

Can Antarctica's shallow zoobenthos 'bounce back' from iceberg scouring impacts driven by climate change?

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Funding information

NERC Core funding

Abstract

All coastal systems experience disturbances and many across the planet are under unprecedented threat from an intensification of a variety of stressors. The West Antarctic Peninsula is a hotspot of physical climate change and has experienced a dramatic loss of sea-ice and glaciers in recent years. Among other things, sea-ice immobilizes icebergs, reducing collisions between icebergs and the seabed, thus decreasing ice-scouring. Ice disturbance drives patchiness in successional stages across seabed assemblages in Antarctica's shallows, making this an ideal system to understand the ecosystem resilience to increasing disturbance with climate change. We monitored a shallow benthic ecosystem before, during and after a 3-year pulse of catastrophic ice-scouring events and show that such systems can return, or bounce back, to previous states within 10 years. Our long-term data series show that recovery can happen more rapidly than expected, when disturbances abate, even in highly sensitive cold, polar environments.

KEYWORDS

benthos, disturbance, polar, recovery, resilience, sea-ice

1 | INTRODUCTION

Ecosystems globally are experiencing an intensification and diversification in the quantity and range of stressors (AghaKouchak et al., 2018; Turner et al., 2020). Anthropogenically introduced stressors including pollution, microplastics and habitat destruction are often highlighted, but of greater, and progressively increasing, concern are climate change intensified natural disturbances such as wildfires, drought or storm events (AghaKouchak et al., 2018). It is unlikely that the climatic drivers causing the acceleration and intensifying of natural disasters will be reversed, or even mitigated, in the foreseeable future (IPCC, 2014). Although some ecosystems are resilient to disturbance and recover quickly, others are more vulnerable and thought unlikely to revert back to their previous states (Lotze et al., 2011). These vulnerable systems, such as coral

reefs, rainforests and polar regions, are often high in diversity but dependent on species characterized by slow growth and low reproduction rates as well as longevity (Lotze et al., 2011). Most ecosystems affected by anthropogenically induced disturbance can recover when conditions improve, for example, if appropriate conservation measures are enacted and anthropogenic pressure is reduced (Jones & Schmitz, 2009). Antarctica is a special case as it remains protected from many direct human impacts by its isolation but is on the forefront of climate-change-driven disturbance, which cannot be mediated by simple measures (Kennicutt et al., 2019; Turner & Comiso, 2017; United Nations, 1959). As such, it is home to some of the least impacted ecosystems—many of which, for example, sub-ice-shelf ecosystems, are already being exposed to open water under the influence of climate warming (Gutt et al., 2020; Ingels et al., 2020).

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West Antarctica has sustained sea-ice losses for two decades while the Southern Ocean as a whole has showed unprecedented sea-ice losses since 2015 (Cook et al., 2016; J. Turner & Comiso, 2017). The West Antarctic Peninsula (WAP) has experienced the most severe consequences of this physical change (Gutt et al., 2020; Rogers et al., 2020). These range from increased air and sea temperature and break up of ice shelves to decreases in annual winter sea-ice duration and accelerated glacial retreat. Consequences of reductions in sea-ice are multifaceted and might range from strongly detrimental community destruction via increased ice-scouring events to changes in community composition owing to increased sedimentation as well as be beneficial since reductions in sea-ice are coincident with extended duration of plankton availability to suspension feeders (Henley et al., 2020; Sahade et al., 2015). Because meal processing times in Antarctic suspension feeders are slow, extended blooms result in more meals per season and are more important than peak concentrations of phytoplankton (Barnes, 2017). This is potentially an important mechanism opposing the destructive force of ice-scouring on benthic communities (Barnes, 2017; Sahade et al., 2015).

