

More losers than winners in a century of future Southern Ocean seafloor warming

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The waters of the Southern Ocean are projected to warm over the coming century, with potential adverse consequences for native cold-adapted organisms. Warming waters have caused temperate marine species to shift their ranges poleward. The seafloor animals of the Southern Ocean shelf have long been isolated by the deep ocean surrounding Antarctica and the Antarctic Circumpolar Current, with little scope for southward migration. How these largely endemic species will react to future projected warming is unknown. By considering 963 invertebrate species, we show that within the current century, warming temperatures alone are unlikely to result in wholesale extinction or invasion affecting Antarctic seafloor life. However, 79% of Antarctica's endemic species do face a significant reduction in suitable temperature habitat (an average 12% reduction). Our findings highlight the species and regions most likely to respond significantly (negatively and positively) to warming and have important implications for future management of the region.

When faced with warming ocean temperatures, many marine species have been shown to exhibit poleward range shifts^{1–3}. These range shifts are dependent on having available suitable habitat at higher (cooler) latitudes⁴. For polar organisms, it could be said that they are at the end of the line, with limited options in terms of northwards or southwards migration^{4,5}. Unlike the Northern Hemisphere, the route of poleward migration of benthic species in the Southern Hemisphere is punctuated by a lack of continuous continental shelf from ~57° S to ~60° S, a sharp temperature gradient across the Subantarctic (SAF) and Polar (PF) fronts and the strong eastward flow of the Antarctic Circumpolar Current, all of which serve to isolate Antarctica both oceanographically and biologically^{6,7}.

Global projections for the response of marine organisms to climate change based on pelagic species and/or sea surface temperature data show the Southern Ocean (south of the PF) to be a hotspot of species turnover, local extinction and invasion^{8,9} and a loss of species richness¹⁰. Benthic animals are, in terms of numbers of species, by far the richest component of Antarctic biodiversity¹¹. The benthic animals of the Southern Ocean shelf have long been isolated from their northern neighbours^{6,7} and how these largely endemic species will react to future projected warming is unknown.

We project likely changes in the potential distribution of 963 shelf-dwelling (water depth <1,000 m) benthic invertebrate species, represented by over 57,000 occurrence records from south of 40° S, under projected seafloor temperatures in 2099 derived from an ensemble of coupled climate models forced by a strong carbon forcing scenario (Representative Concentration Pathway 8.5 (RCP8.5); ref. 12) (Fig. 1). Our findings reveal the species and geographic areas most likely to respond (negatively and positively) to predicted warming of bottom water on the continental shelf and have important implications for future resource management in the region.

Species distribution and projected change

Georeferenced benthic species occurrence records were assigned the modelled present-day seafloor temperature (ensemble averaged

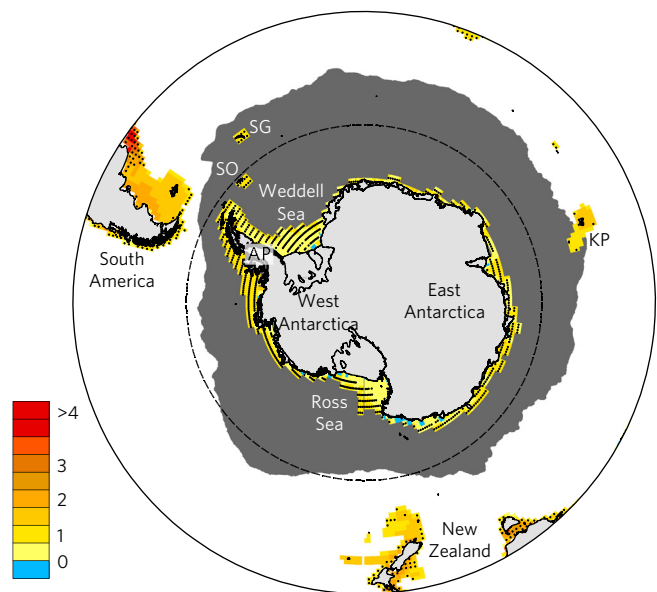


Figure 1 | Temperature anomaly (°C) in 2005 to 2099 using RCP8.5 mean ensemble shelf benthic temperatures (<1,000 m). The black dots indicate that a significant difference exists at the 95% level between the 2005 and 2099 ensembles. The dashed line is 60° S; the grey area is south of the Polar Front (as defined in ref. 32). SG, South Georgia; SO, South Orkney Islands; AP, Antarctic Peninsula; KP, Kerguelen Plateau.

