.* **44**, 1–30 (2019).
3. Ainley, D. G. & Blight, L. K. Ecological repercussions of historical fish extraction from the Southern Ocean. *Fish Fish.* **10**, 13–38 (2009).
4. Agnew, D. J., Hill, S. L., Beddington, J. R., Purchase, L. V & Wakeford, R. C. Sustainability and Management of Southwest Atlantic Squid Fisheries. *Bull. Mar. Sci.* **76**, 579–594 (2005).
5. Kock, K. H., Reid, K., Croxall, J. & Nicol, S. Fisheries in the Southern Ocean: An ecosystem approach. *Philos. Trans. R. Soc. B Biol. Sci.* **362**, 2333–2349 (2007).
6. Nicol, S., Foster, J. & Kawaguchi, S. The fishery for Antarctic krill - recent developments. *Fish Fish.* **13**, 30–40 (2012).
7. Swart, N. C., Gille, S. T., Fyfe, J. C. & Gillett, N. P. Recent Southern Ocean warming and

freshening driven by greenhouse gas emissions and ozone depletion. *Nat. Geosci.* **11**, 836–841 (2018).

8. CBD. *Decision Adopted by the Conference of the Parties to the Convention on Biological Diversity at its Ninth Meeting. UNEP/CBD/COP/DEC/IX/20*. (2008).
9. Visconti, B. P. *et al.* Protected area targets post-2020. *Science* **364**, 239–241 (2019).
10. Hazen, E. L. *et al.* Marine top predators as climate and ecosystem sentinels. *Front. Ecol. Environ.* fee.2125 (2019) doi:10.1002/fee.2125.
11. Constable, A. J. *et al.* Developing priority variables ('ecosystem Essential Ocean Variables' - eEOVs) for observing dynamics and change in Southern Ocean ecosystems. *J. Mar. Syst.* **161**, 26–41 (2016).
12. Reid, K., Croxall, J. P., Briggs, D. R. & Murphy, E. J. Antarctic ecosystem monitoring: Quantifying the response of ecosystem indicators to variability in Antarctic krill. *ICES J. Mar. Sci.* **62**, 366–373 (2005).
13. Cury, P. M. *et al.* Global Seabird Response to Forage Fish Depletion—One-Third for the Birds. *Science* **334**, 1703–1706 (2011).
14. Nicol, S. *et al.* Ocean circulation off east Antarctica affects ecosystem structure and sea-ice extent. *Nature* **406**, 504–507 (2000).
15. Hays, G. C. *et al.* Translating Marine Animal Tracking Data into Conservation Policy and Management. *Trends Ecol. Evol.* **34**, 459–473 (2019).
16. Ropert-Coudert, Y. *et al.* The Retrospective Analysis of Antarctic Tracking Data Project. *Sci. Data*.
17. Hindell, M. A. *et al.* Foraging habitats of top predators, and Areas of Ecological Significance, on the Kerguelen Plateau. in *The Kerguelen Plateau: marine ecosystem and fisheries* (eds. Duhamel, G. & Welsford, D.) 203–215 (Societe Francaise d'Ichtyologie, 2011).
18. Tittensor, D. P. *et al.* Global patterns and predictors of marine biodiversity across taxa. *Nature* **466**, 1098–1101 (2010).
19. Hindell, M. A. *et al.* Decadal changes in habitat characteristics influence population trajectories of southern elephant seals. *Glob. Chang. Biol.* **23**, 5136–5150 (2017).
20. Sallée, J.-B., Speer, K. G. & Rintoul, S. R. Zonally asymmetric response of the Southern Ocean mixed-layer depth to the Southern Annular Mode. *Nat. Geosci.* **3**, 273–279 (2010).
21. Davies, R. G., Irlich, U. M., Chown, S. L. & Gaston, K. J. Ambient, productive and wind energy, and ocean extent predict global species richness of procellariiform seabirds. *Glob. Ecol. Biogeogr.* **19**, 98–110 (2010).
22. Ardyna, M. *et al.* Delineating environmental control of phytoplankton biomass and phenology in the Southern Ocean. *Geophys. Res. Lett.* **44**, 5016–5024 (2017).
23. Ropert-Coudert, Y. *et al.* Chapter 8. Biogeographic pattern of birds and mammals. in *Biogeographic Atlas of the Southern Ocean* (eds. De Broyer, C. et al.) 364–387 (Scientific

Committee on Antarctic Research, 2014).

24. Atkinson, A. *et al.* Oceanic circumpolar habitats of Antarctic krill. *Mar. Ecol. Prog. Ser.* **362**, 1–23 (2008).

25. Nicol, S. & Raymond, B. Pelagic Ecosystems in the Waters off East Antarctica (30° E-150° E). in *Antarctic Ecosystems* 243–254 (John Wiley & Sons, Ltd, 2012). doi:10.1002/9781444347241.ch8.

26. Constable, A. J. *et al.* Climate change and Southern Ocean ecosystems I: How changes in physical habitats directly affect marine biota. *Glob. Chang. Biol.* **20**, 3004–3025 (2014).

27. Meijers, A. J. S. The Southern Ocean in the Coupled Model Intercomparison Project phase 5. *Philos. Trans. R. Soc. A* **372**, 20130296 (2014).

28. Dayton, P. K., Thrush, S. F., Agardy, M. T. & Hofman, R. J. Environmental effects of marine fishing. *Aquat. Conserv. Mar. Freshw. Ecosyst.* **5**, 205–232 (1995).

29. Kroodsma, D. A. *et al.* Tracking the global footprint of fisheries. *Science* **359**, 904–908 (2018).

30. Mormede, S., Dunn, A., Parker, S. & Hanchet, S. Using spatial population models to investigate the potential effects of the Ross Sea region Marine Protected Area on the Antarctic toothfish population. *Fish. Res.* **190**, 164–174 (2017).

31. Massom, R. A. & Stammerjohn, S. E. Antarctic sea ice change and variability – Physical and ecological implications. *Polar Sci.* **4**, 149–186 (2010).

32. Vaughan, D. *et al.* Observations: Cryosphere. in *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (eds. Stocker, T. F. et al.) 317–382 (Cambridge University Press, 2013).

33. Game, E. T. *et al.* Pelagic protected areas: the missing dimension in ocean conservation. *Trends Ecol. Evol.* **24**, 360–369 (2009).

34. Harrison, A.-L. *et al.* The political biogeography of migratory marine predators. *Nat. Ecol. Evol.* **2**, 1571–1578 (2018).

35. Hilborn, R. Marine biodiversity needs more than protection: to sustain the seas, advocates of marine protected areas and those in fisheries management must work together, not at cross purposes, urges. *Nature* **535**, 224–226 (2016).

36. Phillips, R. A. *et al.* The conservation status and priorities for albatrosses and large petrels. *Biol. Conserv.* **201**, 169–183 (2016).

37. Constable, A. J., De LaMare, W. K., Agnew, D. J., Everson, I. & Miller, D. Managing fisheries to conserve the Antarctic marine ecosystem: Practical implementation of the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR). *ICES J. Mar. Sci.* **57**, 778–791 (2000).

