Iceberg killing fields limit huge potential for benthic blue carbon in Antarctic shallows

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Abstract

Climate-forced ice losses are increasing potential for iceberg-seabed collisions, termed ice scour. At Ryder Bay, West Antarctic Peninsula (WAP) sea ice, oceanography, phytoplankton and encrusting zoobenthos have been monitored since 1998. In 2003, grids of seabed markers, covering 225 m^2, were established, surveyed and replaced annually to measure ice scour frequency. Disturbance history has been recorded for each m^2 of seabed monitored at 5–25 m for ~13 years. Encrusting fauna, collected from impacted and nonimpacted metres each year, show coincident benthos responses in growth, mortality and mass of benthic immobilized carbon. Encrusting benthic growth was mainly determined by microalgal bloom duration; each day, nanophytoplankton exceeded 200 μg L^{-1} produced ~0.05 mm radial growth of bryozoans, and sea temperature >0 °C added 0.002 mm day^{-1}. Mortality and persistence of growth, as benthic carbon immobilization, were mainly influenced by ice scour. Nearly 30% of monitored seabed was hit each year, and just 7% of shallows were not hit. Hits in deeper water were more deadly, but less frequent, so mortality decreased with depth. Five-year recovery time doubled benthic carbon stocks. Scour-driven mortality varied annually, with two-thirds of all monitored fauna killed in a single year (2009). Reduced fast ice after 2006 ramped iceberg scouring, killing half the encrusting benthos each year in following years. Ice scour coupled with low phytoplankton biomass drove a phase shift to high mortality and depressed zoobenthic immobilized carbon stocks, which has persevered for 10 years since. Stocks of immobilized benthic carbon averaged nearly 15 g m^{-2}. WAP ice scouring may be recycling 80 000 tonnes of carbon yr^{-1}. Without scouring, such carbon would remain immobilized and the 2.3% of shelf which are shallows could be as productive as all the remaining continental shelf. The region's future, when glaciers reach grounding lines and iceberg production diminishes, is as a major global sink of carbon storage.

Keywords: benthos, blue carbon sink, climate change, feedback, phytoplankton, Southern Ocean

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Introduction

Climate is driving rapid changes in Arctic and West Antarctic seas, with global consequences. These include coastal ice sheet thinning, ice shelf collapses, glacier retreat, sea ice losses, marine warming and likely extreme sensitivity to acidification (Meredith & King, 2005; Orr *et al.*, 2005; Stammerjohn *et al.*, 2008; Cook *et al.*, 2016). This is superimposed on biodiversity which include some of the highest endemism (www.SCAR-MarBIN.be), greatest thermal sensitivity and slowest recovery rates (Peck, 2015). However, there is little direct, hard evidence of biological response to physical change (Gutt *et al.*, 2015) perhaps due to remoteness and cost of sampling, combined with lack of long-term baseline. Some increases in primary (Arrigo *et al.*, 2008; Peck *et al.*, 2010) production have been measured, but may ultimately decline (Legge *et al.*, 2015). Varying secondary production changes have been found with taxon (salps vs. krill, see

Atkinson *et al.*, 2004), water column and depth (Barnes, 2015; Sahade *et al.*, 2015). West Antarctic marine biology is very important to monitor, as not only might it be the most sensitive to change, but is an important sink, in terms of carbon cycling (Legge *et al.*, 2015), benthic accumulation (Peck *et al.*, 2010) and longer term immobilization (Barnes *et al.*, 2016). Furthermore, such carbon drawdown and capture lead to powerful feedbacks. Loss of ice in time and space is a positive feedback on climate change, as increasing exposure of ocean surface leads to albedo change, increased heat absorption, warmer water, more melting and less gas (e.g. CO_2) holding capacity but increased secondary production can be a negative feedback on climate change (Peck *et al.*, 2010; Barnes, 2015). Trends in carbon accumulation and immobilization, which occur on the seabed, could be considered most important as these involve long-term carbon storage – and are perhaps the largest negative feedback on climate change (Barnes, 2015; Barnes *et al.*, 2016). By far the location of most physical, and likely biological, change is the continental shelf and in particular the coastal shallows (Meredith & King, 2005; Cook *et al.*, 2016).

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West Antarctica's shallows (here defined as 50 m – see Fig. S1) comprise just 2.3% of the vast 806k km^2 of continental shelf area, which is typically very deep compared with elsewhere in the world. The shallows are the marine region about which we know most about, because of ease of access – satellite penetration of water is limited, most Antarctic research stations are coastal, and SCUBA only allows direct access to ~50 m. Amongst the most important coastal, climate-forced changes seems to have been fast-ice losses (the winter sea surface freeze has decreased in space and time). This has not only altered albedo, heat absorption and gas exchange potential but also mediated increases in phytoplankton (Arrigo et al., 2008) and iceberg scour to the seabed (Barnes & Souster, 2011; Barnes et al., 2014). Iceberg scour, one of the most significant natural disturbance events (Gutt & Starmans, 2001), is little quantified in the shallows (but see Scrosati & Heaven, 2006; Smale, 2007; Smale et al., 2007) but could lead to less benthic carbon (by crushing and grinding up calcareous organism deposits). Thus, sea ice losses potentially lead to antagonistic impacts on benthic carbon, more phytoplanktonic food for benthos increasing 'blue carbon' (marine carbon storage) but more scouring preventing long-term build up of blue carbon. This study asks how (carbon stocks in) benthic secondary production are changing with time, and in response to changes in ice scour and primary production.