over model means between 1976 and 2005, see Supplementary Table 1) for their location, and the thermal range of each species was calculated (maximum and minimum temperature values from their present-day known locations). Multivariate analyses of the modelled present-day temperature ranges of all studied species resulted in ten distinct groupings with similar distributions (see Methods). Of these groupings, four are only Antarctic, one is Antarctic and subantarctic, two are Antarctic to temperate, one is limited to the subantarctic

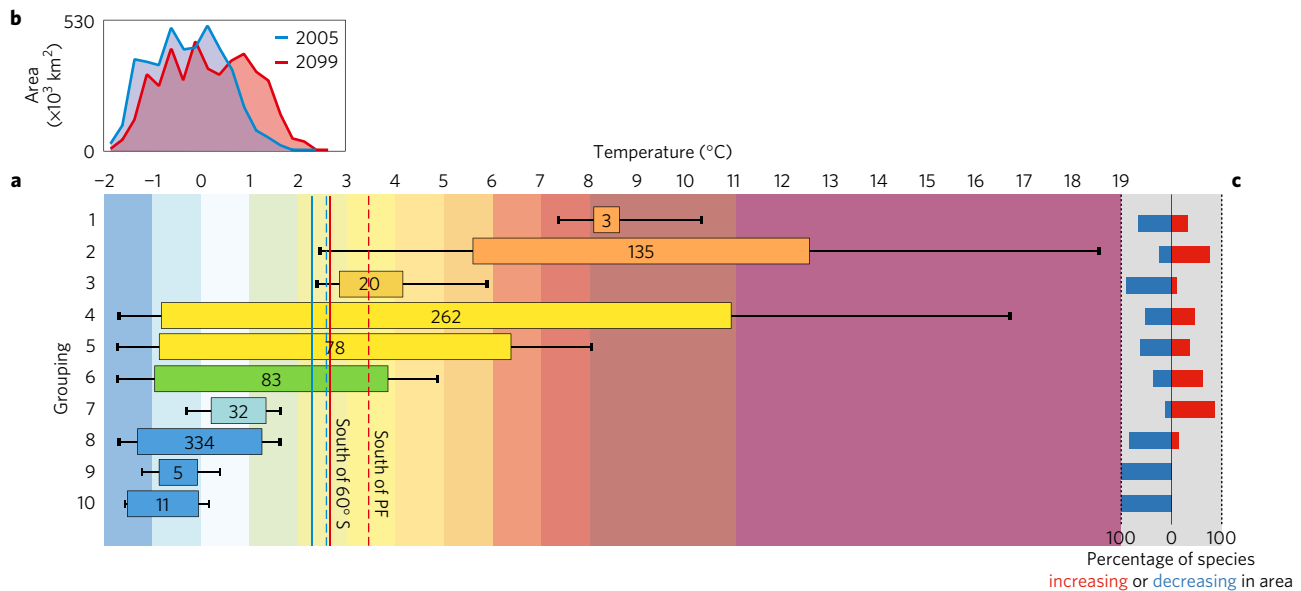


Figure 2 | Temperature ranges of benthic invertebrates from south of 40° S and projected change in seafloor temperatures south of the Polar Front.

a, Temperature ranges of seafloor invertebrates grouped by >80% similarity in their thermal distribution patterns. The coloured bars show the mean temperature range experienced by a group; numbers are the number of species represented by each group. The black bars show the maximum and minimum temperature range experienced by any of the species within a group (more detail is given in Supplementary Table 2). The 2005 (blue) and 2099 (red) maximum temperatures for the shelf area (<1,000 m deep) south of 60° S (solid line) and that south of the Polar Front (dashed line) are shown. The area represents the area of seabed south of 60° S experiencing a given temperature. **b**, Area covered by present and projected future seafloor temperatures (RCP8.5 ensemble mean) south of 60° S. **c**, The percentage of species within each group projected to gain or lose potential habitat area. The red and blue bars indicate the percentage of species experiencing an increase (red) and decrease (blue) in their suitable temperature habitat.

and two are only temperate (Fig. 2). Each of these groupings will be affected differently by the projected increases in temperature. All analyses of potential distributions under projected temperatures were carried out using the pointwise mean of a 19-member model ensemble of seafloor temperatures (Supplementary Table 1) temporally averaged over 2070–2099 under the Coupled Model Intercomparison Project Phase 5 (CMIP5) RCP8.5 forcing scenario (Fig. 3). To address the differences between models, particularly on the Antarctic shelf, we used a mean of the 19-member ensemble as well as examining the most extreme regional cases.

