

# Intermediate ice scour disturbance is key to maintaining a peak in biodiversity within the shallows of the Western Antarctic Peninsula Robinson, Ben; Barnes, David; Grange, Laura; Morley, Simon

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### 34 Abstract

- 35 Climate-related disturbance regimes are changing rapidly with profound consequences for
- 36 ecosystems. Disturbance is often perceived as detrimental to biodiversity; however, the literature is
- 37 divided on how they influence each other. Disturbance events in nature are diverse, occurring across
- 38 numerous interacting trophic levels and multiple spatial and temporal scales, leading to divergence
- 39 between empirical and theoretical studies. The shallow Antarctic seafloor has one of the largest
- 40 disturbance gradients on earth, due to iceberg scouring. Scour rates are changing rapidly along the
- 41 Western Antarctic Peninsula because of climate change and with further changes predicted, the
- 42 Antarctic benthos will likely undergo dramatic shifts in diversity. We investigated benthic macro and
- 43 megafaunal richness across 10-100 m depth range, much of which, 40-100m, has rarely been
- sampled. Macro and megafauna species richness peaked at 50 60m depth, a depth dominated by a
   diverse range of sessile suspension feeders, with an intermediate level of iceberg disturbance. Our
- 46 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
- 48 key to maintaining high biodiversity in Antarctica's shallows.

#### 49 Introduction

- 50 Disturbance events occur in almost all natural ecosystems and tend to be a significant driver,
- 51 influencing assemblage diversity, structure and function<sup>1</sup>. However, the disturbance literature is
- 52 divided. Some studies conceptualise disturbance as departures from a 'stable' state<sup>2,3</sup> and
- 53 detrimental to biodiversity<sup>4</sup>, whereas, others present cases where disturbance maintains high
- <sup>54</sup> biodiversity<sup>5</sup> and promotes resilience to further change<sup>6</sup>. This paradox can be addressed with the
- 55 Intermediate Disturbance Hypothesis (IDH), which posits stable coexisting states under
- 56 "intermediate" disturbance conditions where species diversity is predicted to be highest<sup>7,8</sup>. The IDH
- 57 itself however is disputed on both theoretical and empirical grounds, with studies rarely finding the
- predicted peaked relationship<sup>9,10</sup>. Literature that has found evidence for peaks in diversity include
- 59 successional, post-iceberg disturbance studies<sup>11,12</sup> and theorectical models<sup>13</sup>. In contrast, a meta-
- analysis of disturbance studies found that a key factor in the detection of species richness peak was
- 61 the inclusion of a broad range of disturbance levels, which has not been achieved in the majority of
- 62 empirical studies<sup>14,15</sup>. The Western Antarctic Peninsula has one of the largest disturbance gradients
- 63 on earth<sup>16</sup> and is considered a hotspot of benthic diversity<sup>17-19</sup>, making it an ideal natural laboratory
- 64 for analysing the relationship between disturbance and diversity.
- 65 The shallow Antarctic seafloor (<40m depth) is home to one of the most naturally disturbed
- 66 assemblages, due to frequent iceberg scouring disturbance<sup>16,20</sup>. Ice scour disturbance, defined as
- 67 when the keel of an iceberg impacts the seafloor, are distinct events in both time and space<sup>21</sup>
- resulting in high mortality of >98.5% for macro and megafauna<sup>22,23</sup>. Here, we consider any contact of
- 69 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 ice bergs<sup>24</sup>. The frequency of ice scour
- 71 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 depth<sup>25</sup>. Typically ice scours are
- 13 limited to ~500 m depth, though they may rarely occur deeper<sup>26,27</sup>. Ice scour is the key factor driving
- biodiversity and structure in the Antarctic shallows<sup>21,28-31</sup>. However, its influence has been little
- explored between 40 m and 100 m despite this depth range being an area of significant change in ice
- $rac{1}{5}$  scour frequency<sup>32</sup>, so a broader study between 10 to 100m 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<sup>33-36</sup>. This is particularly true along the