Reductions in winter sea-ice extent and duration, coupled with glacial retreat, lead to greater mobility of icebergs (Barnes & Souster, 2011). In shallow polar seas, such as the WAP coastal zone this means that icebergs, which can extend hundreds of meters below sea level, scour the seabed more frequently, thereby decimating benthic communities (Figure 1; Barnes & Souster, 2011; Dowdeswell & Bamber, 2007). Conditions in Antarctica's seas are unique and include glacial

cycling, constant low temperatures, extreme seasonality of primary production and high oxygen concentrations among others (Clarke, 2008). So far, data are limited on the life histories of the vast majority of benthic species. The facts we do know seem to confirm slow growth rates, longevity and a low reproductive output as well as prolonged gametogenic cycles, which are heavily dependent on seasonal primary production (Clarke, 1979; Peck, 2018). Infrequent rates of disturbance by iceberg scour, however, have been part of the evolutionary history of shallow polar benthos for millennia. Intermediate disturbance rates by icebergs, thus, have helped maintain high levels of β -diversity by contributing to patchiness in polar benthic ecosystems (Connell & Keough, 1985; Gutt & Piepenburg, 2003). This means, assemblages in areas generally affected by ice-scour (all coastal habitat lacking permanent ice cover) can be expected to be in various successional stages and to rarely reach maturity. Thus, we ask the questions of how resilient communities inhabiting shallow polar benthic systems are to the predicted intensification of ice-scouring impact and how sensitive near-shore coastal Antarctic systems will be to this particular consequence of climate change?

In normal years, at Ryder Bay, Adelaide Island, on the Antarctic Peninsula, approximately 24% of the shallow seafloor is impacted by ice-scouring events, but exceptionally high rates of ice-scouring (up to 50% per year) were observed along the WAP between 2007 and 2009 (Barnes et al., 2014). Such a major pulse of large-scale disturbance has the potential to alter community structure, a shift which was observed during the time of the impact (Figure 1; Barnes et al., 2014). Until now it was unknown whether the affected ecosystems had permanently phase-shifted into new steady states, defined by pioneers and scavengers with high mortality and low competition for space (Barnes & Souster, 2011; Sutherland, 1974) or whether, given suitable conditions, slow recovery was possible. To test this, long-term datasets linking climate-induced change to the state of benthic Antarctic ecosystems are needed. These are, however, rare, because repeated measurements over decades are costly and difficult in such challenging environments.

Here, we present data on the status of benthic assemblages in Ryder Bay (Rothera, WAP) for 23 years, prior to (1997–2006), during (2007–2009) and post (2010–2019), the period of high impact (PHI) caused by high-frequency catastrophic ice-scour disturbance events driven by exceptionally low seasonal sea-ice coverage (Barnes et al., 2014; Barnes & Sands, 2017). We estimated species richness of sessile and mobile epifauna as well as mortality rates and competitive interactions of sessile fauna at four locations within Ryder Bay (Figure S2). We aimed to answer the question of how resilient benthic polar systems are to dramatic, sustained disturbance events, and how long recovery might take. To our knowledge, no Antarctic ecosystem has been fully monitored from before, during and after recovery, perhaps in part because of the isolation of the continent and the considerable period of sustained, in situ effort required.

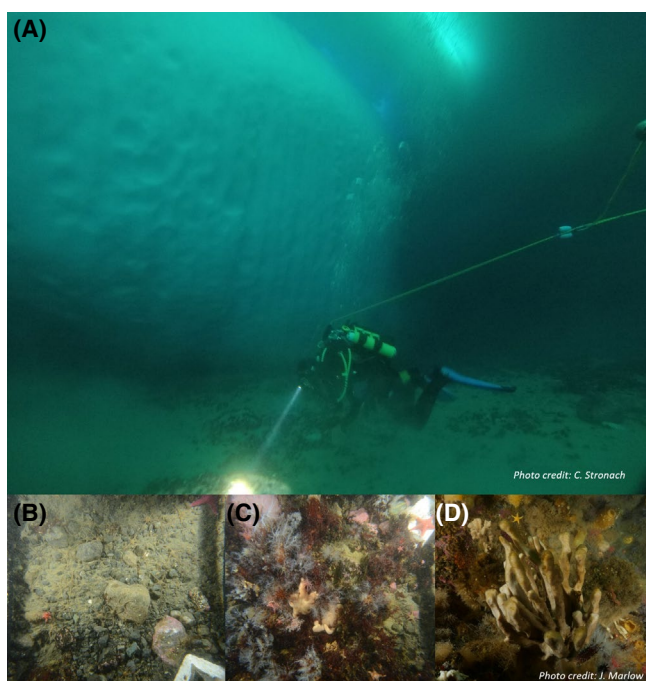


FIGURE 1 Impact of icebergs and stages of recovery: Photos show (A) a grounded iceberg frozen immobile in the sea-ice and the state of benthic communities (B) immediately after impact, (C) 11 years post-impact and (D) sheltered from ice-scouring impact