Temperature changes over the Antarctic and subantarctic shelves showed warming in most regions, especially the West Antarctic Peninsula, the Kerguelen Plateau and parts of the Ross and Weddell seas. The waters south of the PF are expected to warm by an average of 0.4 °C (± 0.3 °C), with a maximum regional mean projected increase of 2.15 °C (Fig. 1).

Species found only in Antarctic bottom waters between -1.8 °C and ~ 1.2 °C, Groups 8 to 10, faced a projected reduction in suitable habitat (Fig. 2). Only the Antarctic endemic species that cannot tolerate sub-zero water, Group 7, increased in potential area. Species with geographic ranges crossing the PF, Groups 4 to 6, experienced a warming at the upper limit of their extent, reducing their range; however, the warming of cold Antarctic waters allowed for range expansion for some species south of the PF. These Antarctic species that cannot tolerate sub-zero water increased their potential range southwards and into East Antarctica.

Species currently found only north of the PF, Groups 1 to 3, are unable to cross into Antarctic waters, other than some species that are able to reach the warmer waters of the Kerguelen Plateau at a projected temperature range of between 3 and 5.8 °C (compared with a present-day range of 2.2 to 4.4 °C). Waters south of 60° S and the South Georgia shelf have not warmed sufficiently to provide suitable conditions for animals from north of the PF, reaching a maximum projected summer temperature of ~ 2.6 °C (Fig. 3). Present-day (1976–2005) modelled mean minimum

seafloor temperatures, shallower than 1,000 m, for southern South America are in the region of 3.8 °C.

Of the 963 benthic species analysed, 577 are likely to experience a reduction in thermally suitable habitat with projected warming (Fig. 4). Of these, 398 (41% of all species) are expected to experience a range loss of under 10% of their present-day suitable temperature potential habitat. A calculated 18.6% of species are projected to lose between 10 and 40% of their present-day potential habitat.

The greatest predicted reduction in area is for a single species of echinoid, *Sterechinus diadema* (Group 3)—native to the Kerguelen Plateau and Crozet, projected to lose $\sim 43\%$ of its present-day potential range. The majority (536) of the species losing potential habitat are found living south of the PF (308 of which are found only in Antarctic waters). Approximately 79% of species endemic to Antarctic waters are projected to experience a reduction in suitable habitat.

All seven of the species projected to more than triple their potential range are from Group 7 and are native to South Georgia, at the northern limit of Antarctic waters, and currently experience a narrow temperature range of between 0.9 and 1.6 °C. However, this projected increase in range is dependent on these species being able to migrate across deep water to reach the Antarctic continental shelf to occupy suitable habitat because South Georgia is projected to warm beyond their current thermal range (Supplementary Figs 1 and 2). Species with ranges that cross the PF are found to both lose (53.5%) and gain (46.5%) potential habitat. The majority (72.1%) of non-Antarctic species included in the study showed a potential range expansion with warming, although it is unlikely that this study accurately represents the effects at the true northern limits of their ranges.

Species turnover and regional change

The projected changes in species distribution (assuming no adaptation to higher temperatures) will have an effect on regional and local species richness, with some areas increasing in diversity