- 79 Western Antarctic Peninsula (WAP)<sup>37</sup>, a hotspot of regional physical change<sup>38</sup>. In the Western
- 80 Antarctic the seasonal sea-ice maximum area and duration have reduced over the last four
- 81 decades<sup>39</sup> (although the signal is noisy). As a result, there has been an increase in iceberg movement
- 82 (because of less time locked into seasonally frozen sea ice), increasing the frequency of ice scour
- 83 impacts (~0.6 scours for each day of sea ice loss at 10 m depth)<sup>32</sup>. Increasing numbers of glaciers and
- 84 ice shelves in retreat  $(87\% \text{ along the WAP})^{33}$ , have led to high rates of iceberg calving<sup>32</sup>, where rates
- of ice scour across all depth ranges are likely to increase substantially over the next century<sup>32,40</sup>.
- 86 Longer-term predictions estimate there will be an eventual decrease in ice scour events as glaciers
- 87 pass the grounding line and retreat onto land<sup>40-43</sup>.
- 88 Understanding how marine ice losses and ice scour will change the ecology of the Antarctic benthic
- 89 macrofauna is key to understanding the future of this ecosystem<sup>1</sup>, and provides insights into
- 90 disturbance ecology. Disturbance is a heavily debated topic, and despite progress in this field, there
- 91 is a lack of consensus on how this impacts systems when disturbance ranges move outside the
- 92 historical norms<sup>44</sup>. It is proposed through the Intermediate Disturbance Hypothesis that within a
- 93 broad range of disturbance, species richness is maximised at intermediate levels due to
- 94 competitively inferior, disturbance-tolerant species and competitively dominant, disturbance-
- 95 sensitive species coexisting<sup>7,8</sup>. However, many reports, which have been critical of the Intermediate
- 96 Disturbance Hypothesis, only test the diversity-disturbance relationship across a small range of
- potential disturbance values<sup>14,15</sup> or struggle to isolate relative, legacy and absolute disturbance<sup>2,25</sup>.
   Therefore, sampling macro and megafaunal assemblages across one of the largest disturbance
- 99 gradients on Earth, occurring over a small spatial scale, provides an ideal opportunity to test
- 100 Intermediate Disturbance Hypothesis, and investigate relationships between disturbance and
- 101 biodiversity. Furthermore, the fauna itself is data poor, between 40-100 m depth, probably due to
- 102 poor overlap of sampling methods at this depth range<sup>32</sup>. Gathering comprehensive data from this
- 103 assemblage before further climate-driven disturbance change is essential, if we are to understand
- 104 the impacts of long-term change in this environment.
- 105 We surveyed benthic macro and megafaunal 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
- 107 materials, Figs S1). Most Antarctic species are relatively long-lived with extremely slow growth,
- 108 reproduction and movement when compared to lower latitudes<sup>45,46</sup>. It follows that these taxa are
- 109 particularly good indicators of ice scour disturbance, with some recovery times predicted to be
- 110 decades long (although exception exists<sup>47</sup>). The broad ranges of disturbance regimes provide an
- 111 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 anaylsis and then compare mulitple diversity
- biodiversity from 10 to 100 m depth using multivariate analysis and then compare mulitple diversity indicies against the disturbance gradient, alongside mulitple other environmental variables using
- 116 mulitple regression modelling. If ice scour is a driving influence behind biodiversity within the
- 117 shallow Antarctic benthos, linear and polynomial regressions will be used to assess with the
- 118 disturbance-biodiversity relationships are congruent with the IDH.

## 119 Methods

- 120 **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 10-100 m depths. Three sites were
- selected along the North coast of Ryder Bay, with similar topography (Supplementary Materials S2)
- 123 and exposure to predominant current flow and iceberg scour, providing homogenous conditions.
- 124 Adjacent to these sites, the Rothera Time Series (RaTS)<sup>48</sup> provided long-term (since 1997)