2 | METHODS

Our experimental system for monitoring annual seafloor ice-scour (IceBergs Impact Study—IBIS) is located in Ryder Bay, near Adelaide Island, WAP ($-67^{\circ}33'59.99''\text{S}$ – $68^{\circ}07'60.00''\text{W}$; Figures S1 and S2; Brown et al., 2004; Smale et al., 2008). Another similar array has recently been established further north on King George Island (WAP; Deregibus et al., 2017). IBIS is a grid system laid out in concrete blocks on the seafloor (Figure S2). Concrete blocks were deployed in nine sets of 5×5 m grid systems. Blocks were set 1 m apart (25 blocks per 5×5 m grid). Three grids were set-up at each of three different depths (5, 10 and 25 m) in South Cove, close to Rothera Research Station in 2002–2003 (Smale et al., 2008). Since then, the grids were monitored annually (December–January) to quantify disturbance, and manually replace blocks damaged by icebergs. Thus, annual iceberg disturbance was monitored for 18 years over an area of 225 m^2 . The extent, intensity and frequency of ice-scour at this location are described in detail in Barnes (2017). The different depths of IBIS meant that a true representation of impacts was measured for shallow assemblages. Shallower sites tend to be more often affected by ice-scour, but the impacts are smaller in size (Smale et al.,

2007). This dataset provides an estimate of the number of how many one m^2 in a 25 m^2 grid have been hit at least once during 1 year in Ryder Bay, as such it is representative of the minimum mean disturbance for each 25 m^2 area or seabed each year.

Duration of annual nano-phytoplankton bloom (chlorophyll concentrations $>200 \mu\text{g L}^{-1}$) and fast-ice duration in Ryder Bay were extracted from data collected for the Rothera Time Series (RaTS) environmental monitoring programme (Venables et al., 2020). Nano-phytoplankton was used as a proxy, since many suspension feeders in Antarctica feed on this size group (see Barnes, 2017 and references therein).

Sampling to monitor the proxies for the status of the ecosystem was carried out opportunistically; thus, samples were not taken every year and at a subset of different sites dependent on accessibility (see Table 1). Generally, three random locations within Ryder Bay and one random IBIS grid in South Cove were chosen ($N = 4$) during each sampling event (Table 1; Figure S1). To prevent any bias of depth stratification on community assemblages, all sites were sampled at ~ 10 m depth (Barnes & Brockington, 2003). Substratum at all sites was similar and was comprised of a steeply sloping seafloor made of boulders and cobbles interspersed with shallow

TABLE 1 Monitoring a shallow Antarctic location for disturbance and its biological consequences. Data availability varied across years for physical and biological parameters: The duration of fast ice (and phytoplankton above threshold of $200 \mu\text{g L}^{-1}$) was measured in days year $^{-1}$ (left) and ice-scour is represented as total ice-scours per total seabed markers (i.e. total/ 225 m^2). Years when the biological assemblage status was sampled are marked by 'x'

	Fast-ice Duration	Ice-scour	Phytoplankton	Mortality	Competition	Mega faunal species richness	Epifaunal species richness
2019	146	61	149	x	x	x	x
2018	94	44	149				
2017	47	65	250				
2016	183	56	120	x	x	x	x
2015	94	50	150		x	x	x
2014	99	48	180				
2013	69	63	210	x	x	x	x
2012	63	84	210				
2011	84	47	150	x	x	x	x
2010	30	77	150				
2009	67	98	180	x	x	x	x
2008	13	120	180				
2007	9	100	180	x	x	x	x
2006	160	39	150	x	x	x	x
2005	201	26	180				
2004	78	51	210	x			
2003	61	55	300	x	x	x	x
2002	207	24	210	x	x	x	x
2001	37		150				
2000	158		210				
1999	61		180				
1998	42		150		x		
1997				x		x	x