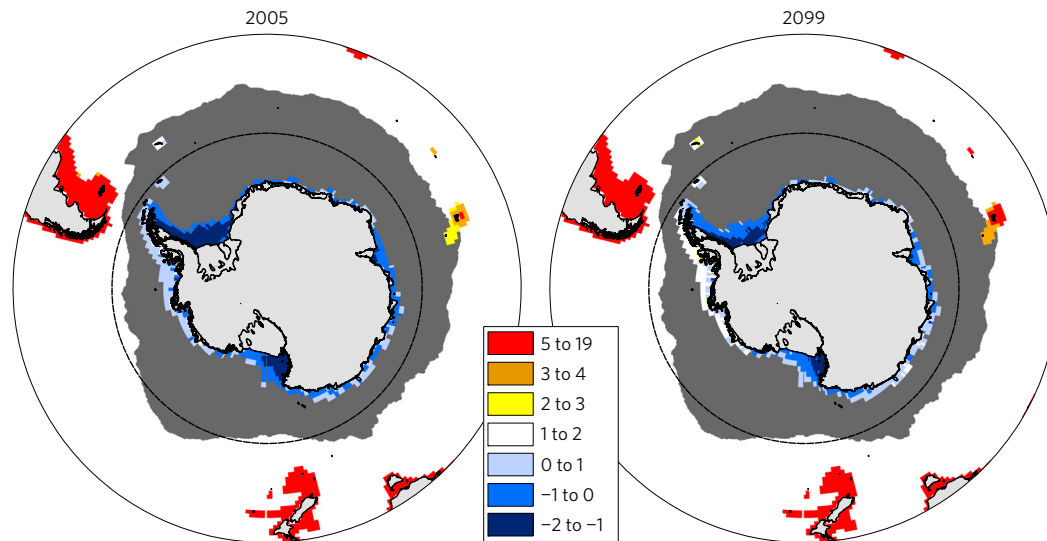


Figure 3 | Mean ensemble seafloor temperatures (°C) averaged over the historical scenario (1976–2005) and over 2070–2099 under RCP8.5 projections. The dashed line is 60° S; the grey area is south of the Polar Front (as defined in ref. 32).

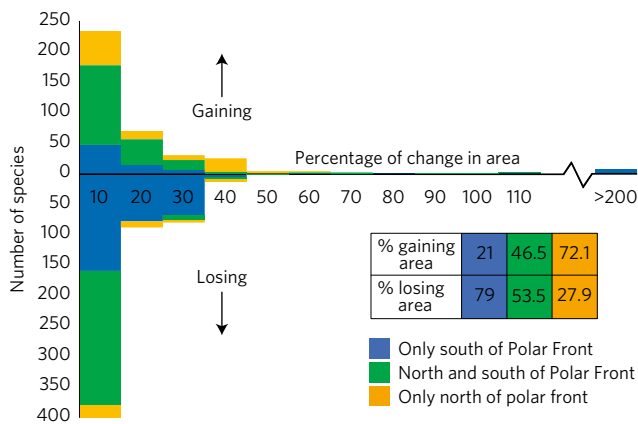


Figure 4 | The number of species that are predicted to experience a change (increase or decrease) in potentially available area of seafloor at suitable temperatures by 2099 under the RCP8.5 scenario.

and others decreasing. Species turnover (Fig. 5) showed a projected overall reduction in species numbers in West Antarctica, the South Orkney Islands and South Georgia. This is due to temperatures reaching a threshold that excludes many cold-water specialists from Antarctica (Groups 7–10) but are still not warm enough for more northerly species to colonize.

The projected loss of species in most of the more northerly regions (South America, New Zealand and Tasmania) is probably due to limitations of the data used in the analyses, as those data do not include species from further north, which are likely to spread southwards into these regions (north of the PF). The Weddell Sea, Ross Sea and parts of East Antarctica showed a projected increase in diversity. This is due to a slight increase in temperatures that favoured a greater number of Antarctic species (Groups 4–6) without excluding the cold-water specialists (Groups 8–10).

Regional upper bounds of warming

Using the ensemble local maximum projected temperature increase for each pixel from the climate model ensemble to explore the (probably unphysical) upper bound of the warmest future scenario (Fig. 6), we saw significantly higher temperatures across the entire study region, with no one outlying model dominating everywhere. However, temperatures south of 60° S showed a lower anomaly

(mean value of 1.13 °C) between the ensemble mean and maximum values than those further north (mean anomaly value of 4.19 °C). This extreme upper bound would allow species from north of the PF to colonize South Georgia but would still not warm the waters south of 60° S sufficiently to allow a southern temperate fauna to survive in Antarctica. This scenario would allow more subantarctic endemic species (Group 3) to survive at the Antarctic Peninsula but they would lose their original suitable habitat. No habitat colder than 0 °C would exist under this most extreme hypothetical case, except for under floating ice shelves, meaning that only species from Groups 4 to 7 would be capable of inhabiting most of the Antarctic shelf, potentially causing the extinction of many Antarctic endemic species (Groups 9 and 10) and restricting the majority (Group 8) to the Weddell Sea and part of the Ross Sea.