- oceanographic measurements across all sample depths including light levels, temperature, salinityand standing stocks of phytoplankton.
- 127 Ice Scour: Ice scour is directly measured in the shallows around Rothera and Carlini stations in
- 128 Antarctica, but the density of deeper scours is surveyed using ship-borne multibeam echo sounding.
- 129 Where measured, ice scour occurrences are high<sup>1,6,7,9</sup> and there has been a dramatically increased
- 130 shift in density and/or frequency within the top 100  $m^{21,27,29}$ . Our ice scour counts were collected
- 131 through analysis of scours per square kilometre in multibeam bathymetry from the JR17001
- 132 (ICEBERGS1) cruise around Ryder Bay<sup>44</sup>, between 0-500 m depth. Raw counts showed large
- 133 variations in absolute values. Therefore, a log transformation was used to constrain the data range.
- 134 An asymptotic regression curve (supplementary material, S3) provided the best fit for the data. Ice
- scour disturbance values between 10-100 m were then interpolated from this regression model.
- 136 **Environmental factors:** Environmental variables were collated from the Rothera time series (RaTS).
- 137 As Antarctic macro and megafauna can be very long lived<sup>45,46</sup>, 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
- 141 years at each specific depth. Benthic growth was calculated from bryozoa and serpulidae (spirobid
- 142 worm) growth ring analysis<sup>49</sup> from 5-500 m depth. Bryozoa growth is considered to represent a
- 143 median value for growth across all benthic taxa<sup>50</sup>. A quadratic spline curve provided the best fit for
- 144 the data; from this, we interpolated values for each 10 m depth interval across our study area
- 145 (Supplementary material on spline regression, S4).
- 146 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
- 149 replicate images per station recorded via ROV, giving 1,500 samples in total. A modified DeepTrekker
- 150 DTG2 was used to collect images and sample morphotypes (more details in supplementary material
- 151 S5). Species accumulation curves were constructed for each station to ensure representation of rare
- 152 species.
- 153 For each sample, a random area of seabed was selected and photographed (approximately 1.5 m<sup>2</sup>).
- 154 Images were corrected for lens distortion with *Hugins* photo editing software and cropped to
- remove areas with insufficient detail or those that were beyond the focal plane of the image.
- 156 Macrofauna within the image were counted and identified into morphotypes. Specimens collected
- 157 were later used to aid species identification and increase taxonomic resolution (188 specimens
- 158 collected). Sample area could not be quantified as the seafloor was not uniform in shape, structure
- 159 or composition. Attempts were made to ensure sampling was as uniform as possible and all images
- 160 were scaled using two lasers but there remains an unquantifiable variability across each sample.
- 161 **Data Analysis:** Biodiversity was expressed as species richness, the number of macrofaunal species
- 162 present within a sample, Shannon-Weiner index  $^{51}$  and Fisher's  $\alpha^{52}$ . Shannon-Weiner and Fisher's  $\alpha$
- 163 were analysed as Shannon-Weiner includes an evenness measure and Fisher's  $\alpha$  is independent of
- 164 sample size, to ensure that neither evenness nor sample size significantly alter the results. We
- 165 preformed linear and polynomial (quadratic and cubic) regression analyses to determine the best-fit
- 166 shape of biodiversity-disturbance relationship. Variance Inflation Factors (VIF) were used to identify
- any collinearity (VIF values between 1-5 = moderately correlated and >5 = highly correlated<sup>53</sup>).
- 168 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 statisticalanalyses were preformed using R 3.5.2 and Minitab 19.
- 171 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
- 173 multidimensional scaling (nMDS), using a Bray-Curtis resemblance matrix was used to compare
- 174 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.