patches of coarse sediment and mud (Clarke, 1996; Smith et al., 2015; Figure S2). Sampling was carried out during the Antarctic summer months of January and February. In each sampling year, species richness of abundant benthic megafauna was assessed in situ in five randomly chosen 1 m² quadrats which were at least 5 m apart at each year. To estimate epifaunal species richness, we examined rocks collected from all five of these quadrats (a total of 20 rocks per site, each with a surface area between 50 and 500 cm² constituting approximately 0.4 m²/quadrat). We counted the number of species until we covered 1 m² in area examined at each site. Competition was estimated by counting overgrowth of colonies or individuals by other sessile epifaunal species (e.g. Bryozoa, Porifera, Polychaeta) until 456 competitive interactions were counted (for comparability). These were divided by the total number of colonies or individuals counted on each rock to give interaction density (number of interactions per recruit). Mortality was determined by the survival age of bryozoan colonies (following Barnes & Souster, 2011). Bryozoans grow in distinct patterns which allows colony age to be assessed. Mortality rate was calculated between each year class: $1 - N_x / (N_x + N_{(x-1)})$, where x is the age group being assessed (e.g. 2, 3 years). This method assumes a constant recruitment rate, which seems reasonable from previous monitoring of settlement and recruitment at the same location (Ashton et al., 2017; Bowden et al., 2006).

2.1 | Statistical analysis

To determine whether frequency of disturbance events varied between periods of years, a generalized linear model (GLM) with a Poisson distribution was used to compare number of impacts per 25 m² between individual years. A Tukey post-hoc test showed distinct groupings between certain period of years (2002–2007: Prior PHI; 2007–2009: PHI; 2009–2019: Post-PHI). We used GLMs to compare species richness of benthic macro- and epifauna, competition and mortality rates among the period before and during impact as well as the individual sampling years after impact to distinguish between years of recovery and the time when recovery was achieved. Distributions used in the model were adjusted for the dependent variable (e.g. Poisson distribution for count data, Gaussian for normally distributed data and Gamma for positively skewed data). To determine differences between individual groups, Tukey post-hoc tests were used on all relevant analyses.

To determine whether any other explanatory variables, such as fast-ice duration or extent of phytoplankton bloom, could explain variability in the data we carried out correlations between all variables. We used Pearsons and Spearman's correlation coefficients to account for non-normally distributed data. We found no difference between both coefficients; thus, results represented here have been calculated using the Pearsons correlation coefficient (Table S1). All data analyses were carried out in R version 3.5.2 (R Core Team, 2020).

3 | RESULTS

3.1 | Fast-ice cover and frequency of ice-scouring in Ryder Bay

Between 2007 and 2009, there was anomalously low sea-ice duration in the Bellinghousen Sea (9–67 days in Ryder Bay). Monitoring IBIS showed that, during this period, some sites experienced up to a minimum of 1 ice-scour impact m⁻² per year (Barnes, 2017). Prior to 2007, Ryder Bay as well as other locations around the WAP experienced a high duration of annual fast ice (average of ~92 days) and a lower frequency of ice-scour events (Table 1; Figure 2; Barnes, 2017; Barnes et al., 2014). While the intensity of ice-scouring significantly dropped after 2009, it did not return to the low levels prior to the PHI (GLM: $F_{2,159} = 16.23$, $p < 0.001$; Figure 2). Ice-scouring events significantly increased with a decrease in annual fast-ice cover (Correlation: $r^2 = -0.76$, $n = 105$, $p < 0.001$).

3.2 | Importance of plankton availability

Annual duration of nano-plankton availability weakly increased with decrease in annual fast-ice cover (correlation: $r^2 = -0.18$, $n = 118$, $p = 0.054$; Figure S3; Table S1). This relationship, however, was not significant. Duration of plankton availability was also not significantly correlated with epifaunal (correlation: $r^2 = 0.08$, $n = 41$, $p = 0.633$; Table S1) and megafaunal species richness (correlation: $r^2 = -0.11$, $n = 41$, $p = 0.505$; Table S1) nor with mortality (correlation: $r^2 = 0.14$, $n = 49$, $p = 0.346$; Table S1) and competition rates (correlation: $r^2 = -0.08$, $n = 145$, $p = 0.588$; Table S1).