Remotely sensed data would typically be a useful tool in the current type of investigation, with advantages in wide geographic coverage and upscaling, but it is unreliably close to the coast for either phytoplankton or separation of different types of ice (e.g. icebergs compared with fast ice) (Barnes et al., 2016). Station-based sampling over long periods of time is proving crucial for monitoring biological responses to climate-forced physical change (e.g. Sahade et al., 2015). Ryder Bay (adjacent to Rothera Research station), Adelaide Island on the West Antarctic Peninsula, is one of the very few stations with year-round marine environmental sampling, has one of the longer term Antarctic data time series and is central to the hot spot of sea ice losses (Venables et al., 2013), CO$_2$ flux (Legge et al., 2015). Iceberg scouring and benthic mortality (Barnes & Souster, 2011) and competition (Barnes et al., 2014) have also been monitored yearly. The scour monitoring has probably become the longest continuously running direct measurement of disturbance on the seabed anywhere in the world. This study focussed on the immobilization of carbon on an Antarctic shallow seabed, by asking what determines values of benthic carbon stock in Antarctic shallows? However, this was tested for encrusting (sessile) benthos only, which form about 10% of biomass at such depths (Barnes & Brockington, 2003). The hypotheses were that (i) duration of phytoplankton abundance limits annual accumulation rate of carbon in the shallows and that (ii) iceberg scour frequency determines mortality rates, thus restricting carbon immobilization (long-term storage in benthos).

Materials and methods

The study was undertaken at Ryder Bay, Adelaide Island, West Antarctic Peninsula (Fig. S1). Water column characteristics, such as temperature, salinity, PAR and size-fractionated (micro, nano and pico) phytoplankton standing stock, have been measured weekly since 1997 (Venables et al., 2013). Monthly means of these data were compiled for 5, 10 and 25 m depth, for 1997 to present. Duration of 'summer' temperature was taken as the number of days for which the sea temperature at each depth was 0 °C or warmer. Duration of food availability was counted as the number of days each year for which nanophytoplankton was measured to exceed 200 μg L^{-1} (~6 μg L^{-1} of carbon) (following Barnes et al., 2016). Grids of 75 ice scour markers on the seabed at each of 5, 10 and 25 m depths have been surveyed (and replaced annually) using SCUBA, such that the frequency of scour at each depth can be calculated. The identity of each particular m^2 hit by icebergs is recorded so that its disturbance history is known, enabling calculation of frequency of hits at m^2 scale, as well as entire grid scale and time since last disturbance. This has been augmented by additional observations from certain years, of ice scour frequency in the intertidal zone and 40 m depth. Annual collections of encrusting fauna on boulders have been made from random m^2 grid squares incorporating the range of disturbance levels at each depth. Each year at each of the 5–25 m depths of faunal collections included those hit by icebergs that year – with and without neighbouring m^2 being hit, as well as m^2 not hit by icebergs, also with and without neighbouring m^2 being hit. This gives four potential levels of disturbance but with the added dimension of historical disturbance to each m^2.

Addition boulder samples were collected from 40 m in three austral summers (1998/1999, 2001/2002 and 2002/2003) and from 200 m depth in 2010/2011) to compare growth and mortality in the shallows with those in deeper water. Growth was measured on the two taxonomic groups, which were most abundant and largest space occupiers: spirorbid polychaete worms and cheilostome bryozoans. Maximum radius was measured of 200 randomly selected spirorbids and bryozoans on boulder collections from each m^2 sampled. The size of cohort increase was directly checked against the size of cohorts of known age on settlement panels. Growth of some cheilostome bryozoans shows feint radial, annual check lines which enabled multiyear growth to be measured in specimens >1 year old.

Mortality of encrusting benthos was determined by the slope of survivorship of annual cohorts (i.e. in a given year x% were 1 year old, y% were 2 years old etc., see Barnes & Souster, 2011). We defined growth as annual increments of drymass, carbon accumulation as the carbon proportion of this

and immobilized carbon as that held by fauna with hard skeletons. Annually incremented growth was measured as mass differences between cohorts (ground-truthed from adjacent settlement panels repeat photographed and periodically harvested to give growth, carbon accumulation and immobilization values). Faunal mass was measured by scraping them off boulders and drying. Following standard drymass and ash-free drymass drying oven and furnace protocols, skeletal mass was calculated (see Barnes *et al.*, 2016). Carbon 'immobilization' was computed by multiplying ash-free dry (organic) mass by 0.5 (Salonen *et al.*, 1976) and adding to the carbon proportion of skeletal mass ~13.3% (±2.5%). The study functional group (sessile suspension feeders) was estimated to constitute ~10%, respectively, of benthos within the shallows (up to 15% of deeper shelf depth benthos, see Barnes *et al.*, 2016), but being cemented to boulders means their burial and sequestration potential is probably amongst the highest of any blue carbon.

Results

Variability in environment, primary and secondary production in WAP shallows

Near-surface temperatures and PAR duration and peaks show both how intensely seasonal and predictable environmental conditions are, and how
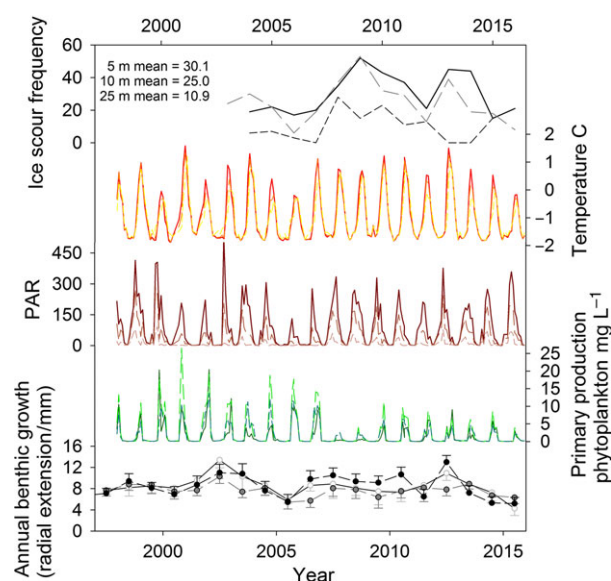