#### 176 Results

- 177 Depths between 10-30 m were dominated by mobile grazers such as by *Nacella concinna* (limpets)
- and *Sterechinus 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
- 180 depth. Between 40-50 m depth, a mixed assemblage of sessile suspension feeders and mobile
- 181 grazers/scavengers were dominant with species such as *Cnemidocapra verrucosa* (solitary ascidian),
- 182 *S. neumayeri* and *Ophionotus victoriae* (brittle star). At 60-100 m depth, sessile suspension feeders
- 183 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
- 185 made and found two bryozoan morphotypes represent multiple species. Bryozoan diversity is likely
- 186 under reported but did coincide with the species richness peak between 50-60 m depth. Suspension
- 187 feeders included, *Neofungella* sp. (Stenoleamate byrozoan), *Perkinsiana littoralis* (feather worms)
- 188 and Anoxyclalyx joubeni (structure-forming hexactinellid sponge).
- 189 No clear zonation was observed between 10-100 m depth; rather a gradual shift between
- assemblages with a broad overlap in species ranges (Supplementary materials Figs S6). Across all
- 191 depths the assemblage composition showed large degree of variability or 'patchiness', typical of
- 192 Antarctic benthos and the resulting from spatial heterogeneity in iceberg scours<sup>54</sup>. Gastropoda,
- 193 Asteroidea and Anthozoa groups showed no depth trend with individual taxa having wide depth
- ranges, although Actiniaria (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.
- 196 (Ctenostomata Bryozoa) and Cnemidocarpa verrucosa. Sterechinus neumayeri and O. victoriae had a
- 197 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 Holothuroidea (sea
- 199 cucumbers), Hydrozoa and Entoprocta were more prevalent at intermediate depths (30-70 m).
- 200 Counts of scours per square kilometre on seabed mapping (vessel multibeam) data spanning
- 201 Marguerite Bay showed that ice scour disturbance varied considerably across all depths. Scour
- 202 density decreased from 1.75x10<sup>5</sup> 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.
- 204 We found an average species richness of 5.77 per image at 10 m depth, increasing to 22.49 between
- 50-60 m depth, before decreasing to 14.77 species richness by 100 m depth. The peak in species
- 206 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
- 208 between biodiversity and disturbance (Figure 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*,
- 211 across all depths). We found similar diversity-disturbance trends with all diversity indices
- 212 (Supplementary materials Figs S7). As Shannon-Weiner ( $r^2$ =32.6, p<0.001) and Fisher's  $\alpha$  ( $r^2$ =26.7,



213 p<0.001) diversity indicies had lower r<sup>2</sup> values than the relationship between depth and species 214 richness (r<sup>2</sup>=48.7, p<0.001), further analyses used species richness.

> Figure 1. Relationship between species richness and disturbance. Line (model) of best fit was nonlinear 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/.

Growth data for selected macrofauna interpolated from the literature<sup>49</sup> rose from 0.08 g day<sup>-1</sup> m<sup>-2</sup> at 215 10 m to peak at 0.14 C g day<sup>-1</sup> m<sup>-2</sup> at 40 m depth, decreasing to 0.12 g day<sup>-1</sup> m<sup>-2</sup> at 100 m depth 216 (supplementary material S8). Growth correlates with ice scour disturbance (VIF = 1.68) and therefore 217 218 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 40-100 m depth, was 0.02 g day<sup>-1</sup> m<sup>-2</sup>. These values 219 are below the signal noise threshold, of 0.05 g day<sup>-1</sup> m<sup>-2</sup>, and cannot be distinguish from experimental 220 221 error. Average annual salinity varied by a maximum 0.54 ‰ across all stations, which is in line with 222 previous work on coastal Southern Ocean salinity being stable and constant throughout the year 223 (except in the intertidal zone)<sup>55</sup> (supplementary material S5). The range of growth and salinity were 224 not considered large enough to detect any correlation with species richness, so were removed from 225 the analysis.

226 Average annual sea temperature was -1.04°C at 10 m depth. This variable decreased to a minimum 227 of -1.09°C at 25 m depth, before increasing to -0.73°C at 100 m (supplementary material S3). 228 Average annual sea temperature was correlated with ice scour disturbance (VIF=1.78) but did not 229 correlate with species richness. Maximum sea temperature range at 10 m depth was 4.00°C, which 230 decreased exponentially with depth, reaching 2.71°C at 100 m depth (supplementary material S3). Chlorophyll  $\alpha$  concentration decreased at an exponential rate with depth from 1.85 mg m<sup>-3</sup> at 10 m 231 to 0.16 mg m<sup>-3</sup> at 100 m, as did photosynthetically active radiation, from 47.70 µmol m<sup>-2</sup> s<sup>-1</sup> to 0.18 232  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup> (supplementary material S3). Sea temperature range, chlorophyll  $\alpha$  and light levels 233 234 exponentially decreased with depth, with the majority of change occurring in the top 20 m depth. All 235 variables had a strong collinearity with scour density (VIF = 20.09, 205.47, 25.24 respectively) and 236 were therefore removed from the model. Linear and polynomial regression analyses for sea 237 temperature range, chlorophyll  $\alpha$  and light levels had a similar unimodal relationship, as ice scour 238 disturbance. However, all environmental variables had lower r<sup>2</sup> values and poorer overall fit, 239 particularly past 30-40 m depth. In addition, there were only small differences between sites, and

- 240 the inclusion of sediment and site did not significantly improve the model (Supplementary
- 241 information on multiple regression analysis S4). These were tested to account for variation in ice
- abundance, topography and current between all 3 sites.