38. Sala, E. *et al.* Assessing real progress towards effective ocean protection. *Mar. Policy* **91**,

11–13 (2018).
39. Roberts, C. M. *et al.* Marine reserves can mitigate and promote adaptation to climate change. *Proc. Natl. Acad. Sci.* **114**, 6167–6175 (2017).
40. Moss, R. H. *et al.* The next generation of scenarios for climate change research and assessment. *Nature* **463**, 747–756 (2010).
41. Peters, G. P. *et al.* The challenge to keep global warming below 2 °C. *Nat. Clim. Chang.* **3**, 4–6 (2013).
42. Péron, C., Weimerskirch, H. & Bost, C.-A. Projected poleward shift of king penguins' (*Aptenodytes patagonicus*) foraging range at the Crozet Islands, southern Indian Ocean. *Proc. R. Soc. B* **279**, 2515–2523 (2012).
43. Atkinson, A. *et al.* Krill (*Euphausia superba*) distribution contracts southward during rapid regional warming. *Nat. Clim. Chang.* **9**, 142–147 (2019).
44. Atkinson, A., Siegel, V., Pakhomov, E. & Rothery, P. Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* **432**, 100–103 (2004).
45. Weimerskirch, H., Louzao, M., de Grissac, S. & Delord, K. Changes in Wind Pattern Alter Albatross Distribution and Life-History Traits. *Science* **335**, 211–214 (2012).
46. Cristofari, R. *et al.* Climate-driven range shifts of the king penguin in a fragmented ecosystem. *Nat. Clim. Chang.* **8**, 245–251 (2018).
47. Southwell, C. *et al.* Recent studies overestimate colonization and extinction events for Adelie Penguin breeding colonies. *Auk* **134**, 39–50 (2017).
48. Jacquet, J., Blood-patterson, E., Brooks, C. & Ainley, D. ' Rational use ' in Antarctic waters. *Mar. Policy* **63**, 28–34 (2016).
49. Grémillet, D. *et al.* Persisting Worldwide Seabird-Fishery Competition Despite Seabird Community Decline. *Curr. Biol.* **28**, 4009-4013.e2 (2018).
50. Block, B. A. *et al.* Tracking apex marine predator movements in a dynamic ocean. *Nature* **475**, 86–90 (2011).

METHODS

Analytical overview

We assembled tracking data from 17 species of seabirds and marine mammals, collected between 1991 and 2016, from across the Antarctic predator research community[16]. Birds and mammals comprise the majority of top predator species in the Southern Ocean, which has few other large, highly mobile marine predator taxa (bony and cartilaginous fishes). These include toothfish, southern bluefin tuna (*Thunnus maccoyii*, which occur in the northernmost part of our study area), and a small number of shark species. Very few of these fish and shark species have been tracked, with very few tracking data available south of 40°S[51]. However, this does not detract from the underlying logic of our approach: that by using the at-sea distributions of an ecologically diverse suite of predators we can identify areas of ecological importance. This benchmark dataset represents 4060 individual tracks and more than 2.9 million location estimates (Fig. 1a). After filtering and quality control, we retained 2823 tracks comprising 2.3 million locations[16]. The ~30% of tracks that were excluded were those with poor quality location fixes that could not be properly filtered, tracks from individuals that did not actually depart the colony, or tracks other problems detected during the rigorous quality control process that we implemented. The full process is described in our companion data paper[16], which makes available all of the data for use by the broader community, without providing further analytical investigation to consider the matters raised here. The environmental covariate values along each of these tracks (the *used* habitat) were compared statistically with the habitat *available* to each animal, thereby allowing each species' habitat selection to be determined (e.g., [52,53]; see Extended Data 1 and 2). We fitted habitat selection models for different life-history stages within a species. Despite the considerable size of the data set, it is not an exhaustive representation of animals from all known colonies (for central-place foragers) or geographic regions (for non-central-place foragers). To account for incomplete tracking coverage, we used the fitted habitat selection models to map habitat importance for each life-history stage of each species across the entire Southern Ocean, including areas around colonies without tracking deployments (Extended Data 3). For each species we calculated the average habitat importance across life-history stages. For colony-breeding species, colony sizes were used to weight the habitat importance values, upweighting areas important to large colonies (Extended Data 8). Southern Ocean predator species can be clustered into Antarctic and sub-Antarctic species (Extended Data 9). We mapped assemblage-level habitat importance (Extended Data 10) for each of these two groups (hereafter "overall habitat importance" maps) by averaging across species-level maps. To calculate the overall map, we took the maximum of the two assemblage-level importance values in each cell. Areas with high values of overall habitat importance (in the top decile of values) indicate areas that are attractive to many species; these represent Areas of Ecological Significance[17]. We then compared the overall habitat importance values inside and outside Areas of Ecological Significance in the context of fishing effort and changes in physical environmental conditions (duration of sea-ice cover, sea surface temperature (SST) and wind speed). We finally quantified the spatial protection afforded to Areas of Ecological Significance under current and proposed spatial management plans.

We describe the methods in more detail in the Supplementary Information. We conducted all the analyses in R[54].

Tracking data

The data represent output from a variety of tracking tag types, providing location estimates at different spatio-temporal resolution and accuracy. We applied a state-space model[55] to estimate most probable locations at regular temporal intervals while accounting for potential errors in the location estimates with automatic and manual quality control before and after filtering[16]. While this procedure does not make the track from a light-based tag as accurate as one from GPS device, it does provide a consistent characterization of the positional accuracy across different tag types, allowing the uncertainty in position to propagate into the uncertainty in the parameters of the fitted movement model and in the track simulation step (see below). We further note that the light-based tag deployments were made almost exclusively on sub-Antarctic animals (albatrosses and fur seals). The spatial scale of our results (Areas of Ecological Significance) in the sub-Antarctic zone (~5 million km^2) is considerably larger than the likely scale of positional error of light-based tags (~100 km) and so we do not believe that using a mixture of tag types has adversely affected our results.

Life-history stages

Most of the species in the study are central-place foragers (*i.e.*, they return periodically to land or sea-ice to breed, moult or rest). The constraints faced by these predators at different stages in their life-history cycle mean that their movements differ markedly across these stages. We therefore fitted models separately for up to five predefined life-history stages in each species' breeding cycle. We automatically assigned tracks to these stages based on calendar date, with manual reassignment where necessary following examination of individual movement patterns. This resulted in 40 data subsets (17 species * 1–4 life-history stages) with sufficient data for habitat selection modelling (Supplementary Information Table S1).

Simulating tracks to estimate available space

The observed locations only provide information about where animals occur, not about where they could have gone. To estimate the geographic space potentially available to animals, we simulated sets of tracks for each observed track. For each observed track, we simulated 50 tracks using the movement model described above[55]. This yielded simulated tracks with movement characteristics (distributions of step length and turning angle) that are the same as the observed track, but they are random and independent of environmental effects. Thus, the simulated tracks offer an estimate of the geographic space that each animal could have occupied (given its movement characteristics and track length) if it had no habitat preferences. The environmental differences between the available geographic space and the utilized geographic space allow the habitat selection of the organisms to be estimated, as detailed below. Locations at the animal's home colony, and locations at known terrestrial resting sites, were fixed at the corresponding time and date in the simulated tracks in order to accurately simulate central place foraging behaviour (Supplementary Information).