Fig. 1 Interannual and seasonal variability with depth in the nearshore marine shallows at Ryder Bay, West Antarctic Peninsula. The data are mean ice scour frequency (top), monthly means of sea temperature (middle top), photosynthetically active radiation (PAR – middle) and phytoplankton standing stock (mg L^{-1} – middle bottom) from the Rothera Time Series (RaTS). Mean growth of encrusting benthic bryozoans (mm yr^{-1} – bottom) is also shown with standard deviation.

similar values can be, across the shallow 5–25 m depths (Fig. 1). Similarly, primary production reflects this strongly seasonal but predictable cycle; however, there were notably brief blooms in 2007, 2008 and 2016. Since 2003, when it was first measured in Ryder Bay, ice scour has been less predictable and more variable (than many other environmental variables), both across years and depths (Fig. 1 top). Secondary production (growth of benthic primary consumers) was measured as radial growth of bryozoans and spirorbids (just the former shown, Fig. 1 bottom). This was consistent, with some interannual variability but no significant temporal trend. It was most significantly influenced by phytoplankton duration, but also by temperature (Table 1). Each day of phytoplankton standing stock above 200 µg L^{-1} resulted in 0.047 mm radial growth of bryozoans and each day of sea temperature above 0 °C added 0.002 mm radial growth (Fig. S2). Fast ice duration was also found to be a significant factor, but this was interpreted as caused by being a covariate of both phytoplankton and temperature durations.

Table 1 ANOVA showing factors influencing growth of encrusting biota in the shallows of Ryder Bay, West Antarctic Peninsula

Source of variation	df	Adj. SS	Adj. MS	F	P
Phytoplankton duration	7	184.2	26.32	13.1	<0.001***
Phytoplankton peak	19	49.2	2.59	1.3	0.192
Temperature duration	4	32.0	8.00	4.0	0.004**
Temperature peak	4	15.4	3.85	1.9	0.109
Fast ice duration	10	41.9	4.19	2.1	0.026*
Frequency of ice scour	6	25.3	4.21	2.1	0.055
Depth	1	0.05	0.05	0.02	0.88
Error	233	1046.5	6.06		
Total	284	1394.5			

Significance levels are shown (*<0.05, **<0.01 and ***<0.001). Phytoplankton duration is the number of days yr^{-1} standing stock was measured to exceed 200 µg L^{-1}, peak was the maximum measured mass L^{-1}, temperature duration was the numbers of days yr^{-1} that sea temperature exceeded 0 °C, temperature peak was the maximum measured sea temperature, fast ice duration was the number of days yr^{-1} during which the sea surface was frozen, ice scour was the number of impacts measured that year, and depth categories were 5, 10, 25 and 40 m.

Table 2 Iceberg scour with depth in South Cove, Ryder Bay, West Antarctic Peninsula, from 2003 to 2016

Per m² seabed	Intertidal	5 m	10 m	25 m
Annual scour probability	0.97 (0.02)	0.34 (0.11)	0.25 (0.05)	0.14 (0.51)
Mean time since last scour (years)	0.7 (0.1)	2.4 (0.15)	3.1 (0.29)	3.6 (0.40)
% Seabed not scoured for >5 years	0.1	6.7	18.7	38.7
% Mortality due to ice scour	Unknown	58.2 (4.1)	47.8 (6.2)	26.1 (3.2)

Data are mean annual chance of each m² of study seabed being hit by icebergs, the proportion of seabed hit, survivorship of benthos and recovery time since last hit, from annual monitoring. Mean % benthic mortality from collections at 40 and 200 m were 31.3% and 20.1%, respectively.

Iceberg scour rates and benthic mortality

Ice scouring is quantifiably very frequent in the shallows – on average, 29% of the study seabed area, from 5 to 25 m, was hit each year. In just over a decade of monitoring ice scour in Ryder Bay, only 7% of the shallows were not hit by icebergs at some point, and these areas were all 10 m or deeper. Iceberg scouring decreases rapidly with depth. An average square metre was hit more than three times in a decade at 5 m decreasing to just over once by 25 m depth. In a given year, the chances of ice scouring any particular square m, increase from 1 in 7 at 25 m, through 1 in 4 at 10 m, 1 in 3 at 5 m to near certainty in the intertidal (Table 2). Thus, the mean time period since any spot was last scoured changes from 3.6 years at 25 m depth to just over 6 months in the intertidal. The time that ecosystems or communities have had to recover from disturbance is a key factor in ecology and is shown in Fig. 2 for 5, 10 and 25 m. Whilst ~40% of the seabed at 25 m has had at least 5 years recovery time, this is less than 7% by 5 m depth (note the increase in light colours on the right of Fig. 2 with increasing depth – showing more seabed with long recovery times).

