Intermediate ice scour disturbance is key to maintaining a peak in biodiversity within the shallows of the Western Antarctic Peninsula

B. J. O. Robinson1,2, D. K. A. Barnes2, L. J. Grange3 & S. A. Morley2

Climate-related disturbance regimes are changing rapidly with profound consequences for ecosystems. Disturbance is often perceived as detrimental to biodiversity; however, the literature is divided on how they influence each other. Disturbance events in nature are diverse, occurring across numerous interacting trophic levels and multiple spatial and temporal scales, leading to divergence between empirical and theoretical studies. The shallow Antarctic seafloor has one of the largest disturbance gradients on earth, due to iceberg scouring. Scour rates are changing rapidly along the Western Antarctic Peninsula because of climate change and with further changes predicted, the Antarctic benthos will likely undergo dramatic shifts in diversity. We investigated benthic macro and megafaunal richness across 10–100 m depth range, much of which, 40–100 m, has rarely been sampled. Macro and megafauna species richness peaked at 50–60 m depth, a depth dominated by a diverse range of sessile suspension feeders, with an intermediate level of iceberg disturbance. Our results show that a broad range of disturbance values are required to detect the predicted peak in biodiversity that is consistent with the Intermediate Disturbance Hypothesis, suggesting ice scour is key to maintaining high biodiversity in Antarctica’s shallows.

Disturbance events occur in almost all natural ecosystems and tend to be a significant driver, influencing assemblage diversity, structure and function1. However, the disturbance literature is divided. Some studies conceptualise disturbance as departures from a ‘stable’ state2,3 and detrimental to biodiversity4, whereas, others present cases where disturbance maintains high biodiversity5 and promotes resilience to further change6. This paradox can be addressed with the Intermediate Disturbance Hypothesis (IDH), which posits stable coexisting states under “intermediate” disturbance conditions where species diversity is predicted to be highest7,8. The IDH itself however is disputed on both theoretical and empirical grounds, with studies rarely finding the predicted peaked relationship9,10. Literature that has found evidence for peaks in diversity include successional, post-iceberg disturbance studies11,12 and theoretical models13. In contrast, a meta-analysis of disturbance studies found that a key factor in the detection of species richness peak was the inclusion of a broad range of disturbance levels, which has not been achieved in the majority of empirical studies14,15. The Western Antarctic Peninsula has one of the largest disturbance gradients on earth16 and is considered a hotspot of benthic diversity17–19, making it an ideal natural laboratory for analysing the relationship between disturbance and diversity.

The shallow Antarctic seafloor (< 40 m depth) is home to one of the most naturally disturbed assemblages, due to frequent iceberg scouring disturbance16,20. Ice scour disturbance, defined as when the keel of an iceberg impacts the seafloor, are distinct events in both time and space21 resulting in high mortality of > 98.5% for macro and megafauna22,23. Here, we consider any contact of ice with the seafloor that results in scour as ice scour disturbance, the majority of disturbance recorded here are likely caused to be small to large icebergs24. The frequency of ice scour disturbances varies due to bathymetry, latitude and topography with the highest frequency in the shallows; at some sites > 35% seabed is scoured per year at 5 m depth25. Typically ice scours are limited to ~ 500 m depth, though they may rarely occur deeper26,27. Ice scour is the key factor driving biodiversity and structure in the Antarctic shallows26,28–31. However, its influence has been little explored between 40 and 100 m

1National Oceanography Centre Southampton, University of Southampton, European Way, Southampton SO14 3ZH, UK. 2British Antarctic Survey, National Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK. 3School of Ocean Sciences, Bangor University, Bangor, Gwynedd LL57 2DG, UK. *email: benson@bas.ac.uk
Despite this depth range being an area of significant change in ice scour frequency, a broader study between 10 to 100 m depth is required.

In recent decades, there have been drastic shifts in the cryosphere through atmospheric and marine warming due to greenhouse gas-driven climate change. This is particularly true along the Western Antarctic Peninsula (WAP), a hotspot of regional physical change. In the Western Antarctic the seasonal sea-ice maximum area and duration have reduced over the last four decades (although the signal is noisy). As a result, there has been an increase in iceberg movement (because of less time locked into seasonally frozen sea ice), increasing the frequency of ice scour impacts (~0.6 scour for each day of sea ice loss at 10 m depth). Increasing numbers of glaciers and ice shelves in retreat (87% along the WAP) have led to high rates of iceberg calving, where rates of ice scour across all depth ranges are likely to increase substantially over the next century. Longer-term predictions estimate there will be an eventual decrease in ice scour events as glaciers pass the grounding line and retreat onto land.