Environmental data

To characterize the biophysical environment at observed and simulated locations, we compiled a suite of 19 environmental covariates (Extended Data 2, Supplementary Information Table S2) and extracted the value of these at each location. The covariates were remotely-sensed, measured *in-situ* or model-estimated and represent biophysical features that influence the movement, distribution and density of marine predators (e.g., [52,53]). It was not computationally feasible to temporally match environmental data to each location estimate. Rather, we created a climatology spanning each tracking data subset (species by life-history stage combination), using the predefined stage dates. We took the mean (or standard deviation) of the environmental data that fell on these days of the year (stage dates) over the whole study period (November 1991 to June 2016). Some covariates (e.g., salinity difference) were only available as monthly climatologies, and we used the months corresponding with the stage dates to calculate the mean (or standard deviation). All covariates were resampled to a 0.1° x 0.1° grid; hereafter we refer to the pixels of this grid as 'cells'. We checked the covariates for each data subset for missing values and if >10% of values were missing we excluded the covariate from that model. This influenced mainly chlorophyll-a concentration, which was excluded from 17 of the 40 habitat models (Supplementary Information Table S1). This affected life-history stages with a large proportion of winter days, since chlorophyll-a data has poor winter satellite coverage due to being obscured by high cloud cover. However, chlorophyll-a was rarely an important predictor in the models in which it was included; thus, excluding chlorophyll-a from models probably had only a negligible effect.

Habitat selection models

We used a habitat selection modelling framework[56] to model and predict the space use of marine birds and mammals of the Southern Ocean. These models use the observed locations of each individual animal and an estimate of the geographic space available to each individual, along with covariates that characterize their environment. The environmental differences between the habitat that was utilized and the habitat that was available allow the habitat selection of the organisms to be estimated. To fit the models, we used boosted regression trees, a machine-learning algorithm that produces an ensemble of regression trees that have been iteratively fitted in a boosting process to improve accuracy[57]. We tested several other algorithms but boosted regression trees showed the best predictive performance in another study[53] and in our tests. For a given location, the response variable was whether the location was an observed or simulated (available) location, and the explanatory covariates were the associated environmental covariates. Boosted regression trees have four parameters that must be set: the number of trees (boosting iterations), the maximum tree depth, the learning rate (shrinkage) and the minimum number of observations in a node. We chose these values as the combination that minimised the area under the receiver operating characteristic curve (a measure of model predictive performance) during 10-fold cross-validation. We also used this metric to evaluate the final fitted models. We used the fitted model to generate spatial predictions for the entire study region and we estimated the uncertainty associated with these predictions using a bootstrap approach (Supplementary Information)

Accessibility model

The modelling procedure described above does not account for the accessibility of a given location to an individual animal (in effect, it estimates the habitat selection of a given location in terms of its environmental characteristics, but without considering whether or not the animal could actually reach that location). For central-place foragers in particular, this is an important consideration. We therefore used a second set of models to account for this[53]. We modelled accessibility in terms of the number of observed + simulated locations in a given cell as a function of that cell's distance to the deployment colony. We fitted binomial models with a smooth, monotonic decreasing constraint[58], under the assumption that the accessibility of cells should decrease with geographic distance. To estimate uncertainty, we sampled curves from the posterior distribution of each fitted accessibility model to use in a bootstrap approach (Supplementary Information).

We used these models to predict the accessibility of each cell over the study region to each species during each life-history stage (that is, given the distance of a cell from a colony, the fitted accessibility model provides an estimate of the probability that animals from that colony would be able to visit that cell). For colony-breeding species (those other than humpback whales, crabeater and Weddell seals), colony sizes were used to weight this accessibility estimate: for a given cell, the accessibility from all known colonies of that species was calculated. A weighted mean of these accessibilities was then taken, using colony sizes as weights. Thus, this weighted accessibility represents the probability that a randomly-selected individual from the global population would be able to visit that cell, effectively upweighting cells in the vicinity of large colonies.

For the non-colony breeding, ice-associated seals (crabeater and Weddell seals), we modelled accessibility as a function of distance beyond the ice edge (15% ice concentration contour), rather than distance to the colony. For humpback whales, we assumed that the whole study area was equally accessible.

Habitat Importance

Transforming output and combining models

The habitat selection models predict the value of the habitat at a location given that the animals could access that location. The predictions of the habitat selection models were therefore multiplied by the predictions of the accessibility models to yield an index that reflects both the habitat selection of each cell and its accessibility to the animals. This is not an estimate of the probability of a species using a given cell, because that probability also depends on the prevalence of the species[59]. Since prevalence varies between species, our habitat selection estimates cannot be compared directly between species. We therefore partitioned the cells into decreasing percentiles based on area[52] in order to obtain a habitat importance map expressed in terms of area (e.g., cells with values of 90 or higher represent the top 10% most important habitat by area for that species). We refer to this as habitat importance, and these maps can be compared among species. To create a single habitat importance layer for each species, we averaged the stage-specific habitat importance layers.

Species grouping

We calculated community-level habitat importance by averaging species-specific habitat importance maps. Sub-Antarctic regions are naturally more species-diverse than those of the Antarctic, and so a simple average of all species together tended to strongly favour sub-Antarctic areas simply because of their greater species diversity. To account for the differences in species richness between the Antarctic and sub-Antarctic, we first defined two species groups using an Unweighted Pair Group Method with Arithmetic Mean hierarchical clustering with Manhattan distance, applied to habitat importance scores (Extended Data 9). This produced two clear groups: an Antarctic species group (emperor penguin, crabeater seal, Antarctic petrel, Adélie penguin, Weddell seal) and a sub-Antarctic species group (Antarctic fur seals, black-browed albatross, wandering albatross, sooty albatross, grey-headed albatross, king penguin, macaroni/royal penguin, light-mantled albatross, white-chinned petrel). The wide-ranging humpback whales and elephant seals did not clearly fall into either cluster, and so were treated as belonging to both groups. The mean habitat importance was calculated for each of these groups separately and then combined (Extended Data 10) by taking the maximum of the two values (Antarctic and sub-Antarctic) in each pixel. We refer to this final layer as the overall habitat importance.

Areas of Ecological Significance

To identify the most important areas, we calculated the 90th percentile (top decile) of the overall habitat importance values. Cells with overall habitat importance values above this threshold together comprised Areas of Ecological Significance.