Comparison of benthic mortality (slopes on survivorship with age plots) on square metres of seabed hit by icebergs compared with those unscoured revealed that ice scour causes nearly 60% of mortality at 5 m but this decreases to just 26% by 25 m (bottom of Table 2). Total mortality (compared with just the proportion attributable to ice scour) also rapidly declines with depth (middle plot, unfilled circles, Fig. 3). Decreasing total mortality and iceberg caused mortality is driven by decreased frequencies of ice scour as mortality associated with each individual scour conversely increased with depth (middle plot, filled circles Fig. 3). ANOVA of potential driving factors mortality showed that depth was a significant covariate, so each depth was analysed separately (left, Table 3). By far the most important factor of mortality level on the seabed was, unsurprisingly, whether the exact spot was hit by icebergs in the study year. However, the next most important factor
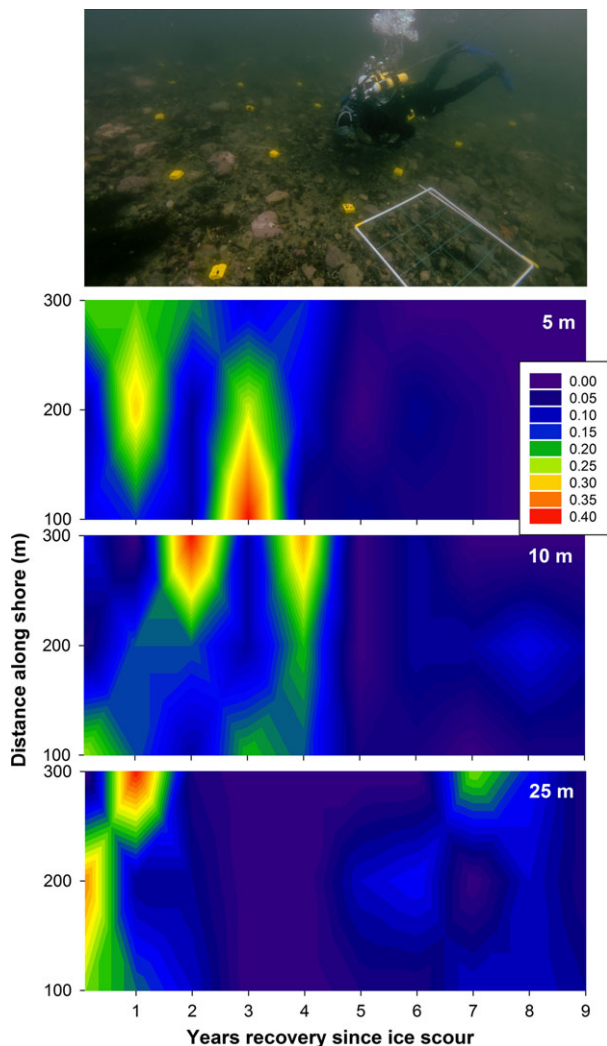

Fig. 2 Ice scour monitoring at Ryder Bay, Adleaide Island, West Antarctic Peninsula. Diver resurvey, recording and replacing ice scour impact markers in a grid of 225 (top), photograph courtesy of Ashley Cordingley. Recovery times of seabed areas from last iceberg impact with time (years), space (distance between marker grids). The data are proportion of seabed (ice scour markers) at different recovery times since last scoured, see legend on right.
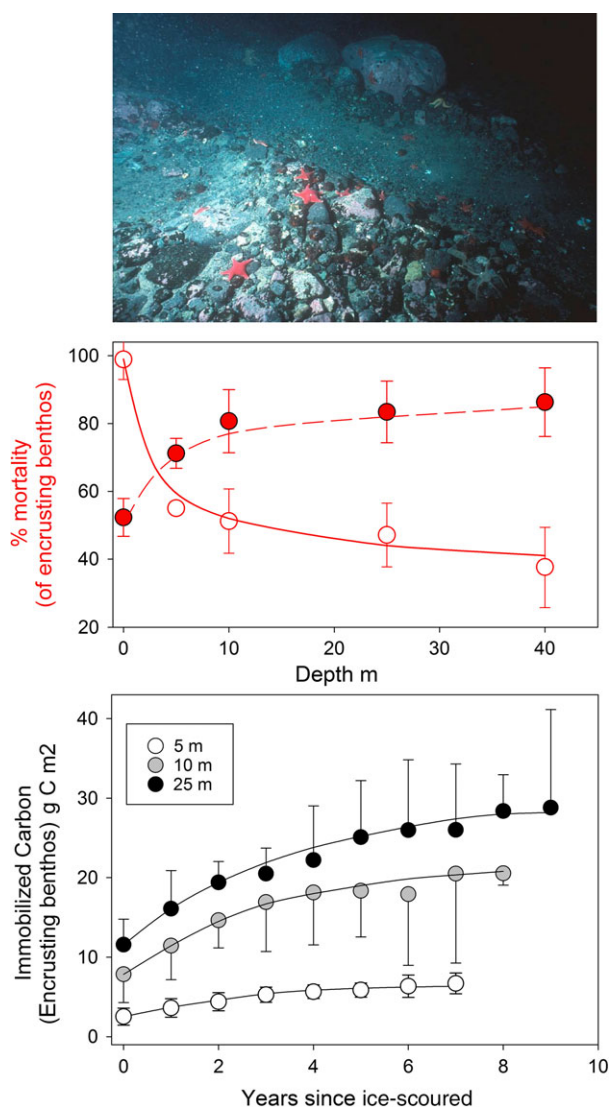
Fig. 3 Ice scour, benthic mortality and immobilization of carbon in the shallows of Antarctica. Furrow caused by iceberg blown into the shallows of Ryder Bay at 10 m (Top – photograph Kirsty Brown). Mortality changes with depth (middle); mean annual mortality of encrusting benthos decreased with depth (unfilled circles), but mortality from direct iceberg hits increased with depth (filled circles). Standing stock of immobilized carbon m^{-2} yr^{-1} with recovery time (since last scoured by icebergs). Data are shown by depth, as mean and standard deviation, with curves fitted by eye.

was whether any immediately neighbouring areas were hit, showing indirect as well as direct impacts of ice scouring on benthos. Other factors, such as overall frequency of scouring at that depth, were also important at some but not other depths. So whilst phytoplankton duration seemed to be the major driver of growth, ice scour was the key factor for mortality.