Understanding how marine ice losses and ice scour will change the ecology of the Antarctic benthic macrofauna is key to understanding the future of this ecosystem, and provides insights into disturbance ecology. Disturbance is a heavily debated topic, and despite progress in this field, there is a lack of consensus on how this impacts systems when disturbance ranges move outside the historical norms. It is proposed through the Intermediate Disturbance Hypothesis that within a broad range of disturbance, species richness is maximised at intermediate levels due to competitively inferior, disturbance-tolerant species and competitively dominant, disturbance-sensitive species coexisting. However, many reports, which have been critical of the Intermediate Disturbance Hypothesis, only test the diversity-disturbance relationship across a small range of potential disturbance values or struggle to isolate relative, legacy and absolute disturbance. Therefore, sampling macro and megafaunal assemblages across one of the largest disturbance gradients on Earth, occurring over a small spatial scale, provides an ideal opportunity to test the Intermediate Disturbance Hypothesis, and investigate relationships between disturbance and biodiversity. Furthermore, the fauna itself is data poor, between 40 and 100 m depth, probably due to poor overlap of sampling methods at this depth range. Gathering comprehensive data from this assemblage before further climate-driven disturbance change is essential, if we are to understand the impacts of long-term change in this environment.

We surveyed benthic macro and mega fauna samples across 100 m depth from three sites on a steeply sloping marine rocky shore on Adelaide Island, WAP (67°35′ S, 068°07′ W, Supplementary materials, Figs S1). Most Antarctic species are relatively long-lived with extremely slow growth, reproduction and movement when compared to lower latitudes. It follows that these taxa are particularly good indicators of ice scour disturbance, with some recovery times predicted to be decades long (although exception exists). The broad ranges of disturbance regimes provide an opportunity to test disturbance-biodiversity relationships, within a similar environment and provide insights into the likely fate of the Antarctic benthos as they undergo dramatic disturbance changes over the next century. In this study, we aim to describe the patterns in macro and megafauna biodiversity from 10 to 100 m depth using multivariate analysis and then compare multiple diversity indices against the disturbance gradient, alongside multiple other environmental variables using multiple regression modelling. If ice scour is a driving influence behind biodiversity within the shallow Antarctic benthos, linear and polynomial regressions will be used to assess with the disturbance-biodiversity relationships are congruent with the IDH.

Methods

Study area. The study area was steeply sloping rocky shores (67°35′ S, 068°07′ W) around Ryder Bay, Adelaide Island, Western Antarctic Peninsula between 10 and 100 m depths. Three sites were selected along the North coast of Ryder Bay, with similar topography (Supplementary Materials S2) and exposure to predominant current flow and iceberg scour, providing homogeneous conditions. Adjacent to these sites, the Rothera Time Series (RaTS) provided long-term (since 1997) oceanographic measurements across all sample depths including light levels, temperature, salinity and standing stocks of phytoplankton.

Ice Scour. Ice scour is directly measured in the shallows around Rothera and Carlini stations in Antarctica, but the density of deeper scours is surveyed using ship-borne multibeam echo sounding. Where measured, ice scour occurrences are high and there has been a dramatically increased shift in density and frequency within the top 100 m. Our ice scour counts were collected through analysis of scours per square kilometre in multibeam bathymetry from the JR17001 (ICEBERGS1) cruise around Ryder Bay, between 0 and 500 m depth. Raw counts showed large variations in absolute values. Therefore, a log transformation was used to constrain the data range. An asymptotic regression curve (supplementary material, S3) provided the best fit for the data. Ice scour disturbance values between 10 and 100 m were then interpolated from this regression model.

Environmental factors. Environmental variables were collated from the Rothera time series (RaTS). As Antarctic macro and megafauna can be very long lived, this RaTS long-term data were used to describe the ambient environment experienced by the study taxa. All RaTS data were averaged across month to ensure even representation of the annual variation from 2011 to 2018. Maximum temperature range was calculated as the maximum and minimum recorded temperature from all 7 years at each specific depth. Benthic growth was calculated from bryozoa and serpulidae (spirobid worm) growth ring analysis from 5 to 500 m depth. Bryozoa growth is considered to represent a median value for growth across all benthic taxa. A quadratic spline curve provided the best fit for the data; from this, we interpolated values for each 10 m depth interval across our study area (Supplementary material on spline regression, S4).

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Macrofauna. Samples were collected at every 10 m depth interval between and including 10–100 m depth from 3 sites along Ryder Bay for a total of 30 stations. At each site the macrofauna assemblage and substrate were surveyed between February 2016 and June 2016, through 50 replicate images per station recorded via ROV, giving 1500 samples in total. A modified DeepTrekker DTG² was used to collect images and sample morphotypes (more details in supplementary material S5). Species accumulation curves were constructed for each station to ensure representation of rare species.