3.3 | Recovery of a benthic system

Disturbance (the PHI), significantly increased mortality during the PHI, but mortality decreased after 2009 although not consistently throughout the recovery period (GLM: $F_{5,48} = 3.87$, $p = 0.005$; Figure 2). Correlations showed that mortality increased with increasing ice-scour frequency ($r^2 = 0.42$, $n = 49$, $p = 0.002$; Table S1).

As found previously (Barnes et al., 2014), the incidence of competition declined during and after the PHI (Figure 2; GLM: $F_{6,37} = 5.54$, $p = 0.0004$). This continued for several years after, up to 2013. At which point competition was significantly below pre-impact levels. Hereafter, competition rates started to increase, though they remained statistically similar to levels prior to and during the PHI until 2019. Only then were they different to competition levels during (and even prior to) PHI (Figure 2).

Throughout the survey, we found 21 taxa of megafauna and 19 taxa of epifauna (Table S2). Mega- and epifaunal species richness were affected very differently by the PHI. Although decreasing, megafaunal species richness was not significantly changed by the PHI. After 2009, megafaunal species richness increased steadily until, by 2019, megafaunal species richness was significantly higher

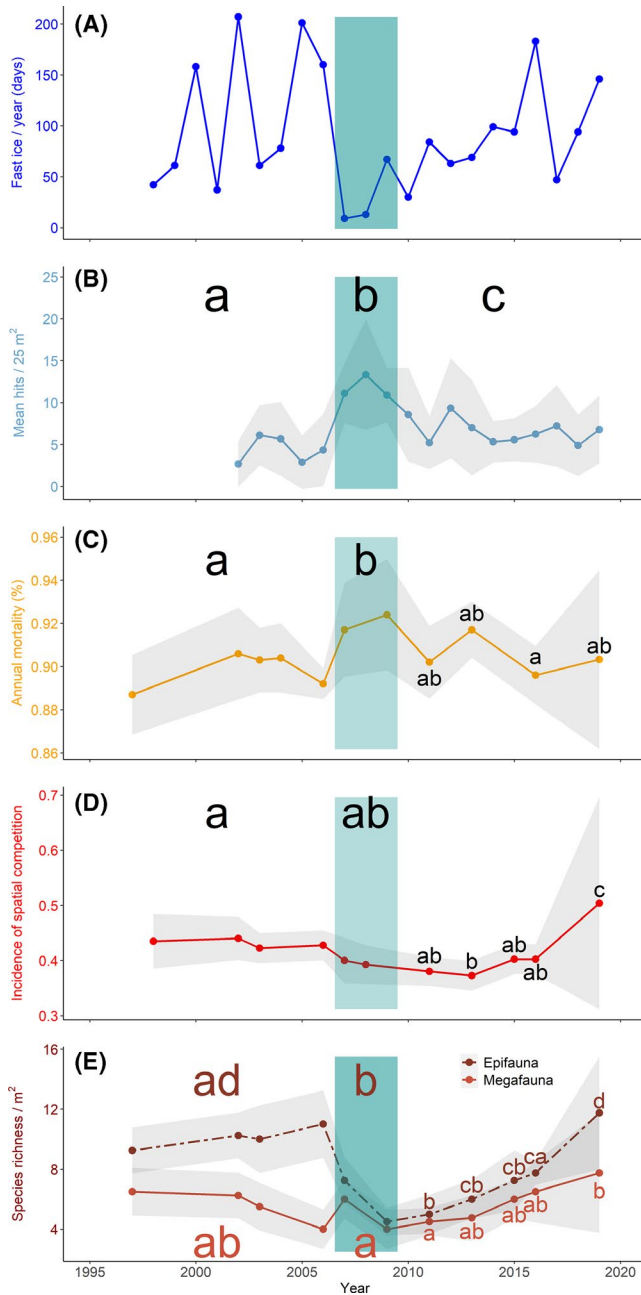


FIGURE 2 A shallow Antarctic ecosystem before, during and after impact. The high impact period is shown by the light blue box. The duration of fast ice reaches a minimum following 2006 (A). This allows more iceberg movement leading to peak ice-scour (B). The high ice-scour drives a rise in benthic mortality rates (C), depressed competition rates (D) and changes in biodiversity (E). Biodiversity is shown as mean megafaunal (dark brown) and epifaunal (light brown) species richness per m^2 between 1997 and 2019. Grey shading represents 95% confidence intervals. Different letters denote statistically different values

than that observed during the PHI (GLM: $F_{7,37} = 2.73$, $p = 0.022$; Figure 2).