No temporal trend was found with growth (Fig. 1 bottom) or mortality (Fig. 3 bottom). However, there

was a discontinuity between 2006 and 2007, before which overall annual mortality was 10% lower. This was coincident with an unusual brief duration of fast ice, high ice scour frequency and two subsequent years of low phytoplankton durations (Fig. 1). In 2008, 2009 and 2010, approximately half the seabed from 5 to 25 m was hit by icebergs, which was twice the average level of impact of other study years. Two-thirds of the encrusting fauna were killed in 2009, and more than half this fauna in the seabed study area was killed each year between 2007–2011 and 2013–2015. However, Fig. 3 shows some evidence that mortality has started to recover to pre-2007 levels.

Iceberg scour and benthic carbon immobilization

As with mortality, ice scouring was the most important factor associated with standing stocks of biomass, measured as immobilized zoobenthic carbon (i.e. carbon bound in skeletelized benthos) (right, Table 3). So the biggest predictor of benthic carbon stocks at a particular square metre was whether it had been scoured in that year (rather than growth or primary production). Typically whether neighbouring areas were scoured that year was next most important, but different combinations of factors differed in importance across the study depths. Comparison of the mean carbon immobilization values by depth and the two outstanding predictors, ice scour hits and ice scour neighbour hits, show how considerable these effects are (Table 4). Areas that were not hit in a given year had approximately half the benthic carbon of areas that were both hit and had immediately neighbouring areas hit, across all depths (top row vs. bottom row of Table 4). Benthic carbon increased with the number of years since last directly ice-scoured (i.e. with increased recovery time), approaching plateau within the study period (Fig. 3 bottom).

On average across the study period, the standing stock of immobilized benthic carbon was 14.5 g m^{-2} (see calculation, bottom Table 4). The carbon mass reported in Table 4 upscales to between 6 and 25 (mean 17.5) tonnes km^{-2} for completely unscoured areas and 2.3–15.4 (mean 8.6) tonnes km^{-2} for completed scoured areas. Comparison of 0% scouring mean (17.5) with 100% scouring mean (8.6) suggests that theoretical ice scouring has potential to half the value of benthic immobilized carbon in the Ryder Bay shallows. The actual greatest values of recycling of immobilized carbon were observed in 2007 and 2009, which had means of 12.7 and 10.9 g m^{-2} compared with 18.2 and 15.2 g m^{-2} if upscaled from just the unscoured values from those years (28–30%).

Table 3 Significant factors influencing mortality and benthic carbon (immobilized in encrusting calcareous skeletelized benthos)

Source of variation	Mortality			Benthic carbon		
	5	10	25	5	10	25
Ice scour year	**263*****	**231*****	**22.3*****	**116.9*****	**27.0*****	**22.3*****
Neighbour m^2 scoured	16.8***	11.8***	2.5	17.1***	4.7*	2.5
Local ice scour freq.	1.0	11.6***	0.5	0.9	6.4**	0.5
Phytoplankton duration	0.5	0.5	3.2**	3.2*	4.3*	3.2*
Growth	3.8	0.6	0.3	3.2	9.3**	0.3
Temperature duration	1.0	0.9	0.1	2.7*	1.3	0.1

Initial analysis showed most variance with depth, so analyses were performed separately for 5, 10 and 25 m. ANOVA F values are shown with significance levels (*<0.05, **<0.01 and ***<0.001). The most important factor (highest F value) for each depth-mortality and depth-benthic carbon combination is shown in bold. Factors as in Table 1 but with the addition of whether the particular m^2 sampled was ice-scoured in the sampled year and whether the neighbouring m^2 sampled was ice-scoured in the sampled year.

Table 4 Carbon immobilization with depth in the shallows at Ryder Bay, West Antarctic Peninsula

Study m^2	Neighbour m^2	0 m	g C m^{-2} 5 m	Freq.	g C m^{-2} 10 m	Freq.	g C m^{-2} 25 m	Freq.
Not hit	Not hit	–	5.9 (2.0)	15%	21.5 (6.4)	28%	24.9 (8.6)	53%
Not hit	Hit	–	5.4 (1.2)	44%	18.4 (6.1)	43%	23.4 (5.7)	31%
Hit	Not hit	–	2.9 (1.1)	3%	10.8 (4.9)	4%	15.7 (5.3)	2%
Hit	Hit	<1	2.3 (1.1)	38%	8.1 (3.4)	26%	15.4 (3.4)	14%
Calculation 5 m	$(5.9 \times 0.15) + (5.4 \times 0.44) + (2.9 \times 0.03) + (2.3 \times 0.38)=$							4.2
Calculation 10 m	$(21.5 \times 0.28) + (18.4 \times 0.43) + (10.8 \times 0.04) + (8.1 \times 0.26)=$							16.3
Calculation 25 m	$(24.9 \times 0.53) + (23.4 \times 0.31) + (15.7 \times 0.02) + (15.4 \times 0.14)=$							22.9
	Mean benthic carbon tonnes^{-1} km$^{-2}=$							14.5
Multiplied by area of West Antarctic shallows/1000 tonnes=								267

Immobilization is reported as mean g C m^{-2} with standard deviation for $n > 10$ of all encrusting fauna. This lithophyllic biota (tubicolous polychaetes, cheilostome and cyclostome bryozoans, some demosponges and calcarea) all represent the functional group – sessile suspension feeders. The mean annual frequency of each category is shown as per cent (of total ice scour marker grid squares). Bottom rows show calculation for mass of benthic immobilized carbon in study area and scaled up for West Antarctic shallows.