Environmental pressures

To assess past environmental stressors on the Southern Ocean ecosystem, we calculated change in SST, wind speed and sea-ice duration. We selected SST and wind because they were frequently the most important predictor variables in the habitat models (Extended Data 4), and sea-ice concentration since this was an important predictor for Antarctic species. Moreover, these variables are considered important drivers of ocean and ecosystem dynamics (e.g., [18,60]) and key axes on which environmental change in the Southern Ocean has been detected (e.g., [26]). For each cell, we calculated change in SST (°C) or wind speed (m/s) as the difference between mean SST or wind speed in 1987–1999 and 2007–2017. For sea-ice duration, we calculated the difference in the mean number of days per year that each pixel had a sea-ice concentration >15%, for the same periods. These periods represent the decades at the beginning and end of a 30-year period covering our study period. Thirty years is also the recommended period for climate assessments[61]. We also obtained data on fishing effort, which is considered to be a major environmental stressor in many regions of the Southern Ocean (e.g., [29,62]) from the Global Fishing Watch dataset, covering the period 2012–2016[29]. We compared the values of these four stressors in the Areas of Ecological Significance and outside cells using random permutation tests with 10,000 permutations. The null hypothesis is that stressor values inside and outside Areas of Ecological Significance are from the same distribution.

Future projections of Areas of Ecological Significance

Our predicted AES (under current environmental conditions) are determined by both the oceanographic and climatic conditions of an area, as well as the accessibility of that area to each of our species of interest. In principle it would be possible to use future projections of environmental data and accessibility along with our fitted models in order to obtain future projections of AES. However, some predictor variables are not available from the climate models used for the future projections, and while other variables might appear to be available, they have different properties due to factors such as different temporal and spatial resolution in the output, or the ability of the climate model to resolve the relevant processes. For example, sea surface height from satellite altimetry gives information about frontal and mesoscale features. Yet, while sea surface height is available as an output from many CMIP5 models, those models do not explicitly resolve mesoscale features[63] and so the model-output sea surface height data will not be acting as a proxy for the same oceanographic properties that satellite-derived altimetry does.

To assess future distributions of AES-like habitat, we therefore used a k-nearest neighbour classifier approach, conceptually similar to climate analogues (e.g., [64]). For each grid cell we compiled current (end of 20th century) environmental conditions, as well as projected conditions at the end of the 21st century from climate models (see below). In terms of accessibility, most of our study species breed in colonies, and “accessibility” for these species is determined by both the geographic distribution of their colonies as well as the colony sizes. Currently, future projections of colony location and size do not exist for our study species, although initial work has begun for some species (e.g., [46]). Colony locations and sizes were therefore assumed to remain constant, and so the accessibility of each grid cell to each species was assumed to remain unchanged. For each grid cell, we compared its projected future environmental and accessibility conditions to every cell in the current (20th century) grid and selected the most similar five cells. If the majority of those cells were from current AES areas, the projected cell was labelled as “AES-like”, otherwise “not AES-like”. These projections therefore provide an indication of the future distribution of AES-like environmental conditions, under the assumptions that colonies do not move or change in size, and that the animals do not change their habitat preferences. These assumptions are unlikely to hold in reality; however, examining the changes in AES-like habitat under these assumptions allows us to isolate the effects of environmental change from colony or habitat-usage changes. As environmental change occurs, species are likely to adapt by changing their colony distributions and habitat usage. The AES projections offer insights into the likely distribution of environmental pressures, and thus where adaptation by species might be important.

Climate data were compiled from eight global climate models (ACCESS1.0, BCC-CSM1.1, CanESM2, CMCC-CM, EC-EARTH, GISS-E2-H-CC, MIROC-ESM, and NorESM-M) considered to be most suitable for Southern Ocean studies, by virtue of reliably reproducing extant sea-ice conditions[65]. These models were from phase five of the World Climate Research Programme's Coupled Model Intercomparison Project (CMIP5). For each model, we extracted data for a 30-year period concomitant with our tracking data (1976–2005), and for a thirty-year end-of-21st-century (2071–2100) period. We extracted future (2071–2100) climate data from projections under two Representative Concentration Pathway (RCP) simulations: a medium-forcing scenario (RCP4.5, which assumes that society implements changes to limit future CO_2 emissions in the near future, with peak emissions occurring in 2040) and a more extreme, high-forcing scenario (RCP8.5, which assumes little curbing of emissions and retains a strong reliance on fossil fuels into the foreseeable future)[40]. Reference (1976-2005) data were extracted from hindcast model runs that attempt to simulate historical conditions, and consequently use observed CO_2 concentrations over the past 160 years to guide the models.

A maximum of eight variables were extracted for each model, depending on the available data (not all models provide all variables), at monthly time resolution. The variables used were sea-ice concentration, SST, sea surface salinity, sea surface height, the spatial gradient of sea surface height, near-surface current speed, near-surface wind speed, and surface downward heat flux. The 30-year mean and standard deviation of each variable was calculated over summer (December to February) and winter (July to September) months. All variables were normalized to the range 0–1 prior to further analysis.

The resulting set of up to 48 predictors (mean and SD of up to 8 environmental variables, each for summer and winter, plus accessibility layers for 16 species) naturally showed high correlation between many of the variables. We used a principal components analysis to reduce the dimensionality of this data set, choosing the lowest number of principal components required to explain at least 95% of the variance in the original data; this number ranged from 14–17 components, depending on the model and scenario. For each projected-climate cell, the nearest neighbours in the historical-climate grid were calculated using Euclidean distance on these normalized and dimension-reduced data.

Animal Ethics Statement.

All work was conducted under the appropriate National or Institutional Ethics approvals. There were: Argentina (Dirección Nacional del Antártico), Australia (Australian Antarctic program; the University of Tasmania a, Belgium (Belgian Science Policy Office), Brazil (Brazilian Antarctic Programme; National

Council for Scientific and Technological Development - CNPq; Ministry of Science, Technology, Innovation and Communications – MCTIC; Ministry of the Environment; CAPES), France (Agence Nationale de la Recherche; Terres Australes et Antarctiques Françaises), Germany (Deutsche Forschungsgemeinschaft, Hanse-Wissenschaftskolleg - Institute for Advanced Study), Italy (Programma Nazionale di Ricerche in Antartide, PNRA), Japan (Japanese Antarctic Research Expedition; JSPS Kakenhi grant), Monaco (Fondation Prince Albert II de Monaco), New Zealand (Ministry for Primary Industries - BRAG; Pew Charitable Trusts), Norway (Norwegian Antarctic Research Expeditions; Norwegian Research Council), Portugal (Foundation for Science and Technology), South Africa (Department of Environmental Affairs; National Research Foundation; South African National Antarctic Programme), UK British Antarctic Survey; Natural Environment Research Council, and USA U.S. AMLR Program of NOAA Fisheries; US Office of Polar Programs.