For each sample, a random area of seabed was selected and photographed (approximately 1.5 m²). Images were corrected for lens distortion with Hugin's photo editing software and cropped to remove areas with insufficient detail or those that were beyond the focal plane of the image. Macrofauna within the image were counted and identified into morphotypes. Specimens collected were later used to aid species identification and increase taxonomic resolution (188 specimens collected). Sample area could not be quantified as the seafloor was not uniform in shape, structure or composition. Attempts were made to ensure sampling was as uniform as possible and all images were scaled using two lasers but there remains an unquantifiable variability across each sample.

Data analysis. Biodiversity was expressed as species richness, the number of macrofaunal species present within a sample, Shannon-Weiner index and Fisher’s α. Shannon-Weiner and Fisher’s α were analysed as Shannon-Weiner includes an evenness measure and Fisher’s α is independent of sample size, to ensure that neither evenness nor sample size significantly alter the results. We preformed linear and polynomial (quadratic and cubic) regression analyses to determine the best-fit shape of biodiversity-disturbance relationship. Variance Inflation Factors (VIF) were used to identify any collinearity (VIF values between 1 and 5 = moderately correlated and > 5 = highly correlated). Parameters of regression were estimated using R package lme4 with Loess smoothing using the R package ggplot2 to assess potential nonlinearity between biodiversity and disturbance. All statistical analyses were performed using R 3.5.2 and Minitab 19.

Macrofauna composition was analysed using Primer 7 (version 7.0.17). Taxa abundance was transformed using square root function to reduce the influence of hyper-abundance and non-metric multidimensional scaling (nMDS) using a Bray–Curtis resemblance matrix was used to compare macrofaunal composition across all depths and sites. SIMPER (SIMilarity PERcentages) analysis was used to calculate the contribution of each taxa to group similarity, across the different factor levels.

Results

Depths between 10 and 30 m were dominated by mobile grazers such as by *Nacella concinna* (limpets) and *Stereochinus neumayeri* (sea urchins). These depths were also coincident with the highest prevalence of algae, although coralline algae was still found in reasonably high frequencies at 60 m depth. Between 40 and 50 m depth, a mixed assemblage of sessile suspension feeders and mobile grazers/scavengers were dominant with species such as *Cnemidocarpa verrucosa* (solitary ascidian), *S. neumayeri* and *Ophionotus victoriae* (brittle star). At 60–100 m depth, sessile suspension feeders dominated with some associated fauna, groups of Porifera and Bryozoa in particular. Due to bryozoans only being identifiable to species level under a microscope, multiple collections were made and found two bryozoan morphotypes represent multiple species. Bryozoan diversity is likely under reported but did coincide with the species richness peak between 50 and 60 m depth. Suspension feeders included, *Neofungella* sp. (*Stenoleamate byrozoan*), *Perkinsiana littoralis* (feather worms) and *Anoxycladulina joubenti* (structure-forming hexactinellid sponge).

No clear zonation was observed between 10 and 100 m depth; rather a gradual shift between assemblages with a broad overlap in species ranges (Supplementary materials Figs S6). Across all depths the assemblage composition showed large range of variability or ‘patchiness’, typical of Antarctic benthos and the resulting from spatial heterogeneity in iceberg scours. Gastropoda, Asteroida and Anthozoa groups showed no depth trend with individual taxa having wide depth ranges, although Actinaria (sea anemones) tended to be found deeper (> 60 m depth, but heavily species specific). Bryozoa, Ascidia and Porifera were found deeper, with the exception of *Beania* sp. (*Clenostomatida Bryozoa*) and *Cnemidocarpa verrucosa*. *Stereochinus neumayeri* and *O. victoriae* had a notable prevalence across all depths, although these taxa were found in higher abundance at depths shallower and deeper than 50 m, respectively. Representatives of the Holothuroidae (sea cucumbers), Hydrozoa and Entoprocta were more prevalent at intermediate depths (30–70 m).