As expected, epifaunal species richness declined significantly during the PHI (GLM: $F_{7,37} = 16.23$, $p < 0.001$), which was reflected in a significant correlation with mortality rates (Correlation: $r^2 = -0.46$,

$n = 40$, $p = 0.003$; Table S1; Figure 2; Barnes et al., 2014). Epifaunal species richness gradually increased after 2009, yet did not differ from the PHI until 2016. By 2019, epifaunal species richness was significantly higher than during the recovery period between 2011 and 2016. Increase in epifaunal species richness was significantly correlated with a decrease in ice-scour frequency (Correlation: $r^2 = -0.45$, $n = 41$, $p = 0.003$; Table S1).

4 | DISCUSSION

Our results highlight a concerning trend across the WAP. Although extreme low sea-ice cover, as those observed between 2007 and 2009, might still remain anomalous, the general trend within the last decade indicates that sea-ice cover in the coastal WAP is likely to decline in extent and duration over the coming years (Ducklow et al., 2013; Rogers et al., 2020). As part of this study, we specifically quantified the impact of this ice loss for benthic ecosystems in Ryder Bay. The similar set-up at King George Island will allow us to validate the generality of our findings over time (Deregibus et al., 2017). As far as we know, the dominant species and the physical environment of near-shore systems in Ryder Bay seem representative of most high energy shallow subtidal coastal systems along the WAP. Sea-ice duration is spatially complex but the consequences of a reduction in coastal fast ice are likely to be experienced along the complete WAP (Turner & Comiso, 2017).

We expected that most response variables representing benthic ecosystem status would differ between the years before and during the PHI (Barnes, 2017; Barnes et al., 2014; Barnes & Souster, 2011), but that after 10 years the system would start to show signs of recovery (Conlan & Kvitek, 2005). Surprisingly, this was only partly the case. Megafaunal species richness, for example, was not greatly affected by the increased disturbance. This is surprising as, although, megafauna was comprised primarily of mobile species (Table S2), many taxa including anemones and sea-cucumbers move extremely slowly (Arntz et al., 1994). As such, it is unlikely that this failed response is caused by the mobile species ability to 'flee' from the iceberg, but by their capacity to invade recently impacted systems from neighbouring unaffected areas more rapidly than originally thought (Robinson et al., 2020). It seems that, unlike sessile species, even slow mobile species are less dependent on recruitment events for recolonization or dispersal. The presence of carrion and the chance to evade competition (Dunlop et al., 2014; Peck et al., 1999) may stimulate this migration into recently disturbed patches as food availability for some scavengers can also be highly seasonal and thus limiting in Antarctic benthic ecosystems (Dunlop et al., 2014). In fact, previous research has shown that *Odontaster validus*, a highly abundant, scavenging starfish, will move towards a feeding cue in great numbers within 30 h (Kidawa, 2005; Smale et al., 2007). Further studies have shown that mobile species can recolonize a recently disturbed space within 10 days in sub-Antarctic near-shore systems and within 4 years in the deep sea (Gollner et al., 2017; Peck et al., 1999). Thus, an ability to profit from such disturbance events, for example, by

increased food abundance in terms of carrion in conjunction with high mobility, such as shown by the majority of Antarctic scavengers including *O. validus*, sea urchins (*Sterechinus neumayeri*), a range of amphipod species (Seefeldt et al., 2017), and some primary consumers such as sea cucumbers (*Heterocucumis steineni*) and limpets (*Nacella concinna*), seem to be successful traits in areas with high but localized disturbance regimes (Robinson et al., 2020; Seefeldt et al., 2017; Smale, 2008). This means that megafauna appear to be fairly resilient to iceberg impact. However, population structure and densities in affected communities may have changed during the experimental period, which represents an important unknown and caveat to this interpretation (Jones & Schmitz, 2009).