Data availability

The tracking data are available in[16]o. Computer code is available at https://github.com/SCAR/RAATD

REFERENCES [methods]

51. Queiroz, N. *et al.* Global spatial risk assessment of sharks under the footprint of fisheries. *Nature* **572**, 461–466 (2019).
52. Raymond, B. *et al.* Important marine habitat off east Antarctica revealed by two decades of multi-species predator tracking. *Ecography* **38**, 121–129 (2015).
53. Reisinger, R. R. *et al.* Habitat modelling of tracking data from multiple marine predators identifies important areas in the Southern Indian Ocean. *Divers. Distrib.* **24**, 535–550 (2018).
54. R Core Team. R: A Language and Environment for Statistical Computing. (2018).
55. Jonsen, I. D. *et al.* Movement responses to environment: fast inference of variation among southern elephant seals with a mixed effects model. *Ecology* **100**, 1–8 (2019).
56. Aarts, G., MacKenzie, M., McConnell, B., Fedak, M. & Matthiopoulos, J. Estimating space-use and habitat preference from wildlife telemetry data. *Ecography* **31**, 140–160 (2008).
57. Elith, J., Leathwick, J. R. & Hastie, T. A working guide to boosted regression trees. *J. Anim. Ecol.* **77**, 802–813 (2008).
58. Pya, N. & Wood, S. N. Shape constrained additive models. *Stat. Comput.* **25**, 543–559 (2015).
59. Phillips, S. J. *et al.* Sample selection bias and presence-only distribution models: Implications for background and pseudo-absence data. *Ecol. Appl.* **19**, 181–197 (2009).
60. Rintoul, S. R. The global influence of localized dynamics in the Southern Ocean. *Nature* **558**, 209–218 (2018).
61. World Meteorological Organization. *Guide to Climatological Practices (WMO-No. 100)*. (World Meteorological Organization, 2011).
62. Halpern, B. S., Selkoe, K. A., Micheli, F. & Kappel, C. V. Evaluating and ranking the vulnerability

of global marine ecosystems to anthropogenic threats. *Conserv. Biol.* **21**, 1301–1315 (2007).
63. He, J. *et al.* Impact of Ocean Eddy Resolution on the Sensitivity of Precipitation to CO_2 Increase. *Geophys. Res. Lett.* **45**, 7194–7203 (2018).
64. Williams, J. W., Jackson, S. T. & Kutzbach, J. E. Projected distributions of novel and disappearing climates by 2100 AD. *Proc. Natl. Acad. Sci.* **104**, 5738–5742 (2007).
65. Cavanagh, R. D. *et al.* A Synergistic Approach for Evaluating Climate Model Output for Ecological Applications. *Front. Mar. Sci.* **4**, 308 (2017).

SUPPLEMENTARY INFORMATION

Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

ACKNOWLEDGEMENTS

This contribution is part of the Retrospective Analysis of Antarctic Tracking Data (RAATD), a project of the Expert Group on Birds and Marine Mammals of the Scientific Committee on Antarctic Research (www.scar.org). The RAATD project would not have been possible without the dedication of the many scientists, students and field assistants who helped collect data in the field or process them, including, non-exhaustively, S. Adlard, A. Agüera, M. Biuw, M-A. Blanchet, J. Clarke, P. Cock, H. Cox, M. Connan, A.R. Carlini, S. Corsolini, M. Cottin, J.D. Le Croquant, G.A. Danieri, D. Davies, B. Dilley, R. Downie, M. Dunn, B.M. Dyer, S. Focardi, H.O. Gillett, S. Haaland, L. Jonsen-Humble, H. Kane, B.A. Krafft, C. Kroeger, C.A.E. Lemon, G. Mabille, M. Marczak, T. McIntyre, S. McKooy, J.A. Mennucci, T. Nordstad, C. Oosthuizen, R. Orben, T. Photopoulou, B. Picard, O. Prud'homme, T. Raclot, S. Ramdohr, D.H. Raymond, L. Riekkola, G. Richard, G. Robertson, T. Rogers, K. Ropert-Kato, S. Schoombie, T.N. Snakes, E. Soininen, A. Specht, K. Stevens, J.N. Swærd, C. Tosh, S. G. Trivelpiece, O. S. G. Trolli, T. Truly, L. Upfold, M. Le Vaillant, Y. Watanabe, M. Wege, C. Wheeler, T.O. Whitehead, M. Widmann, A.G. Wood, N. Youdjou and I. Zimmer. We also thank the large number of fieldworkers without whom these valuable data would not have been collected. D. G. Ainley and A. Constable commented on an earlier version of the manuscript. Support and funding were provided by supranational committees and organisations including the Scientific Committee on Antarctic Research, BirdLife International and the European Commission (IUCN BEST program), as well as from various national institutions (see also author affiliations) and foundations, including but not limited to **Argentina** (Dirección Nacional del Antártico), **Australia** (Australian Antarctic program; Australian Research Council; Sea World Research and Rescue Foundation Inc., IMOS is a national collaborative research infrastructure, supported by the Australian Government and operated by a consortium of institutions as an unincorporated joint venture, with the University of Tasmania as Lead Agent), **Belgium** (Belgian Science Policy Office), **Brazil** (Brazilian Antarctic Programme; National Council for Scientific and Technological Development - CNPq; Ministry of Science, Technology, Innovation and Communications – MCTIC; Ministry of the

Environment; CAPES), **France** (Agence Nationale de la Recherche; Centre National d'Etudes Spatiales; Centre National de la Recherche Scientifique; the French Foundation for Research on Biodiversity (FRB; www.fondationbiodiversite.fr) in the context of the CESAB project "RAATD"; Fondation Total; Institut Paul-Emile Victor; Programme Zone Atelier de Recherches sur l'Environnement Antarctique et Subantarctique; Terres Australes et Antarctiques Françaises), **Germany** (Deutsche Forschungsgemeinschaft, Hanse-Wissenschaftskolleg - Institute for Advanced Study), **Italy** (Programma Nazionale di Ricerche in Antartide, PNRA), **Japan** (Japanese Antarctic Research Expedition; JSPS Kakenhi grant; NIPR visiting professor fellowship for M. Hindell), **Monaco** (Fondation Prince Albert II de Monaco), **New Zealand** (Ministry for Primary Industries - BRAG; Pew Charitable Trusts), **Norway** (Norwegian Antarctic Research Expeditions; Norwegian Research Council), **Portugal** (Foundation for Science and Technology), **South Africa** (Department of Environmental Affairs; National Research Foundation; South African National Antarctic Programme), **UK** (Darwin Plus; Ecosystems Programme at the British Antarctic Survey; Natural Environment Research Council; WWF), and **USA** (U.S. AMLR Program of NOAA Fisheries; US Office of Polar Programs).

AUTHOR CONTRIBUTIONS

MAH conceived and led the project.

RA, BA, GB, JB, MNB, LB, HB, C-AB, PB, J-BC, RC, DPC, RJMC, LDR, PJNdB, KD, SD, MD, KD, LE, MF, AF, NG, MG, KTG, CG, SDG, RH, JH, MAH, LAH, AK, KRK, RK, GLK, KMK, KL, AL, CL, MAL, PL, ABM, MEIM, BMcD, CMcM, MM, KN, ESN, SO, RAP, PP, JP, KP, NR, YRC, PGR, MS, ASB, CS, IS, ATak, ATar, LGT, PNT, WT, EW, HW, BW and JX collected and contributed data.

VA-G, HB, J-BC, SC, BD, MAH, LAH, KJ, AK, IJ, MAL, DN, BR, RRR, YRC, DT, LGT, PNT, AVdP and SW processed and analysed the data.