Counts of scours per square kilometre on seabed mapping (vessel multibeam) data spanning Marguerite Bay showed that ice scour disturbance varied considerably across all depths. Scour density decreased from 1.75 × 10⁵ scours per square kilometre at 10 m depth to 3.92 scours per square kilometre at 100 m depth. Species richness showed a peaked relationship with study depth. We found an average species richness of 5.77 per image at 10 m depth, increasing to 22.49 between 50 and 60 m depth, before decreasing to 14.77 species richness by 100 m depth. The peak in species richness coincided with 32 scours per square kilometre. Linear and polynomial regression analysis found a cubic function ($F_{3,1496}=385.94$, $r^2=0.44$, $p<0.01$) and provided the best-fit relationship between biodiversity and disturbance (Fig. 1). The regression line shows a clear unimodal relationship, with a wide range of species richness at each level of disturbance. The maximum range of species richness at each depth was on average, 28.2 species (average Standard Deviation 5.43, across all depths). We found similar diversity-disturbance trends with all diversity indices (Supplementary materials Figs S7). As Shannon-Weiner ($r^2=32.6$, $p<0.001$) and Fisher’s α ($r^2=26.7$, $p<0.001$) diversity indices had lower $r^2$ values than the relationship between depth and species richness ($r^2=48.7$, $p<0.001$), further analyses used species richness.

Growth data for selected macrofauna interpolated from the literature rose from 0.08 g day⁻¹ m⁻² at 10 m to peak at 0.14 g day⁻¹ m⁻² at 40 m depth, decreasing to 0.12 g day⁻¹ m⁻² at 100 m depth (supplementary material S8). Growth correlates with ice scour disturbance (VIF = 1.68) and therefore has a quadratic correlation with species richness ($F_{2,1497}=291.20$, $r^2=0.279$, $p<0.001$). However, the maximum range of values for growth between...
40 and 100 m depth, was 0.02 g day$^{-1}$ m$^{-2}$. These values are below the signal noise threshold, of 0.05 g day$^{-1}$ m$^{-2}$, and cannot be distinguish from experimental error. Average annual salinity varied by a maximum 0.54‰ across all stations, which is in line with previous work on coastal Southern Ocean salinity being stable and constant throughout the year (except in the intertidal zone)\(^5\) (supplementary material S5). The range of growth and salinity were not considered large enough to detect any correlation with species richness, so were removed from the analysis.

Average annual sea temperature was −1.04 °C at 10 m depth. This variable decreased to a minimum of −1.09 °C at 25 m depth, before increasing to −0.73 °C at 100 m (supplementary material S3). Average annual sea temperature was correlated with ice scour disturbance ($VIF = 1.78$) but did not correlate with species richness. Maximum sea temperature range at 10 m depth was 4.00 °C, which decreased exponentially with depth, reaching 2.71 °C at 100 m depth (supplementary material S3). Chlorophyll α concentration decreased at an exponential rate with depth from 1.85 mg m$^{-3}$ at 10 m to 0.16 mg m$^{-3}$ at 100 m, as did photosynthetically active radiation, from 47.70 to 0.18 µmol m$^{-2}$ s$^{-1}$ (supplementary material S3). Sea temperature range, chlorophyll α and light levels exponentially decreased with depth, with the majority of change occurring in the top 20 m depth. All variables had a strong collinearity with scour density ($VIF = 20.09, 205.47, 25.24$ respectively) and were therefore removed from the model. Linear and polynomial regression analyses for sea temperature range, chlorophyll α and light levels had a similar unimodal relationship, as ice scour disturbance. However, all environmental variables had lower $r^2$ values and poorer overall fit, particularly past 30–40 m depth. In addition, there were only small differences between sites, and the inclusion of sediment and site did not significantly improve the model (Supplementary information on multiple regression analysis S4). These were tested to account for variation in ice abundance, topography and current between all three sites.

**Discussion**

The Antarctic marine shallows are home to one of the largest natural disturbance gradients on earth, up to 100% mortality across the entire macrobenthic population within the intertidal (with some exceptions see Waller, et al.\(^5\)), to near 0% mortality\(^21\) around 200 m depth\(^37\). Shallower than 40 m depth ice scour disturbance is a key controlling factor\(^21,28-30\) as only disturbance resilient species are able to persist, reducing species richness.\(^7,8\)

However between 40 and 100 m depth there is little information on which environmental factors influence the