Discussion

Ice scour and secondary production on Antarctic shallow seabeds

Most work on polar secondary production focuses on water column zooplankton such as copepods and euphausiids, but coastal seabeds can be very productive as well (Fillinger *et al.*, 2013). As elsewhere, the most potential for production is in the shallows but it is rarely apparent because of pervasive iceberg scour. The effects of ice scour are highly diverse, from aiding benthos dispersal (Dayton, 1989) and feeding (Peck *et al.*, 2005), to fertilization of primary production (Duprat *et al.*, 2016) and increasing foraging distance and thus mortality of penguins (Wilson *et al.*, 2016). Probably the most significant impact of icebergs is their scouring collisions with the seabed causing mass mortality of benthos, thereby creating a 'patchwork quilt' of seabed areas in differing states of recolonization and succession, maintaining high regional biodiversity (Conlan *et al.*, 1998; Gutt, 2001; Teixido *et al.*, 2004). However, this ice scour destruction of secondary production opens up space for fast-growing pioneers and thus can be considered to also stimulate and renew secondary production (like fire on land). The role of disturbance in terrestrial environments can be similarly pivotal, diverse and contrasting in its effects on primary and secondary production. It is, though, much better quantified (than in the sea), particularly in the case of fire, storms, floods, landslides and larva flows amongst others. Growth and disturbance have been monitored at a number of global locations for decades, such as at Barro Colorado Island, Panama (Condit, 1998). With year-round study of oceanographic conditions and benthos growth, mortality and immobilized carbon since 1998, and quantified iceberg disturbance since 2003, the current study shows the pivotal context, role and

importance of ice scour at a polar site and the value of long-term monitoring in a region of considerable, complex, climate-forced change. Ongoing climate change is likely to drive more ice scour at the poles – through both less fast ice allowing more movement of existing icebergs and retreating glaciers producing more icebergs. Net effects of climate-forced impacts on marine (production) feedbacks are complicated to predict as sea ice losses, in time and space, have resulted in more (blue) open water and thus more heat uptake by the planet (Parkinson, 2014). Offset against this is increased open water, although it can lead to bigger phytoplankton blooms (Arrigo *et al.*, 2008), providing longer meal times for benthos and therefore increased secondary production and benthic carbon capture (Barnes, 2015). However, more open water also leads to increased ice scouring (Barnes *et al.*, 2014) which is shown here results in more recycling of that production and carbon capture gains, rather than long-term seabed storage. Terrestrial high-latitude warming has led to similar complexities in biotic production, carbon sink dynamics and negative feedback effectiveness (Housset *et al.*, 2014).

Annual carbon accumulation on polar continental shelves (estimated as 10^6–10^7 tonnes) is small by comparison with kelp forests, salt marshes, mangrove swamps and terrestrial forests. However, unlike elsewhere much polar benthos is immobilized into skeletelized form, and very buriable in deep water – thus is argued to constitute Earth's largest, most important negative feedback against climate change (Barnes, 2015; Barnes *et al.*, 2016). As peak primary production is both shallow and coastal (Arrigo *et al.*, 2008), potentially the most important part of benthic carbon accumulation and immobilization is in the shallows. The current study shows that secondary production can indeed be considerable in the polar shallows, but there seemed little if any detectable role of ice scour in determining the amount of annual growth (Table 1) despite potential for resuspending food during winter (Peck *et al.*, 2005). As at typical (deeper) shelf depths (Barnes *et al.*, 2016), phytoplanktonic food duration was the dominant factor explaining the magnitude of encrusting benthos growth. However, the additional positive effect of increased sea temperature on growth, although small, is important considering the shallows are the fastest warming component of the ocean, in amongst the fastest warming sea (Meredith & King, 2005). Specific dynamic action (meal processing time) in polar ectotherms is estimated to be reduced by more than 10 days at 1 °C compared with 0 °C sea temperature (Peck, 2015), thereby enabling more mouthfuls for the same length of phytoplankton bloom. Annual growth varied by a factor of three from highs of 2003 and 2013

to lows of 2006 and the last two study years, but showed no gradual temporal trend (Fig. 1). Such annual variability has also been found on the deeper shelf seabed (Winston, 1983; Brey *et al.*, 1998; Barnes, 2015) but from a much lower baseline than in the shallows. However, growth appears to be simply driven by length of exposure to phytoplankton bloom duration (Fig. S2), so benthos grows less in deep water because there is just has less time to feed (and therefore grow). In contrast to accumulating carbon through growth, long-term storage (carbon immobilization) was mainly driven by ice scour (Table 3). This may hold in deeper water, as implied by comparisons of biomass between scoured and unscoured areas, but on much longer time scales (Conlan *et al.*, 1998; Gutt, 2001; Teixido *et al.*, 2004).

Ice scour control over benthic carbon stocks in the shallows

The frequency and magnitude of disturbance to a habitat fundamentally influence the nature of biodiversity in almost every measurable parameter. Nowhere is that more obvious than on polar shelf seabeds, which span the least to most naturally disturbed (underneath ice shelves vs. ice-scoured shallows) habitats on Earth (Dowdeswell *et al.*, 1993; Gutt, 2001). For the last few million years, benthos has been cyclically and predictably bulldozed from polar continental shelves by ice sheet expansion and retreat during glaciations (Thatje *et al.*, 2008). Each interglacial recolonization is less predictably disturbed by ice scour at smaller spatial and temporal scales (Bond *et al.*, 1992). Conditions in the West Antarctic Peninsula, with accelerating glacier retreat, ice shelf collapses and fast ice losses in time and space, are likely to be a 'perfect storm' for maximal iceberg impacts on marine life. Ryder Bay has already proved important in measuring water column carbon exchange (Legge *et al.*, 2015). The current study has shown that the duration of that microagal drawdown is the main factor limiting growth in the shallows (Table 1), that is annual accumulation rate of carbon there (thereby validating the first hypothesis). However, it is here shown that iceberg scour is ultimately the most crucial factor limiting stocks of benthic carbon immobilization, because of recycling carbon through mortality (Tables 2–4).