MAH, HB, J-BC, SC, BD, LAH, IJ, MAL, BR, RRR, YRC, DT, LGT, PNT, AVdP, SW and SLC drafted the paper.

All authors edited and proofread the paper.

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COMPETING INTERESTS

HB, J-BC, BD, MAH, LAH, IJ, MAL, BR, RRR, YRC, DT, LGT, PNT, AVdP and SW are members of the Scientific Committee on Antarctic Research (SCAR) Expert Group on Birds and Marine Mammals. SLC is President of SCAR.

FIGURE CAPTIONS

Figure 1. Areas of Ecological Significance in the Southern Ocean. Tracking data from 17 predator species (a) were used to model the habitat importance for each species. Combining these model outputs gives overall habitat importance (b) and the upper decile of overall habitat importance delimits Areas of Ecological Significance (white contours). (c) shows these Areas of Ecological Significance (blue) in context. In (a), black points indicate tracking data and yellow points indicate tagging locations (location names in [16]). In (b), black points indicate colony locations for the 14 colony-breeding species. In (c), major oceanographic fronts (grey lines) are: Sub-Antarctic Front (SAF), Polar Front (PF) and Southern Antarctic Circumpolar Current Front (SACCF).
[DOUBLE COLUMN]

Figure 2. Fishing effort in the Southern Ocean. (a) Map showing fishing effort (total fishing hours between 2012 and 2016[29]). Contour lines (white) indicate the Areas of Ecological Significance. (b) Kernel density plot showing the distribution of values of fishing effort (zero values not shown) inside (red) and outside (grey) Areas of Ecological Significance (AES). Two-tailed permutation tests (n = 1,098,226 grid cells) indicate a significant difference. (c) Proportion of cells inside and outside AES that had some (>0 hours, yellow) or no (0 hours, purple) fishing effort.
[SINGLE COLUMN]

Figure 3. Spatial protection of Southern Ocean Areas of Ecological Significance. (a) Current (orange polygons) and proposed (magenta polygons) Marine Protected Areas (MPAs) superimposed on overall habitat importance. White contours denote Areas of Ecological Significance (AES), black lines show national Exclusive Economic Zones, and the blue line shows the CCAMLR Convention Area. (b) Area (million km^2) in current (orange) and proposed (magenta) MPAs, and outside MPAs (blue). (c) Area (million km^2) inside and outside AES in national Exclusive Economic Zones, the CCAMLR Convention Area and the international waters outside these two areas.
[DOUBLE COLUMN]

Figure 4. Projected change in distribution of Areas of Ecological Significance (AES) under RCP8.5. a) Cells that were AES in the original results are shown as blue (remain as AES) or orange (become non-AES in the future). The gradation from orange to blue shows the proportion of climate models that indicate loss (orange) or retention (blue) of AES. Similarly, the gradation from white to green shows the proportion of models that indicate non-AES cells will remain as non-AES (white) or become AES (green). Orange and magenta polygons show current and proposed Marine Protected Areas, respectively. b) Shows the percentage change in AES area according to the 8 different climate models (black points), and the mean of these (red points). In boxplots, the box is from the 25^{th} – 75^{th}

percentile, and the whiskers extend to the smallest/largest value that is not further than 1.5 times the interquartile range from the 25^{th}/75^{th} percentile.

[SINGLE COLUMN]

EXTENDED DATA CAPTIONS

Extended Data 1. Overview of the modelling process. a) shows how habitat importance for a given life-history stage (e.g., chick-rearing) of a given species (e.g., king penguin [*Aptenodytes patagonicus*]) is calculated using two models (grey boxes): the habitat selection model and the accessibility model. b) shows how these stage-specific, species-specific habitat importance predictions are combined to calculate mean habitat importance for multiple species (e.g., king penguin and Antarctic fur seal [*Arctocephalus gazella*]). Note that in the habitat accessibility model—Box 2 in (a)—distance to colony can be weighted by relative colony size or not. The unweighted version is shown in this figure.

Extended Data 2. Maps showing the 19 environmental covariates used to model marine predator habitat selection in the Southern Ocean. Grey lines indicate major oceanographic fronts. Abbreviations, sources and units of measurement are defined in the Supplementary Information Table S2.

Extended Data 3. Habitat importance scores for 16 marine predator species in the Southern Ocean. The maps show predicted habitat importance for each species. Predictions for macaroni (*Eudyptes chrysocome*) and royal penguins (*E. schlegeli*) are combined. Black circles show all known colony locations for the 14 colony-breeding species, which we used to predict the models across the whole Southern Ocean.

Extended Data 4. Covariate importance. Relative importance of 19 environmental variables used as predictors in 40 boosted regression tree models of the habitat selection of Southern Ocean marine predators. Higher variable relative importance values indicate that the variable has higher predictive power. Points show the values for each model and boxplots (in grey, behind) show the distribution of values. Variables are ordered (top to bottom) by decreasing median importance. Panels show the results for three different species groups that were identified by hierarchical cluster analysis (see text and Extended Data 7). Full covariate names are given in Supplementary Information Table S2. In boxplots, the median is shown, the box is from the 25^{th} – 75^{th} percentile, and the whiskers extend to the smallest/largest value that is not further than 1.5 times the interquartile range from the 25^{th}/75^{th} percentile.

Extended Data 5. Varied relationships between covariates and habitat selection across species. Scatterplot smooths (black lines) of the relationship between predictions of the species habitat selection models (boosted regression trees) (vertical axis) and the values of covariates used as predictors in our boosted regression tree models (horizontal axis). The smooths were drawn by fitting generalized additive models for large datasets with a thin plate regression spline basis, since loess smoothing was not computationally feasible. Full covariate names and units are given in Supplementary Information

Table S2. Higher habitat selection values indicate higher probabilities of use, irrespective of availability in this case. A smooth is shown for each species. Since each species had 1–5 predictions, for different life-history stages, we took the mean habitat selection estimate per cell for each species. Rug marks on the horizontal axis indicate the distributions of the data points.