Under the RCP8.5 scenario, warming is projected to continue beyond the year 2100 and therefore to set the 2100 projections into a longer-term context we examined a more limited ensemble with RCP8.5 projections available up to 2200 (Supplementary Table 1). The mean of this more limited ensemble revealed a general pattern of further warming, a consequence of which is that the majority of the sub-zero waters are lost along with most of the suitable habitat for endemic Antarctic species (Supplementary Figs 2 and 3). The additional warming brings the 2200 ensemble mean warming to levels similar to, but still less severe than, the previously discussed 2099 ensemble local extreme in projected warming for each pixel (Fig. 6).

Discussion

Marine species have four potential responses to projected warming: species capable of shifting their bathymetric range into cooler, deeper water may be able to maintain their present-day latitudinal distribution^{1,3,13}; poleward migration is an option, but for shelf-restricted organisms, this range shift is dependent on availability of suitable habitat at higher latitudes^{1,3,13}; species may be able to adapt their behaviour or physiology to mitigate against rising temperatures^{3,14,15}; species unable to find suitable habitat elsewhere, and unable to complete their life cycle or are out-competed at higher temperatures are likely to become locally or globally extinct^{3,8,16}.

For Antarctic shelf species, deeper water and southerly migration are not an option as they already inhabit the coldest water on Earth in its most southerly marine locations, both of which are found in the Ross and Weddell Sea shelves. Previous global analysis of

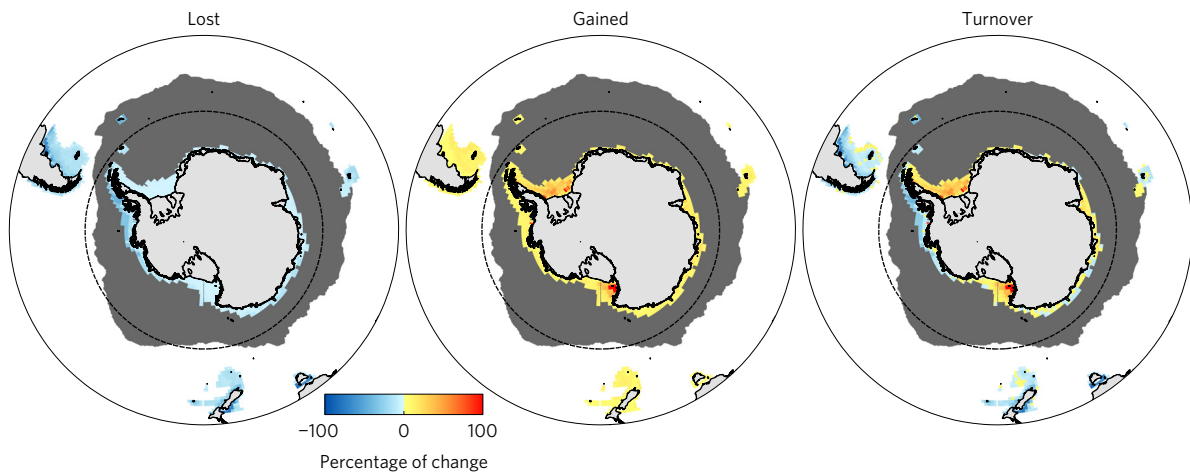


Figure 5 | Species change/turnover (gain + loss) by 2099 as a percentage of the original number of species potentially inhabiting each pixel (based on suitable present-day temperature ranges, using RCP8.5 mean ensemble projections). The dashed line is 60° S; the grey area is south of the Polar Front (as defined in ref. 32).