### 243 Discussion

- 244 The Antarctic marine shallows are home to one of the largest natural disturbance gradients on earth,
- 245 up to 100% mortality across the entire macrobenthic population within the intertidal (with some
- exceptions see Waller, et al. <sup>56</sup>), to near 0% mortality<sup>21</sup> around 200 m depth<sup>57</sup>. Shallower than 40 m
   depth ice scour disturbance is a key controlling factor<sup>21,28-30</sup> as only disturbance resilient species are
- depth ice scour disturbance is a key controlling factor<sup>21,28-30</sup> as only disturbance resilient species
   able to persist, reducing species richness<sup>7,8</sup>. However between 40-100m depth there is little
- 249 information on which environmental factors influence the Antarctic benthos and furthermore what
- 250 species occupy this depth range<sup>32</sup>. Deeper than 40 m we found a unimodal relationship between
- 251 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
- 253 Hypothesis, a widely recognised concept, but one that has produced many reviews and critiques<sup>15</sup>.
- 254 The disturbance-diversity pattern identified across our depth range showed an extreme variability in
- 255 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<sup>22,23</sup>. The variation in
- 257 species richness amongst samples from similar depth likely reflect a patchwork of assemblages at
- 258 different stages of recovery, from previous ice scour events. However, 'patchiness' (or spatial
- 259 heterogeneity) was lowest at 10 m depth, which was dominated by a mobile assemblage, which
- 260 could rapidly re-invade recent iceberg scours, the impact of ice scour impacts across a wider area,
- $261 \qquad \text{enough to homogenise the fauna at this depth}^{25}.$
- 262 The influence of other environmental variables could not be completely isolated from disturbance, 263 although many of them showed minor changes beyond 30 m depth. Additionally, we do not know at 264 what depths lower thresholds of disturbance are reached and species richness starts to be 265 controlled by other factors. Likely the flux of food particles from the surface, which much of the Antarctic seafloor community is reliant on<sup>58</sup>, will become a crucial factor at depth. For example, 266 Jansen, et al. <sup>59</sup> showed that the abundance and richness of types of benthic fauna could be 267 268 predicted by food availability at depths below 200 m. We could not confirm any influence of light 269 level or chlorophyll a concentration on biodiversity; however, they are likely to play a major, but 270 perhaps complex, role in the structuring of benthic biota and ecosystem dynamics<sup>60</sup>, particularly 271 below the depth of peak biodiversity.
- The Western Antarctic Peninsula is a climate change hotspot that is predicted to warm if current
  emissions continue<sup>61</sup>. 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<sup>33-35,41</sup>.
  Over the next century icebergs are likely to calve at an increased rate and with higher mobility as
  they are less likely to be held in place by seasonal sea ice<sup>40</sup>. As argued in this study, ice scour
  disturbance is a key controlling factor down to 100 m depth; if disturbance regimes continue to
  change, we expect benthic biodiversity to alter considerably.
- We suggest two potential futures within the next century for biodiversity in the shallows, based on
  the diversity-disturbance patterns reported in this study and the current composition of the
  Antarctic macro and mega-fauna. First, if scour disturbance increases rapidly the macro and
  megafaunal assemblage will struggle to redistribute, particularly if these species ranges are
  restricted by depth-dependent environmental and biological factors. The majority of macro and
  megafaunal species are long lived with slow growth, locomotion and reproduction, when compared

to lower latitudes<sup>45,46</sup> (but may grow faster with moderate warming<sup>62</sup>). Within this context, a century
 may not be long enough for these species to migrate away from, or adapt to, new conditions.

287 Increasing ice scour is expected to remove many of the competitively-dominant, disturbance-

sensitive species, such as *Mycale acerata* (sponge), which have slow growth and reproduction

rates<sup>63</sup>. However, many macro and megafauna species have wide depth-ranges (*M. acerta* for

example between 20-90 m depth) and so although species richness is controlled by ice scour in the

291 shallows, species may still exist at extremely low frequencies across a wide spectrum of disturbance

292 levels.