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**Figure 1.** Relationship between species richness and disturbance. Line (model) of best fit was non-linear regression (cubic model, black line). Points are samples, with increasing shades of grey representing a greater number of samples. Green lines are 95% confidence intervals. Total sample number is 1500, evenly divided across 10 m depth intervals. Plot constructed in RStudio v1.1.463, [https://www.rstudio.com/](https://www.rstudio.com/).
Antarctic benthos and furthermore what species occupy this depth range\(^1\). Deeper than 40 m we found a unimodal relationship between macro and megafauna species richness and ice scour disturbance, with a peak in species richness at intermediate levels of ice scour disturbance. This concurs with the Intermediate Disturbance Hypothesis, a widely recognised concept, but one that has produced many reviews and critiques\(^2\). The disturbance-diversity pattern identified across our depth range showed an extreme variability in species richness across all depths. This patchiness is suggestive of ice scour disturbance being the driving factor, as a spatially and temporally discrete mass mortality event\(^22,23\). The variation in species richness amongst samples from similar depth likely reflect a patchwork of assemblages at different stages of recovery, from previous ice scour events. However, ‘patchiness’ (or spatial heterogeneity) was lowest at 10 m depth, which was dominated by a mobile assemblage, which could rapidly re-invade recent iceberg scours, the impact of ice scour impacts across a wider area, enough to homogenise the fauna at this depth\(^25\).

The influence of other environmental variables could not be completely isolated from disturbance, although many of them showed minor changes beyond 30 m depth. Additionally, we do not know at what depths lower thresholds of disturbance are reached and species richness starts to be controlled by other factors. Likely the flux of food particles from the surface, which much of the Antarctic seafloor community is reliant on\(^44\), will become a crucial factor at depth. For example, Jansen, et al.\(^37\) showed that the abundance and richness of types of benthic fauna could be predicted by food availability at depths below 200 m. We could not confirm any influence of light level or chlorophyll a concentration on biodiversity; however, they are likely to play a major, but perhaps complex, role in the structuring of benthic biota and ecosystem dynamics\(^49\), particularly below the depth of peak biodiversity.

The Western Antarctic Peninsula is a climate change hotspot that is predicted to warm if current emissions continue\(^25\). This change is also likely to result in a profound impact on ice scour disturbance, as glaciers continue to retreat and sea ice reduces in both extent and duration\(^24,33–35,41\). The second prediction is based on biodiversity regime change, that the increase in ice scour disturbance would redistribute species into deeper waters, as can be seen in small, sheltered areas of the seabed where much deeper species dominate (e.g., Sterechinus neumayeri and Ophionotus victoriae) both found in high abundance\(^70\).
overhangs and caves\(^2\)). However, in the previously high disturbance area between 10 and 30 m there may be small increases in richness and diversity, as macro-algae and their associated fauna increase.

To summarise, even though the Intermediate Disturbance Hypothesis is debated\(^9,14,35,71\), our results are congruent with this explanation for the Antarctic benthos disturbance-diversity pattern which can be detected because of the broad range of disturbance regimes included in this study. The consequences of the diversity-disturbance patterns within shallow Antarctic benthos will have profound impacts, particularly with glacial retreat opening new fjordic habitats and potential providing new carbon sinks and negative climate feedback loops\(^32\). The future of the shallow Antarctic benthos is likely to involve dramatic fluctuations in biodiversity and ecosystem functioning, and should warming continue, could ultimately lead to locally large losses in biodiversity with far-reaching implications.