The high annual mortality found in shallow polar benthos was as expected, but the fact that ice scour only directly caused 58–26% of 5–25 m fauna was surprisingly low (see Barnes & Souster, 2011). It seems likely that specific predators, such as sea spiders and nudibranchs, and general grazers such as echinoids, have a bigger impact on populations than suspected.

Nevertheless, the current study shows that scouring has a considerable impact on mortality and carbon stocks. If unscoured, the standing stock of immobilized benthic carbon at Ryder Bay averaged ~15 g m^{-2} (Table 4), which if representative of wider regional values, could upscale to 15 tonnes km^{-2}. In turn, this could upscale to 11 million tonnes across the 806k km^2 area of West Antarctica's shallows. This would be two orders of magnitude more than at typical Antarctic shelf depths (~400–600 m) (see Arntz et al., 1994; Barnes, 2015) and would make the shallows as potentially productive as the other 97% of the shelf in deeper water.

Ice scour transforms that potential production, such that much of the shallows appears like 'urchin barrens' at some temperate, rocky subtidal sites. Ice scour is extremely destructive in deep water (Dowdeswell et al., 1993; Conlan et al., 1998; Gutt, 2001), but even in the shallow, a scour can cause 99% mortality (Smale, 2007; Smale et al., 2007) and become much more frequent with decreasing depth (Figs 2 and 3). Given this pivotal role of ice scour, but infrequency even by 25 m depth, it is clear that long-term continuous monitoring becomes crucial to meaningful assessment of how disturbance influences ecology. On average, each square metre at 25 m and shallower will be hit at least once in a decade by icebergs, meaning that nearly all of the shallows is recovering from recent ice scour (Fig. 2). The current study revealed the complexity of mortality in the shallows. The proportion of mortality caused by icebergs halved from 5 to 25 m, and overall mortality (of encrusting benthos monitored) decreased with depth, but increased per direct hit by icebergs with depth (Fig. 3). This is because ice scour frequency measurably decreases with depth but hits harder and over a larger area in deeper water (icebergs must be larger to hit the seabed deeper). Casual observations of grounded icebergs at different depths revealed those scouring at 5 m were mostly just 1–10 m in length, whereas those hitting the seabed at 25 m were 20–80 m in size (dkab per sobs). Mean mortality values of 26–58% caused by ice scour were lower than either expected or compared to the literature values (Peck et al., 1999; Lee et al., 2001; Smale et al., 2007) from sediments and mixed substrata but across all benthic groups. This was interpreted as caused by more refuge on hard surfaces but also higher survival of colonial animals because 99% of modules killed in a colony still enables persistence.

The lack of asymptotes at any study depth given in Fig. 3 (bottom) suggests that the entire shallow seabed (within the study region) is still recovering from ice scour. Biological recovery from ice scour has been documented over various periods of time at deep shelf depths in the Weddell Sea (Gutt, 2001) and shallows at Ryder Bay Smale et al. (2007). These show that even similar scours can recover in differing ways and paces, but the current study shows that iceberg impacts have considerable impact on standing stocks of carbon. In deeper water, recovery rates can take from decades to hundreds of years (Conlan et al., 1998; Gutt, 2001) or even thousands from wide-scale ice age level scouring (Barnes et al., 2016). However, Fillinger et al. (2013) showed that deep shelf colonization following ice shelf collapse can be rapid, in just years. Colonization and recolonization of the seabed by benthos, and the subsequent growth, involve massive consumption of microalgae, thereby cycling and accumulating millions of tonnes of carbon. This is minor compared with other such global processes in kelp forests, salt marshes and mangroves, but on the polar shelves, it is of global importance for two reasons. Polar benthic growth increases carbon flow to the seabed with intensifying climate change, as a negative feedback (Peck et al., 2010; Barnes, 2015). Secondly, the skeletelized fauna has the potential to escape normal carbon cycling and become immobilized (Barnes et al., 2016) and ultimately sequestered. The values found by the current study show that polar benthos, despite being life in the slow lane, can yield 17.5 tonnes C km^{-2} where unscoured. The area of seabed shallower than 50 m, within West Antarctica, was calculated to be ~18 400 km^2 (based on GIS within the area in Fig. S1). Upscaling the immobilized benthic carbon values in Ryder Bay shallows to the area of West Antarctic shallows gives a calculated value of 267 000 tonnes. Past SCUBA surveys in the South Shetland, South Orkney and South Georgia (cruises JR109 and JR144) suggest that the biomass within Ryder Bay encrusting biota is representative of that in other regional shallows. If iceberg scouring at Ryder Bay is also typical of other shallows, then ice scouring is recycling up to 80 000 tonnes (but potentially >130 000 tonnes) of immobilized carbon each year. Icebergs may have an important role in increasing carbon recycling through fertilization of algal blooms (Duprat et al., 2016) but their scouring may be as, or more significant at recycling carbon on the seabed.

Are Southern Ocean photic zone biota undergoing phase shifts?