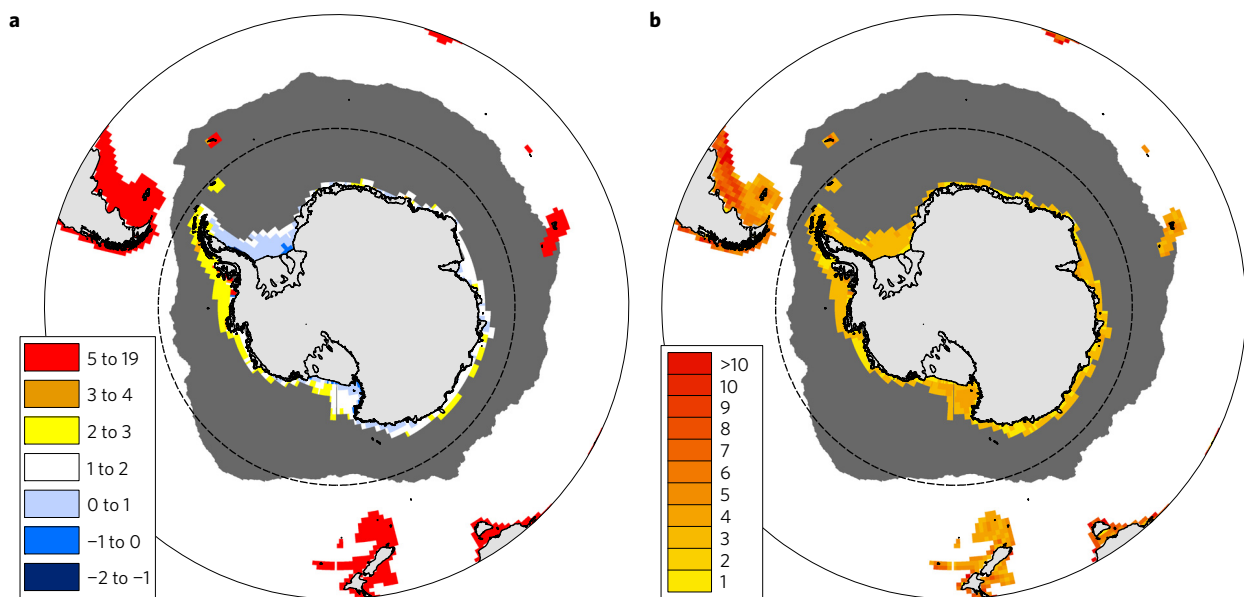


Figure 6 | Maximum projected seafloor temperature values for 2099. a, Maximum projected values of seafloor temperature (°C) per grid cell within the RCP8.5 ensemble. b, The anomaly between the mean model and the maximum individual model value per grid cell (°C). The dashed line is 60° S; the grey area is south of the Polar Front (as defined in ref. 32).

thermal tolerance and latitude in ectotherms suggested that marine organisms from south of 60° S had the narrowest tolerance range of anywhere on the planet². Our results suggest that reduction in range area along with probable localized extinctions will affect around 79% of species endemic to south of the PF.

Antarctic benthos is generally considered to be poorly suited to warmer temperatures¹⁵, with small experimental rises of 2 or 3 °C above normal drastically reducing their ability to carry out critical functions¹⁷. Two to three degrees is a large change in the model mean temperature south of the PF, and most regions are predicted to experience smaller changes (average projected increase of 0.4 °C, with a maximum of 2.15 °C) (Fig. 1). However, limited evidence from environments that are extreme and highly seasonal, even by polar marine standards, the Antarctic intertidal, suggest that some endemic species (for example, *Laternula elliptica*, member of Group 6) are capable of surviving far warmer temperatures (7.5 °C) than would be expected from laboratory experiments¹⁸. Under experimental conditions, *L. elliptica* has been shown to suffer

complete loss of function at 5 °C, although there is some anecdotal evidence that individuals can survive for over a month at 3 °C (refs 19,20). A recent study²¹ found fossils of present-day endemic Antarctic species, including *L. elliptica*, and South American molluscs living side by side in East Antarctica in the Pliocene at temperatures of between 4 and 7.5 °C. On the basis of this evidence, it may be the case that at least some of these cold-water species are capable of tolerating the projected rise in temperatures with limited effect on their distribution.

The potential for marine invasive species in Antarctic waters, similar to those already observed for terrestrial habitats²², has been the subject of much speculation^{7,23}. The existing (and future) meridional temperature gradients across the SAF and PF are larger than the projected warming change either north or south of these fronts, meaning it will still be colder on the southern side of the front in the future than it is on the present northern side. Therefore, these fronts will continue to be significant barriers to potential invasive species; however, very few laboratory-based

physiological studies of the lower thermal tolerances of these species exist². One potential source of invasive species into Antarctica that has only recently been recognized is the introduction of cold-tolerant Northern Hemisphere and Arctic species via ships and ballast water²⁴.