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References

1. Dell, J. et al. Interaction diversity maintains resiliency in a frequently disturbed ecosystem. *Front. Ecol. Evol.* 7, 145 (2019).
2. White, P. S. & Pickett, S. T. A. In *The Ecology of Natural Disturbance and Patch Dynamics* (eds S. T. A. Pickett & P. S. White) 3–13 (Academic Press, 1983).
3. Newman, E. A. Disturbance ecology in the anthropocene. *Front. Ecol. Evolat.* https://doi.org/10.3389/fevo.2019.00147 (2019).
4. Barnosky, A. D. et al. Approaching a state shift in Earth’s biosphere. *Nature* **486**, 52–58 (2012).
5. Yuan, Z., Jiao, F., Li, Y. & Kallenbach, R. L. Anthropogenic disturbances are key to maintaining the biodiversity of grasslands. *Sci. Rep.* 6, 22132 (2016).
6. Hughes, A. R., Byrnes, J. E., Kimbro, D. L. & Stachowicz, J. J. Reciprocal relationships and potential feedbacks between biodiversity and disturbance. *Ecol. Lett.* 10, 849–864. https://doi.org/10.1111/j.1461-0248.2007.01075.x (2007).
7. Connell, J. H. & Slater, R. O. Mechanisms of succession in natural communities and their role in community stability and organization. *Am. Nat.* **111**, 1119–1144 (1977).
8. Connell, J. H. Diversity in tropical rain forests and coral reefs. *Science* **199**, 1302–1310 (1978).
9. Fox, J. W. The intermediate disturbance hypothesis should be abandoned. *Trends Ecol. Evol.* **28**, 86–92. https://doi.org/10.1016/j.tree.2012.08.014 (2013).
10. Sheil, D. & Burslem, D. F. Disturbing hypotheses in tropical forests. *Science* **362**, 525–527 (2018).
11. Newman, E. A. Disturbance ecology in the anthropocene. *Sci. Rep.* **11**, 1 (2021).
12. Teixidó, N., Garrabou, J., Gutt, J. & Arntz, W. Iceberg disturbance and successional spatial patterns: the case of the shelf Antarctic benthic communities. *Ecosystems* **10**, 143–158 (2007).
13. Johst, K., Gutt, J., Wissel, C. & Grimm, V. Diversity and disturbances in the Antarctic megabenthos: Feasible versus theoretical disturbance ranges. *Ecosystems* **9**, 1145–1155 (2006).
14. Mackey, R. L. & Currie, D. J. The diversity-disturbance relationship: Is it generally strong and peaked? *Ecology* **82**, 3479–3492. https://doi.org/10.1890/0012-9658(2001)082[3479:TDRTIA]2.0.CO;2 (2001).
15. Huston, M. A. Disturbance, productivity, and species diversity: Empiricism vs. logic in ecological theory. *Ecology* **95**, 2382–2396. https://doi.org/10.1890/13-1397.1 (2014).
16. Smale, D. A., Brown, K. M., Barnes, D. K., Fraser, K. P. & Clarke, A. Ice scour disturbance in Antarctic waters. *Science* **321**, 371. https://doi.org/10.1126/science.1158647 (2008).
17. Griffis, H. J., Danis, B. & Clarke, A. Quantifying Antarctic marine biodiversity: The SCAR-MarBIN data portal. *Deep Sea Res. Part II* **58**, 18–29. https://doi.org/10.1016/j.dsr2.2010.05.008 (2011).
18. Grange, L. J. & Smith, C. R. Megafaunal communities in rapidly warming fjords along the West Antarctic Peninsula: Hotspots of abundance and beta diversity. *PLoS ONE* **7**, e77917 (2012).
19. Gutt, J., Griffis, H. J. & Jones, C. D. Circumpolar overview and spatial heterogeneity of Antarctic macrobenthic communities. *Mar. Biodivers.* **43**, 481–487. https://doi.org/10.1007/s12526-013-0152-9 (2013).
20. Pothoff, M., Johst, K. & Gutt, J. How to survive as a pioneer species in the Antarctic benthos: Minimum dispersal distance as a function of lifetime and disturbance. *Polar Biol.* **29**, 543–551 (2006).
21. Convey, P. et al. The spatial structure of Antarctic biodiversity. *Ecol. Monogr.* **84**, 203–244 (2014).
22. Peck, L. S., Brockington, S., Vanhove, S. & Beghyn, M. Community recovery following catastrophic iceberg impacts in a soft-sediment shallow-water site at Signy Island, Antarctica. *Mar. Ecol. Prog. Ser.* **186**, 1–9 (1999).
23. Lee, H., Vanhove, S., Peck, L. & Vinx, M. Recolonisation of meiofauna after catastrophic iceberg scouring in shallow Antarctic sediments. *Polar Biol.* **24**, 918–925. https://doi.org/10.1007/s003000100300 (2001).
24. Armstrong, T. World Meteorological Organization. WMO sea-ice nomenclature. Terminology, codes and illustrated glossary. Edition 1970. Geneva, Secretariat of the World Meteorological Organization, 1970. [ix], 147 p. [including 175 photos] + corrigenda slip. (WMO/OMM/BBM, No. 259, TP.145.) 1. *Glaciol.* **11**, 148–149 (1972).