It is not apparent from the long-term monitored data of Ryder Bay in Fig. 1 that there has been any drastic change, but other data show there has. The total (across depths) level of ice scouring at Ryder Bay was very high in 2007–2009, as has a related raised level of benthic mortality (Fig. 4 top and upper middle). Integrated nanophytoplankton production has remained at a
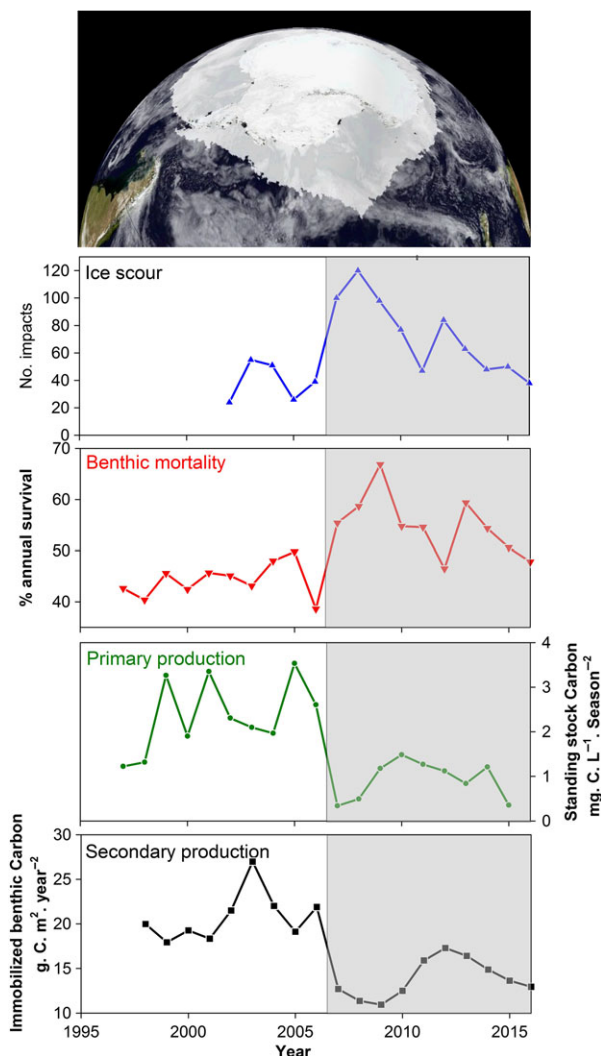
Fig. 4 Fast ice, ice scour, benthic mortality, primary and secondary production with time in the Ryder Bay shallows, Antarctica. Phase shift from 2007 onwards is shown in grey shade. Top image shows West Antarctica during (winter) disturbance minimum due to maximum extent of fast ice. The plots are total number of ice scours per year (top), annual mortality of encrusting benthos (upper middle), integrated biomass (mg C L^{-1} Season^{-2}) of nanophytoplankton primary production and standing stock of immobilized carbon in encrusting benthos.

Fig. 5 Iceberg shape, size and grounding depth can be difficult to predict from above water profile only. Photograph credit Tobias Friedrich.

reduced level since 2007 (Fig. 4 lower middle) and benthic biomass (measured as immobilized carbon in encrusting benthos) remains unrecovered nearly a decade later (Fig. 4 lower). The timing of change in each measured parameter was similar suggesting phase shift.

Southern Ocean phase shifts of krill-salps (Atkinson *et al.*, 2004) and their higher predators (Trivelpiece *et al.*, 2011) on the seabed in response to sedimentation from glacier retreat (Sahade *et al.*, 2015) and ice

scouring (Barnes *et al.*, 2014) have been suggested. The current study provides the most detailed long-term study, with multiple environmental variables, trophic levels, growth, mortality and carbon stocks but at a small spatial scale. The diversity and intensity of measurement collections make such a study difficult to undertake on a larger scale. Detection of change, even at a location as heavily monitored as Ryder Bay, theoretically a hot spot of climate change, can still be non-straight-forward. No phase shift was evident in many biologically relevant measures (Fig. 1), nor does Ryder Bay's nanophytoplankton bloom appear to be increasing with sea ice losses as is happening at regional scale (Arrigo *et al.*, 2008; Stammerjohn *et al.*, 2008). In deeper water, immobilization of carbon by benthos is significantly increasing (Barnes *et al.*, 2016), but not in the shallows. Climate-forced sea ice losses have far exceeded regional values (Barnes *et al.*, 2014) and evidence from the current study of the shallows is that this in turn resulted in massive ice scouring from 2007 to 2009. More than half the study areas benthos was killed off,

but (here demonstrated for the first time) even adjacent areas of seabed were negatively affected (Tables 3 and 4). This may be inability to cope with increased sedimentation (Sahade *et al.*, 2015) or increased predation from scavengers around fresh scours (Dunlop *et al.*, 2014). Coincident depression in nanophytoplankton production and sustained moderately high scouring has prevented recovery for nearly a decade (Fig. 4). Climate-forced phase shifts have been suggested in both the open ocean (Atkinson *et al.*, 2004) and shallows (Barnes *et al.*, 2014; Sahade *et al.*, 2015) around Antarctica. Arguably data from the current study are the most detailed, evidence-rich and convincing of a climate driven shift in an Antarctic ecosystem, even if only at bay scale.

West Antarctica's shallows are likely to continue to be a hot spot of glacier retreat, ice shelf collapses and sea ice losses, and whilst it does, the massive carbon drawdown of microalgal blooms is likely to remain a pool of short term carbon cycling (accumulated by benthos which is then crushed by ice scour). However, as regional ice shelves disappear and glaciers pass their grounding lines intrinsic iceberg production will also rapidly fall. Ultimately if phytoplankton bloom increases are sustained (see Legge *et al.*, 2015), sea temperatures only marginally elevated (Meredith & King, 2005) and iceberg scour (Fig. 5) declines, benthos carbon storage could drastically increase. The region, already a key carbon sink for cycling (Legge *et al.*, 2015), accumulation (Peck *et al.*, 2010) and immobilization (Barnes, 2015), could double its annual carbon storage budget and thus its importance as a negative feedback on climate change. It seems likely that reductions of scouring will also occur in the Arctic shallows. Furthermore, there should be increases in genuine carbon sequestration as more immobilized carbon in deeper shelf habitats will be eventually buried by sedimentation rather than recycled by scouring. However, until then, any benthic carbon gains will continue to be recycled by likely increased ice scouring for at least the coming decades.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Locations of ice scour quantification in Antarctica's shallows.
Figure S2. Factors influencing growth of encrusting benthos.
Figure S3. Proportion of seabed study area scoured by icebergs at Ryder and Borge Bays.