Our findings show that under strongly warming climate change scenarios, species in Antarctic waters are likely to experience a range shift, with some geographic areas losing species and others opening up to a range of previously excluded Antarctic species (Fig. 5). How these changes to communities will affect ecosystem structure and function is unknown¹⁶, although it is likely to lead to some species benefiting and many others being disadvantaged. The timings of season-dependent reproduction and feeding, predator–prey relationships, assemblage structure, habitat complexity, susceptibility to parasites and disease and interspecific competition for resources are all likely to change in a warming environment²⁵ and may have unforeseeable additional effects on species' distribution and abundances.

Projected changes in species richness do not, however, directly equate to changes in biomass or ecosystem function. The addition of new consumers or ecosystem engineers to a community has been shown to have a dramatic effect on communities, even without a change in temperature²⁶. Species such as durophagous king crabs have been a major recent topic of discussion regarding the present and future of the Antarctic benthos^{27,28}. King crabs found at South Georgia (south of the PF) at the present day include species from Group 5 (*Paralomis spinosissima*) and Group 7 (*P. anamerae* and *P. formosa*) that are capable of living at temperatures currently found on the West Antarctic Peninsula shelf but are not found living there today²⁷. However, the present-day distribution of native Antarctic king crabs (south of 60° S) is deeper than 1,000 m (ref. 27) (beyond the bathymetric scope of this study) and those shallower-dwelling species found north of the PF (for example, *Lithodes santolla* from Group 2) will not be able to tolerate temperatures in Antarctic waters given the projected levels of warming.

Warming ocean temperature is not the only physical factor associated with projected environmental change in the Southern Ocean^{29,30}, with shelf regions likely to be most affected by multiple changes³⁰. While we show that temperature changes alone are unlikely to drive significant levels of extinctions, associated changes such as ocean acidification and changes to sea ice and convection patterns have the potential to affect the entire ecosystem, altering food and light availability and causing physiological stress^{16,29,30}, and may have synergistic negative effects on species already facing habitat reduction due to warming. With fishing in the region likely to be of increasing importance to global food supplies^{30,31}, this may represent a further stress on the ecosystem, further affecting those species facing a reduction in suitable habitat.

Our findings highlight the organisms and geographic regions most likely to respond significantly (negatively or positively) to projected seafloor warming in and around the Southern Ocean. Evidence from 963 benthic species, even under the strongly warming RCP8.5 climate projections, suggests that, when considered in isolation, the effect of projected warming on Antarctic shelf seafloor life results in substantial redistribution rather than wholesale extinction or invasion. The cold-adapted endemic species native to the region south of the PF face a reduction in suitable habitat and may require additional management and conservation measures in future to minimize the additional effects of other changes and human impacts.

Methods

Methods, including statements of data availability and any associated accession codes and references, are available in the online version of this paper.

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Author contributions

H.J.G. analysed the data; A.J.S.M. prepared the oceanographic data; all authors wrote the manuscript.

Additional information

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Competing financial interests

The authors declare no competing financial interests.

Methods

Ocean temperature. Models from the CMIP5 coupled climate ensemble were selected from all available output in the UK Centre for Environmental Data Analysis (CEDA) CMIP5 database. Models were selected on the basis of having monthly averaged ocean potential temperature (thetao) output for both the historical (HIST) scenario for the years 1975–2005 and the strong climate Representative Concentration Pathway 8.5 for years 2070–2099 (RCP8.5; ref. 33). RCP8.5 refers to the approximate change in radiative forcing in watts per square metre by the year 2100 and is sometimes referred to as a 'business as usual scenario'¹². It includes a full range of anthropogenic forcing factors (greenhouse gases, aerosols, chemically active gases and land use) along with a repeating 11-year solar cycle³⁴ and drives significant changes in Southern Ocean temperature, circulation, salinity, winds and sea ice extent by 2100³⁵. These changes are more extreme in RCP8.5, but tend to be qualitatively similar in the Southern Ocean to milder climate forcing scenarios such as RCP4.5 (refs 36,37). It is worth noting that while the future projections of the Southern Ocean have significant dynamical disagreements across the CMIP5 ensemble, warming on the continental shelves and upper ocean is a robust feature^{35,38}.