25. Robinson, B. J., Barnes, D. K. & Morley, S. A. Disturbance, dispersal and marine assemblage structure: A case study from the nearshore Southern Ocean. *Mar. Environ. Res.* **160**, 105025 (2020).
26. Gutt, J., Starmans, A. & Dieckmann, G. Impact of iceberg scouring on polar benthic habitats. *Mar. Ecol. Prog. Ser.* **137**, 311–316 (1996).
27. Barnes, D. K. A. & Conlan, K. E. Disturbance, colonization and development of Antarctic benthic communities. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **362**, 11–38. https://doi.org/10.1098/rstb.2016.195 (2007).
28. Smale, D. A. Ecological traits of benthic assemblages in shallow Antarctic waters: Does ice scour disturbance select for small, mobile, secondary consumers with high dispersal potential? *Polar Biol.* **31**, 1225–1231. https://doi.org/10.1007/s00300-008-0461-9 (2008).
29. Barnes, D. K. A. The influence of ice on polar nearshore benthos. *J. Mar. Biol. Assoc. U.K.* **79**, 401–407 (1999).
30. Gutt, J. On the direct impact of ice on marine benthic communities, a review. *Polar Biol.* **24**, 553–564 (2001).
31. Barnes, D. K. A. & Tarling, G. A. Polar oceans in a changing climate. *Curr. Biol.* **27**, R454–R460. https://doi.org/10.1016/j.cub.2017.01.045 (2017).
32. Barns, D. K. A., Fleming, A., Sands, C. J., Quentin, M. L. & Deregbus, D. Icebergs, sea ice, blue carbon and Antarctic climate feedbacks. *Philos. Trans. R. Soc. A Math. Phys. Eng. Sci.* **376**, 20170176. https://doi.org/10.1098/rsta.2017.0176 (2018).
33. Cook, A. J., Fox, A. J., Vaughan, D. G. & Ferrigno, J. G. Retreating glacier fronts on the Antarctic Peninsula over the past half-century. *Science* **308**, 541–544. https://doi.org/10.1126/science.1104335 (2015).
34. Cook, A. J. et al. Ocean forcing of glacier retreat in the western Antarctic Peninsula. *Science* **353**, 283–286 (2016).
35. Clarke, A. et al. Climate change and the marine ecosystem of the western Antarctic Peninsula. Philos. Trans. R. Soc. Lond. B Biol. Sci. 362, 149–166. https://doi.org/10.1098/rstb.2006.1958 (2007).
36. Turner, J. & Comiso, J. Solve Antarctica’s sea-ice puzzle. Nat. News 547, 275 (2017).
37. Meredith, M. P. & King, J. C. Rapid climate change in the ocean west of the Antarctic Peninsula during the second half of the 20th century. Geophys. Res. Lett. https://doi.org/10.1029/2005GL024042 (2005).
38. Barnes, D. K. A. & Souster, T. Reduced survival of Antarctic benthos linked to climate-induced iceberg scouring. Nat. Clim. Chang. 365–368. https://doi.org/10.1038/nclimate1232 (2011).
39. Parkinson, C. L. Global sea ice coverage from satellite data: Annual cycle and 35-yr trends. J. Clim. 27, 9377–9382. https://doi.org/10.1175/jcli-d-14-00605.1 (2014).
40. Rogers, A. et al. Antarctic futures: An assessment of climate-driven changes in ecosystem structure, function, and service provisioning in the Southern Ocean. Ann. Rev. Mar. Sci. 12, 87–120 (2020).
41. Morley, S. A. et al. Global drivers on Southern Ocean ecosystems: Changing physical environments and anthropogenic pressures in an Earth system. Front. Mar. Sci. 7, 1097 (2020).
42. Barnes, D. K. A. Iceberg killing fields limit huge potential for benthic blue carbon in Antarctic shallows. Glob. Chang. Biol. 26, 2750–2755 (2020).
43. Barnes, D. K. A. Blue carbon on polar and subpolar seabeds. In Blue carbon on polar and subpolar seabeds. https://doi.org/10.5772/intechopen.78237.
44. Bowler, D. et al. The geography of the Anthropocene differs between the land and the sea. bioRxiv https://doi.org/10.1101/432880 (2019).
45. Arnitz, W., Brey, T. & Gallardo, V. Antarctic zoobenthos. Oceanogr. Mar. Biol. 32, 241–304 (1994).
46. Clarke, A. Marine benthic populations in Antarctica: Patterns and processes. Antarct. Res. Ser. 70, 373–388 (1996).
47. Fillinger, L., Jauussen, D., Lundålv, T. & Richter, C. Rapid glass sponge expansion after climate-induced Antarctic ice shelf collapse. Curr. Biol. 23, 1330–1334 (2013).
48. Clarke, A., Meredith, M. P., Wallace, M. I., Brandon, M. A. & Thomas, D. N. Seasonal and interannual variability in temperature, chlorophyll and macronutrients in northern Marguerite Bay, Antarctica. Deep Sea Res. Part II 55, 1988–2006. https://doi.org/10.1016/j.dsr2.2008.04.035 (2008).
49. Barnes, D. K. A. Iceberg killing fields limit huge potential for benthic blue carbon in Antarctic shallows. Glob. Chang. Biol. 23, 2649–2659. https://doi.org/10.1111/gcb.13523 (2017).