293 The presence of species across a wide depth gradient, may allow a few individuals found at the

extremes of their ranges to thrive as conditions shift in their favour. The broad depth-ranges of

295 many species support a second prediction, that the increase in ice scour disturbance would 296 redistribute species into deeper waters, as the diversity migrates in response to a new disturbance

297 pattern. The second prediction is based on biodiversity being driven by disturbance, even at the

deeper end of our depth range. Beyond 100 m depth the relative difference in disturbance is minute

and it is likely that primary production (more specifically bloom duration<sup>41</sup>) will be the limiting factor,

300 restricting the depth over which these species can redistribute. However, the pattern between sea-

301 surface chlorophyll and species richness is multifaceted, with trophic dependent relationships and

dependent on multiple physical variables<sup>59</sup>. This study cannot disentangle where, or if, the relative

303 contribution of disturbance is surpassed by primary production as a driving factor and instead

304 asserts that between 60-100 m depth the influence of disturbance is likely to wane.

With both predictions, we can expect species richness loss in the shallows (10-30 m) as disturbance tolerant species reach their limit and either redistribute to deeper waters or are extirpated. Both of the predictions made here are by no means mutually exclusive, there may well be a drop in diversity

308 across all depth ranges, as species are unable to move outside of their established ranges, combined

309 with a shift in the now reduced biodiversity peak, as the intermediate levels of disturbance shift

310 deeper. The eventual limit of the depth shift in biodiversity will likely be dictated by the depth

related reduction in primary production<sup>64</sup>. However, climate change-induced sea ice changes and

associated changes in light regime<sup>65</sup> are predicted to increase bloom duration<sup>41</sup> potentially allowing

313 more species to persist at a greater depth.

314 In particular, species such as *Sterechinus neumayeri* and *Ophionotus victoriae* both found in high

abundance across a large depth range with catholic diets<sup>66,67</sup>, will likely thrive as niches shift and new

316 opportunities become available. A key feature in assemblage response to disturbance shift is

dispersal capability<sup>25</sup>; broadcast-spawning species, such as *Cnemidocarpa verrucosa*<sup>68</sup>, may be

318 better able to redistribute in response to the changing environment. While species that have low

319 reproductive rates but are sensitive to climate forcing, such as *Anoxycalx joubini* (structure-forming

hexactinellid sponge) may spawn to respond to these changing conditions<sup>69</sup>. Generally species with

low reproductive rates are likely to suffer, however this may be countered by mobile species, whose

adults can adjust depth ranges through movement such as *Trematomus bernacchii* (Nototheniidae
 fish)<sup>70</sup>. Ultimately however if warming continues glaciers will retreat past grounding lines and

iceberg calving rates will drop dramatically resulting in a complete reversal to low levels of iceberg

disturbance across all depths<sup>42</sup>. This will likely form a new climax community with lower diversity

and dominated by porifera (sponges) usually found in deeper water, as can be seen in small,

327 sheltered areas of the seabed where much deeper species dominate (e.g., overhangs and caves $^{28}$ ).

328 However, in the previously high disturbance area between 10-30 m there may be small increases in

richness and diversity, as macro-algae and their associated fauna increase.

- 330 To summarise, even though the Intermediate Disturbance Hypothesis is debated<sup>9,14,15,71</sup>, our results
- 331 are congruent with this explanation for the Antarctic benthos disturbance-diversity pattern which
- 332 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 333
- 334 profound impacts, particularly with glacial retreat opening new fjordic habitats and potential
- providing new carbon sinks and negative climate feedback loops<sup>42</sup>. The future of the shallow 335
- 336 Antarctic benthos is likely to involve dramatic fluctuations in biodiversity and ecosystem functioning,
- 337 and should warming continue, could ultimately lead to locally large losses in biodiversity with far-
- 338 reaching implications.

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- 526 Figure legends:

- 527 Figure 1. Relationship between species richness and disturbance. Line (model) of best fit was non-
- 528 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,
- 531 https://www.rstudio.com/.