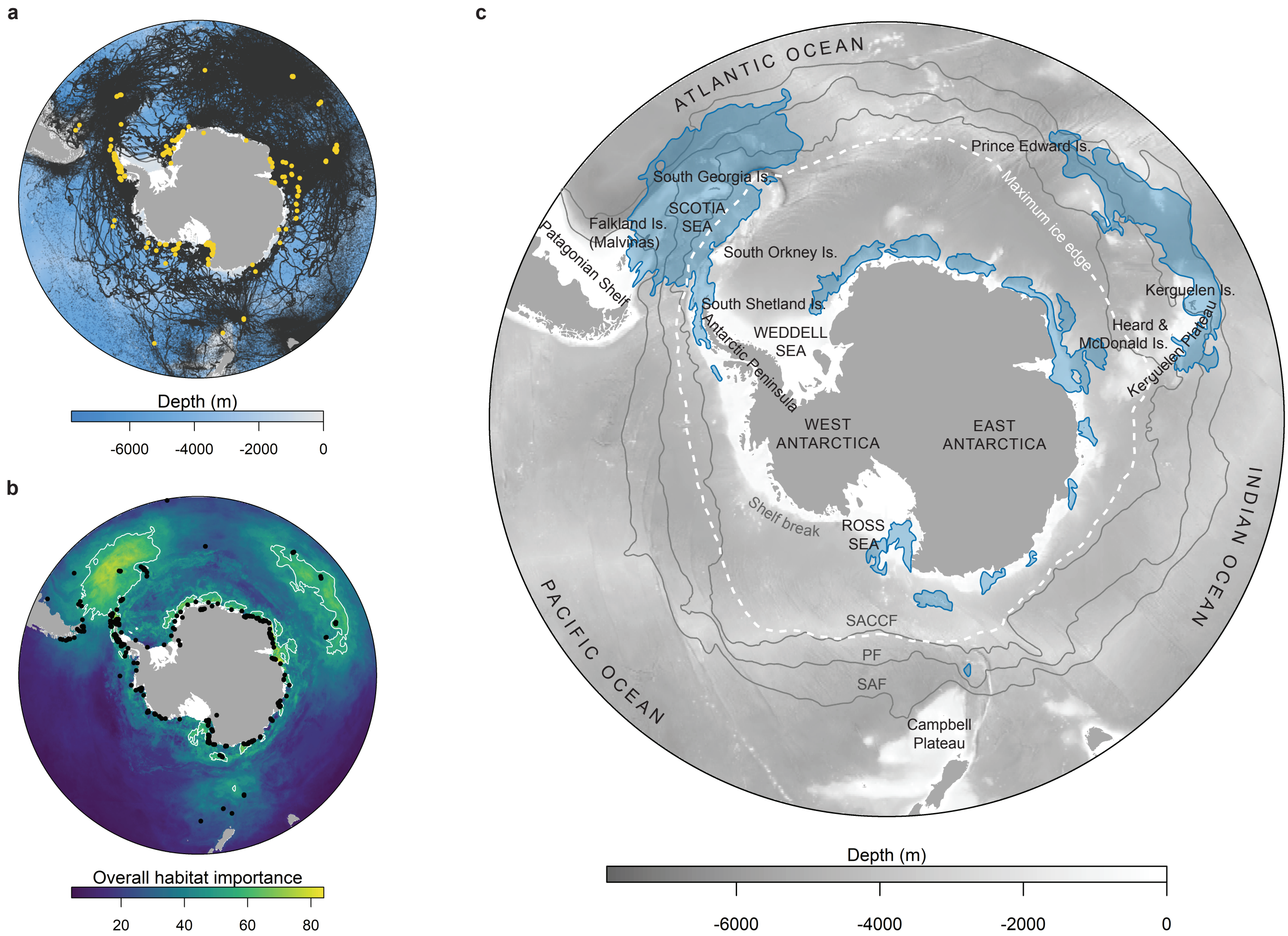
Extended Data 6. Potential environmental stressors in the Southern Ocean. Maps (a-c) showing the change (mean in 1987–1998 compared to mean in 2007–2017) in (a) sea-ice duration (days), (b) sea surface temperature (SST, °C), and (c) wind speed (m/s). Contour lines (black) indicate the Areas of Ecological Significance. Kernel density plots (d-f) show the distribution of values of each of a-c inside (red) and outside (grey) Areas of Ecological Significance (AES). Horizontal lines represent zero change. Two-tailed permutation tests indicate significant differences in each case; the number of grid cells included in the test is given in each case (n).

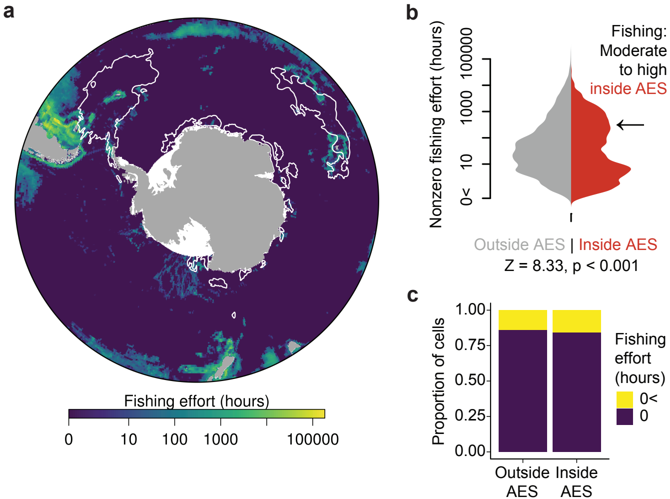
Extended Data 7. Change in AES distribution under RCP4.5. a) Cells that were AES in the original results are shown as blue (remain as AES) or orange (become non-AES in the future). The gradation from orange to blue shows the proportion of climate models that indicate loss (orange) or retention (blue) of AES. Similarly, the gradation from white to green shows the proportion of models that indicate non-AES cells will remain as non-AES (white) or become AES (green). Orange and magenta polygons show current and proposed Marine Protected Areas, respectively. b) Shows the percentage change in AES area according to the 8 different climate models (black points), and the mean of these (red points).

Extended Data 8. Comparison of a) unweighted and b) weighted overall habitat importance. a) shows overall habitat importance calculated without accounting for colony sizes, while b) shows overall habitat importance if colony sizes are taken into account. See Methods and Supplementary Information for details. Black points indicate colony locations for the 14 colony-breeding species, and the white contours indicate the Areas of Ecological Significance.