50. Pinkerton, M., Bradford-Grieve, J., Bowden, D. & Cummings, V. Benthos: Trophic modelling of the Ross Sea. Support. Docum. CCAMLR Sci. 17, 1–31 (2010).
51. Pielou, E. Shannon’s formula as a measurement of species diversity: It’s use and disuse. Am. Nat. 100, 463–465 (1966).
52. Fisher, R. A., Corbet, A. S. & Williams, C. B. The relation between the number of species and the number of individuals in a random sample of an animal population. J. Anim. Ecol. 1, 42–58 (1943).
53. Everitt, B. & Skrondal, A. The Cambridge Dictionary of Statistics. Vol. 1 (Cambridge University Press, Cambridge, 2002).
54. Smale, D. A., Barnes, D. K. A. & Fraser, K. P. The influence of ice scour on benthic communities at three contrasting sites at Adelaide Island, Antarctica. Aust. Ecol. 32, 878–888. https://doi.org/10.1111/1442-9993.2007.01776.x (2007).
55. Peck, L. S., Convey, P. & Barnes, D. K. A. Environmental constraints on life histories in Antarctic ecosystems: Tempos, timings and predictability. Biol. Rev. 81, 75–109. https://doi.org/10.1017/s1464793105006871 (2006).
56. Waller, C., Worland, M., Convey, P. & Barnes, D. Ecophysiological strategies of Antarctic intertidal invertebrates faced with freezing stress. Polar Biol. 29, 1077–1083 (2006).
57. Barnes, D. K. A. Polar zoobenthos blue carbon storage increases with sea ice losses, because across-shelf growth gains from longer algal blooms outweigh ice scour mortality in the shallows. Glob. Chang. Biol. 23, 5083–5091. https://doi.org/10.1111/gcb.13772 (2017).
58. Smith, C. R., Mincks, S. & DeMaster, D. J. A synthesis of bentho-pelagic coupling on the Antarctic shelf: Food banks, ecosystem inertia and global climate change. Deep Sea Res. Part II 53, 875–894 (2006).
59. Jensen, J. et al. Abundance and richness of key Antarctic seafloor fauna correlates with modelled food availability. Nat. Ecol. Evolut. 2, 71–80 (2018).
60. Henley, S. E. et al. Changing biogeochemistry of the Southern Ocean and its ecosystem implications. Front. Mar. Sci. 7, 581 (2020).
61. Marshall, G. J. et al. Causes of exceptional atmospheric circulation changes in the Southern Hemisphere. Geophys. Res. Lett. 31, 14 (2004).
62. Ashton, G. V., Morley, S. A., Barnes, D. K., Clark, M. S. & Peck, L. S. Warming by 1°C drives species and assemblage level responses in Antarctica's marine shallows. Curr. Biol. 27, 2698–2705.e2693 (2017).
63. Riesgo, A. et al. Some like it fat: Comparative ultrastructure of the embryo in two demosponges of the genus Mycale (order poecilosclerida) from Antarctica and the Caribbean. PLoS ONE 10, e0188805 (2015).
64. Tosuzogyova, A. & Storch, D. Global diversity patterns are modulated by temporal fluctuations in primary productivity. Glob. Ecol. Biogeogr. 28, 1827–1838 (2019).
65. Clark, G. F. et al. Light-driven tipping points in polar ecosystems. Glob. Change Biol. 19, 3749–3761 (2013).
66. Brockington, S., Clarke, A. & Chapman, A. Seasonality of feeding and nutritional status during the austral winter in the Antarctic sea urchn Sterechinus neumayeri. Mar. Biol. 139, 127–138 (2001).
67. Pratt, D. B. & Dearborn, J. Feeding biology of the Antarctic brittle star Ophioplatus victoriae (Echinodermata: Ophiuroidea). Polar Biol. 3, 127–139 (1984).
68. Sabade, R., Tatin, M. & Esnail, G. B. Reproductive ecology of the ascidian Cnemidocarpa verrucosa at Potter Cove, South Shetland Islands, Antarctica. Mar. Ecol. Progr. Ser. 272, 131–140 (2004).
69. Dayton, P. K. et al. Recruitment, growth and mortality of an Antarctic hexactinellid sponge, Anoxycalyx joubini. PLoS ONE 8, e56939 (2013).
70. Vacchi, M., Cattaneo-Vietti, R., Chiantore, M. & Dalin, M. Predator-prey relationship between the nototheniid fish Trematodus bernacchii and the Antarctic scallop Adamussium colbecki at Terra Nova Bay (Ross Sea). Antarct. Sci. 12, 64–68 (2000).
71. Shell, D. & Burslem, D. F. Defining and defending Connelly’s intermediate disturbance hypothesis: a response to Fox. Trends Ecol. Evolut. 28, 571–572. https://doi.org/10.1016/j.tree.2013.07.006 (2013).

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The authors declare no competing interests.

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Correspondence and requests for materials should be addressed to B.J.O.R.

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