As expected, epifaunal species richness declined significantly during the PHI, which was also reflected in increased mortality rates and a decline in competition rates. Competition for space is one of the main drivers structuring sessile benthic assemblages (Dayton, 1971; Schoener, 1983). Increased space availability, created by the repetitive removal of established attached fauna via ice-scouring, reduces competitive pressure for primary colonizers such as *Fenestrulina rugula*, an early successional bryozoan (Barnes et al., 2014). Intraspecific competition between early colonizers, however, may be just as intense as interspecific competition between later successional stages (Lubchenco & Menge, 1978), which explains a continuing occurrence of competition in years of high ice-scour. In fact, a previous detailed analysis showed that while interspecific competition decreased during the PHI, rates of intraspecific competition, primarily among *F. rugula* populations, increased (Barnes et al., 2014). This is not only typical of ecosystems in early successional stages but also a common phenomenon found in higher latitudes (Barnes & Neutel, 2016) where harsh environmental conditions and abiotic perturbations, such as ice-scour, limit the dominance of stronger competitors (Barnes, 2002).

An increase in epifaunal species richness in combination with a rise in competition rates suggests that later successional stages in assemblage development have been reached. A decade after disturbance eased at Ryder Bay, sessile communities appear to have 'bounced back' (sensu Lotze et al., 2011). This result also highlights the sensitivity of sessile species, here primarily cheilostome bryozoa, spirorbinae and porifera, to perturbations. Recruitment of most epifaunal species in Antarctica is highly seasonal and predominantly occurs during the summer season. Bryozoans, however, which contribute one of the most speciose groups of epifauna in near-shore Antarctic systems, start recruitment during late winter beginning with weak competitors followed by stronger competitors during the early summer (Bowden, 2005). However, there seems to be a single short recruitment pulse per species per year (Bowden, 2005). Early colonizers often contribute to ameliorating environmental conditions to later successional stages (Potthoff et al., 2006; Turner, 1983). Thus, increased mortality of new early successional colonizers owing to sustained ice-scour disturbance may have far-reaching consequences for the structure and function of benthic communities (Robinson et al., 2020). Although annual recruitment of sessile species will contribute to the resilience of Antarctic near shore benthic systems, short durations and single

occurrence of annual recruitment in conjunction with sessile species inability to evade disturbance make them highly vulnerable to sustained ice-scouring events.

Interestingly, increased phytoplankton duration (food availability for suspension and deposit feeders) was not directly linked with an increase in epifaunal species richness. It seems likely, though, that enhanced phytoplankton duration might aid re-establishment of sessile species by benefiting recruitment success and growth rates of sessile species (Barnes, 2017). Although we were not able to measure this during this study, the question of how far increased duration of phytoplankton abundance ameliorates detrimental effects of ice-scouring on recruitment success of epifaunal species would be a sensible priority for future research to determine drivers underpinning recovery of benthic ecosystems in Antarctica.

With the exception of mortality rate, we found evidence that three of our four descriptors of ecosystem status seem to have reverted to, or increased above, levels prior to impact. The inconsistent decrease in mortality rates after the PHI may be because frequencies of ice-scour (a key driver of shallow benthic mortality; Barnes & Conlan, 2007) still remained higher than pre-impact levels. This relatively high level of disturbance may have also curbed the recovery of sessile components of communities (Connell, 1978; Jones & Schmitz, 2009).

Marine benthic systems, in general, seem to be very resilient to disturbance. With an average recovery time of less than 10 years globally, many of them are among the fastest ecosystems to recover from perturbations. This is in contrast to, for example, terrestrial forest system which have an average recovery time of 40 years (Jones & Schmitz, 2009). Many benthic systems, such as rocky shores or exposed shallow subtidal benthic systems, including the one studied here, are in a constant state of perturbation. These physical conditions hinder or make less likely the establishment of an apex community, which, in Ryder bay includes prominent large sponges, octocorals and brachiopods (pers. obs. D. K. A. Barnes). The 10-year recovery time, that has been demonstrated here for Antarctic near coast benthic systems, still seems remarkably fast, yet is comparable to a similar study following the recovery of benthic systems in Arctic fjord systems which reported recovery times for similar ecosystems between 13 and 24 years (Keck-Al-Habahbeh et al., 2020).