Each model was interpolated onto a regular $1^\circ \times 1^\circ$ latitude and longitude grid and the austral summer months (January–March) temporally averaged over the respective HIST and RCP8.5 30-year periods. Bottom properties were then extracted on the basis of the deepest non-empty thetao value at each latitude–longitude grid point. Note that this represents the temperature over the entire bottom cell, which in deeper model layers may extend for 250 m or more vertically, rather than the temperature at the exact sea bed. For layers shallower than 1,000 m, vertical cell extents are on the order of 10–100 m depending on the model.

The model ensemble was further reduced by rejecting the CNRM-CM5 models due to significantly outlying (warm) bottom temperature properties and the HadGEM2-AO due to issues identifying the bottom cell. This left us with 19 models (Supplementary Table 1) with both HIST and RCP8.5 averaged austral-summer-time bottom temperatures for the given years. Mean ensemble temperatures and standard deviations for each ensemble were then calculated elementwise at each latitude and longitude cell. To test whether the elementwise model changes between the two scenarios are statistically significant, we applied a dependent *t*-test for paired samples on the differences. Excluding some grid points abutting the coastline where model topographies varied due to differing resolutions, and regions of the abyssal ocean where temperature changes were small, most of the model domain shows significant bottom-temperature changes between the HIST and RCP8.5 scenarios at the 95% confidence level, agreeing with similar studies of Southern Ocean properties³⁸.

Austral winter (June–August) mean temperatures were calculated and it was found that they produced similar patterns of change between the HIST and RCP8.5 scenarios, but tended towards slightly weaker average temperature changes. We therefore proceeded to use the summer values as an example of the peak temperature changes experienced in a seasonal cycle. To investigate the extremes of the future ensemble we also constructed a local ensemble maximum benthic temperature change map, where the model with the most extreme RCP8.5 temperature change at each grid point was used, rather than the ensemble average. This represents the most extreme change predicted at each grid point, and is not consistent with any one model output. No one model completely dominated this output, meaning we can be relatively confident that it is not driven entirely by one spurious ensemble member. This method is also more susceptible to biases induced by intra-model variability in the averaging periods. At regional scales, interannual temperature variability within a single model often overwhelms the climate signal, so this analysis should be viewed only as a hypothetical exploration of extreme upper bounds of the ensemble, rather than a reasonable prediction of potential change.

Biogeographic records. The biological data were extracted from the expert-validated database for Part 5. Biogeographic Patterns of Benthos of the Scientific Committee on Antarctic Research Biogeographic Atlas of the Southern Ocean³⁹ with additional records for taxa with limited data from north of 50° S (Sipuncula, Annelida, Mysida and Crinoidea) extracted from the Ocean Biogeographic Information System (<http://iobis.org>). All benthic species with 20 or more records, at depths shallower than 1,000 m and from south of 40° S were selected. All species names were validated using the World Register of Marine Species (<http://www.marinespecies.org>). The 963 selected species included 10 phyla (Annelida, Arthropoda, Bryozoa, Chordata, Cnidaria, Echinodermata, Mollusca, Nematoda, Porifera and Sipuncula) representing 21 classes. A total of 57,827 benthic occurrence records were used. Of these species, 390 were found only south of the Polar Front (PF), 426 had ranges that crossed the PF and 147 were known only from north of the PF.

Biological record locations were overlaid onto the modelled seafloor temperature data and present-day temperature values were assigned to each record. As the georeferenced biological data were limited to occurrence and had no abundance data, the thermal range of each species was defined uniformly as any temperature between the minimum and maximum temperatures of its present-day distribution. Species were clustered into groups of species with similar thermal limits and temperature range size using Bray–Curtis similarity in PRIMER 6 (ref. 40). All analyses of potential distributions under projected temperatures were carried out using RCP8.5 mean ensemble seafloor temperatures for 2099. Present-day and projected future species potential range areas are based on the area of seafloor habitat anywhere in the study region at temperatures suitable for that species, irrespective of whether that species had been found in that geographical area. Species turnover analyses assumed that all species are equally capable of migrating to any part of the study region with a suitable temperature, irrespective of life history traits. Depth ranges of species were not included in the analyses, with all pixels at depths shallower than 1,000 m treated equally.

Data availability. The authors declare that the data supporting the findings of this study are available from Biodiversity.aq, the Ocean Biogeographic Information System and the UK Centre for Environmental Data Analysis.

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