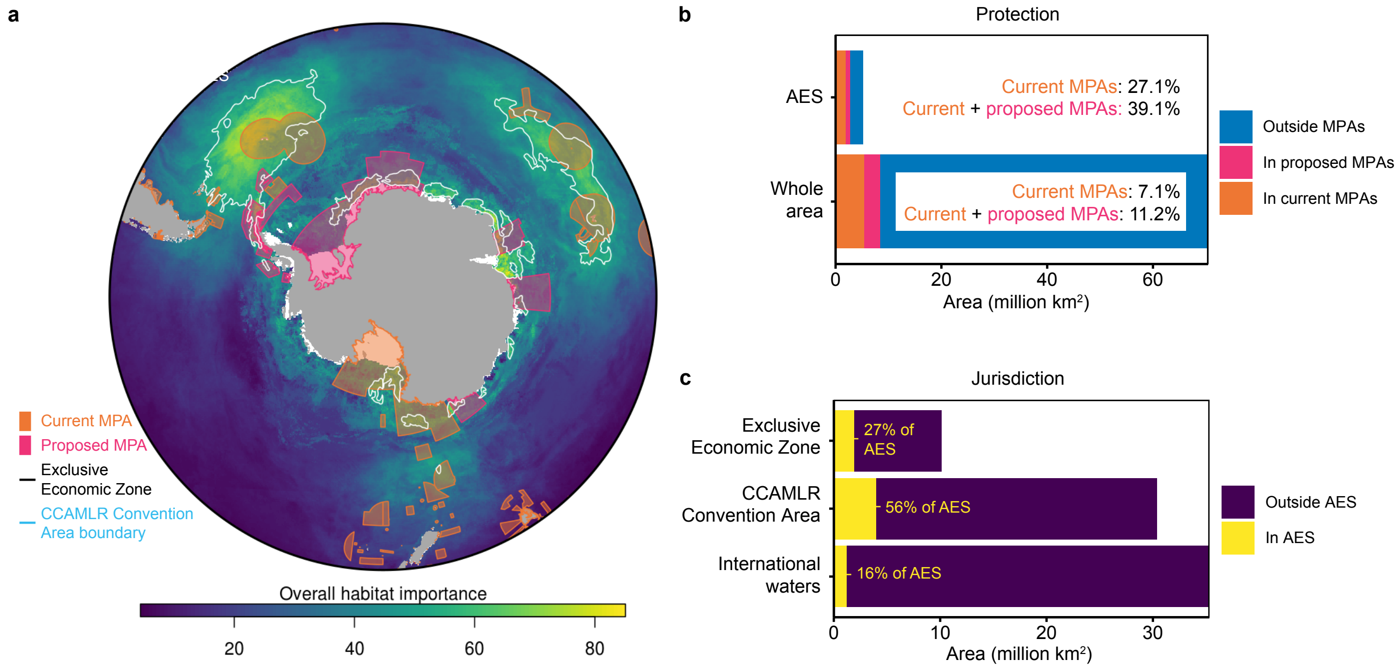
Extended Data 9. Dendrogram of hierarchical cluster analysis showing species groups in the dataset. We performed UPGMA (Unweighted Pair Group Method with Arithmetic Mean) hierarchical cluster analysis on the Manhattan distance among species, calculated from the habitat importance scores. The results show two clear species groups (Antarctic - blue, and sub-Antarctic - magenta). Humpback whales and southern elephant seals (orange) did not fall into either group and we assigned them to both groups for subsequent analyses. The cophenetic correlation coefficient between the distance matrix and the dendrogram was 0.86, which means the dendrogram is a good representation of the Manhattan distance values among the species. Values can range from 0 (no correlation) to 1 (perfect correlation).

Extended Data 10. Mean habitat importance of a) Antarctic and b) sub-Antarctic species. To account for regional differences in species richness we defined two species groups (see Methods and Extended Data 5) and calculated mean habitat importance for these two groups separately. These two mean habitat importance layers—(a) and (b)—were then combined into a single overall habitat importance layer by choosing the maximum value in each cell. Black points indicate the colony locations of colony-breeding species in each species group.

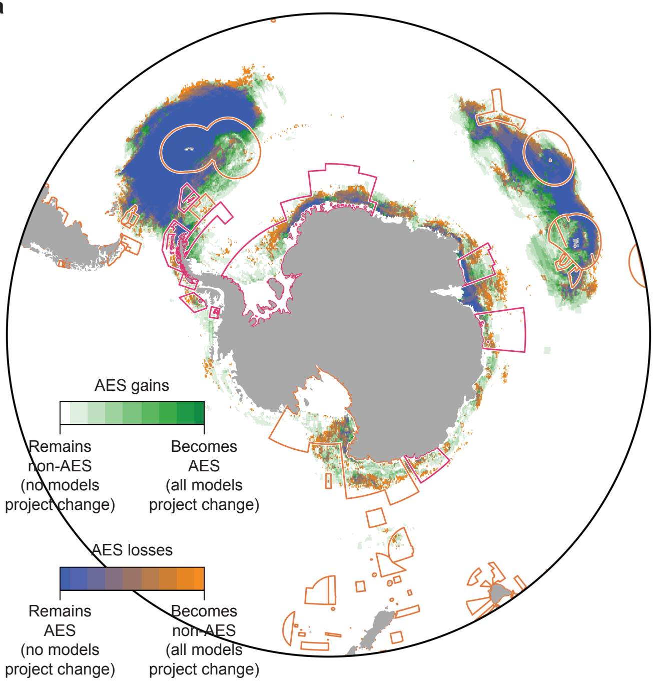

a
Depth (m)
-6000
-4000
-2000
0
b
Overall habitat importance
20
40
60
80
c
ATLANTIC OCEAN
INDIAN OCEAN
PACIFIC OCEAN
Prince Edward Is.
South Georgia Is.
SCOTIA SEA
Falkland Is. (Malvinas)
Patagonian Shelf
South Orkney Is.
South Shetland Is.
Antarctic Peninsula
WEDDELL SEA
Maximum ice edge
Kerguelen Is.
Heard & McDonald Is.
Kerguelen Plateau
WEST ANTARCTICA
EAST ANTARCTICA
Shelf break
ROSS SEA
SACCF
PF
SAF
Campbell Plateau
Depth (m)
-6000
-4000
-2000
0



a
Fishing effort (hours)
0
10
100
1000
100000
b
Nonzero fishing effort (hours)
0<
10
1000
100000
Fishing:
Moderate
to high
inside AES
Outside AES | Inside AES
Z = 8.33, p < 0.001
c
Proportion of cells
1.00
0.75
0.50
0.25
0.00
Outside AES
Inside AES
Fishing effort (hours)
0<
0

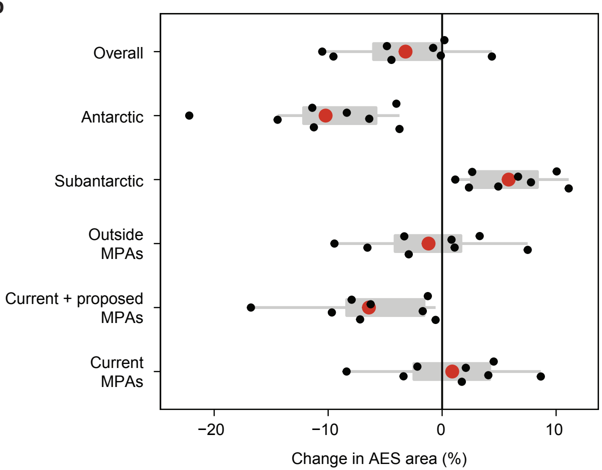

a
Current MPA
Proposed MPA
Exclusive Economic Zone
CCAMLR Convention Area boundary
Overall habitat importance
20
40
60
80
b
Protection
AES
Whole area
Current MPAs: 27.1%
Current + proposed MPAs: 39.1%
Current MPAs: 7.1%
Current + proposed MPAs: 11.2%
Outside MPAs
In proposed MPAs
In current MPAs
0
20
40
60
Area (million km²)
c
Jurisdiction
Exclusive Economic Zone
CCAMLR Convention Area
International waters
27% of AES
56% of AES
16% of AES
Outside AES
In AES
0
10
20
30
Area (million km²)

a



AES gains
Remains non-AES (no models project change)
Becomes AES (all models project change)
AES losses
Remains AES (no models project change)
Becomes non-AES (all models project change)

b



Overall
Antarctic
Subantarctic
Outside MPAs
Current + proposed MPAs
Current MPAs
−20
−10
0
10
Change in AES area (%)