Although our study does not include proxies for ecosystem functioning, we could clearly show that mobile and sessile communities display varying degrees of resilience to disturbance caused by iceberg scouring. The fact that disturbance remained significantly greater during the recovery period than prior to the PHI indicates that the resilience of benthic Antarctic systems is greater than the life histories of the dominant species would suggest (Clarke, 1979; Potthoff et al., 2006). However, recovery time also depends on the magnitude and frequency of disturbance (Lotze et al., 2011). Current climate models, as well as our observations, predict decreases in sea-ice along the WAP (Roach et al., 2020). This means that, as long as the ~240 marine terminating glaciers along the WAP (90% of which are currently retreating; Cook et al., 2016) have not receded to firm ground, increased ice-scouring periods such as those observed here

during 2007–2009 might not be an exception but become a new normality for most of the WAP. While the capacity for resilience in benthic Antarctic ecosystems, shown during the present study, will provide a more optimistic view of potential persistence throughout the realization of these predictions, it is still unclear how far this capacity will stretch in increasingly stressed conditions.

Scale dependency of disturbance recovery has already been considered at larger scale in deeper water (Gutt et al., 2011; Gutt & Piepenburg, 2003). Our design incorporated multiple spatial scales from 1 m to hundreds of metres but did not specifically test for the effect of scale on resilience. Thus, the possibility still exists that the ecosystem will shift to a state of greater biotic impoverishment once the disturbance becomes chronic and spatially more extensive (Keck-Al-Habahbeh et al., 2020). This could result in reduced time available for the recovery of the ecosystem alongside a decrease in non-disturbed patches acting as sources for recolonization (Sutherland, 1974).

The extent of this study covered a miniscule spatial area in comparison to the vast extent of the WAP. Thus, the generality of our assumptions needs to be challenged with any new information that is being revealed about WAP's near shore coastal systems in the future. However, this is the only long-term data that show the state of aspects of a physical–biological system, before and during a PHI and at the cusp of recovery in Antarctica. Thus, these data contribute significantly to our understanding of the resilience of Antarctic benthic systems to the effects of climate change in a way that was unknown previously.

ACKNOWLEDGEMENTS

We would like to thank the current and all previous Rothera winter and summer marine teams and the Rothera 2019 wintering team. Especially C. Stronach, Z. Waring, A. Lines for constant support and R. Grant, G. Raymond, T. King, B. Sasikandarajah, J. Law, M. Phillips for helping out so much. D. Lewis, T. Hume and M. Washington for fixing the camera, T. Back, B. Mack, C. Mirfin and M. Porter for instructive tea breaks, A. Flink for help with the Stork project, P. Young, D. Stojanovic, M. Steel, J. Tighe and D. Routledge for keeping us running one way or another. Thanks to A. Kitchiner for useful comments. We would also like to thank P. Dayton for very helpful comments on the manuscript. A. Clarke was important in the initiation of the impact monitoring programme and its early management. This study was funded by Natural Environment Research Council (NERC) core funding to the Biodiversity, Evolution and Adaptations Team of the British Antarctic Survey.

CONFLICT OF INTEREST

The authors declare no competing interest.

AUTHORS' CONTRIBUTIONS

Nadescha Zworschke: Contributed to data collection and analysis, statistical analysis and writing of first draft. Simon Morley: Management and maintenance of impact monitor. Assistance with data collection over 15 years, contribution to writing. Lloyd Peck:

Co-conception of impact monitor with DKAB and A. Clarke, assistance with data collection and management of impact monitor over 22 years. David Barnes: Co-conception of impact monitor with LSP and A. Clarke. Prime manager of project for 20 years, contributed to data collection, analysis and writing.

DATA AVAILABILITY STATEMENT

Data available on request from the authors.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Zwerschke N, Morley SA, Peck LS, Barnes DK. Can Antarctica's shallow zoobenthos 'bounce back' from iceberg scouring impacts driven by climate change? *Glob Change Biol.* 2021;00:1–9. <https://doi.org/10.1111/gcb.15617>