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Altered Sea Ice Thickness and Permanence Affects Benthic Ecosystem Functioning in Coastal Antarctica

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ABSTRACT

Antarctic sea ice and the cold waters surrounding the continent are key elements of the global climate system, influencing heat redistribution, oceanic circulation and the absorption of carbon dioxide from the atmosphere. However, the Southern Ocean is predicted to warm by 1–6°C over the next century, altering sea ice extent, thickness and permanence. To better understand the connections between coastal sea ice conditions and the functioning of Antarctica's unique marine benthic ecosystems, we performed manipulative experiments on the seafloor at two southwestern Ross Sea sites with contrasting sea ice conditions. Benthic systems at both study sites were net heterotrophic during the study period (early November), with primary production most likely limited by light availability rather than nutrients. There was five times more fresh algal detrital material in benthic sediments at the site with the thinner, snow-free, annually formed sea ice, relative to the site with thicker, multiyear sea ice. This elevated quantity and quality of algal detrital matter corresponded with a significantly greater rate of sediment oxygen utilization by the benthos and an altered pathway of nitrogen regeneration (tighter coupling between nitrification and denitrification). Large benthic animals (brittle stars, *Ophionotus victoriae*) enhanced the efflux of dissolved inorganic nutrients from the sediment to the water column and played a greater role in nutrient regeneration at the site with more food. Although changes in sea ice characteristics in the Western Ross Sea are difficult to predict at present, large benthic organisms can be expected to have an expanded role in mediating the effects of elevated coastal productivity and detritus supply on ecosystem dynamics in this part of Antarctica.

Key words: coastal Antarctic marine benthos; under-ice algal detritus; sediment oxygen demand; nutrient flux; *Ophionotus victoriae*.

INTRODUCTION

Major changes in climate are expected to profoundly affect the coastal ecosystems of Antarctica (Thomas 2004). Although these changes in climate are expected to vary both spatially and with the progression of global warming, a much higher degree of uncertainty lies in how these changes will

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manifest themselves ecologically (Smetacek and Nichol 2005; Smith and others 2006). Coastal marine sediments contribute to key ecosystem functions such as organic matter degradation and nutrient regeneration as a result of interactions between biogeochemical processes and resident organisms (Mermillod-Blondin and others 2005; Norling and others 2007). Although knowledge of these processes is growing for temperate, tropical and Arctic ecosystems (Rysgaard and others 1998; Lohrer and others 2004; Eyre and others 2011), little information is available for Antarctic sediments, especially from in situ experiments (McMinn and others 2010). The extreme cold, low light, low sediment organic content and often coarse grain size of Antarctic sediments may all affect the linkage between local sedimentary processes and wider water column productivity.

Coastal benthic communities in the western Ross Sea, Antarctica—including the southernmost accessible marine ecosystems on the planet—are unique and diverse, with many sites exhibiting high animal abundance and biomass (Dayton and others 1974; Dayton 1989; Kim and others 2007; Thrush and others 2010). These community characteristics exist despite a lack of primary production during winter due to the absence of sunlight from May to July, which can lead to food limitation (Dayton and Oliver 1977; Dayton and others 1986; Thrush and others 2006). The presence of sea ice extending many km offshore further limits coastal primary production, even during the months of November to January when there is sunlight 24 h d^{-1} (Norkko and others 2007; Thrush and Cummings 2011; Wing and others 2012), as the ice reduces the availability of photosynthetically active radiation (PAR) in underlying marine habitats by more than 99% (Schwarz and others 2003). Although microalgae, mainly diatoms, can be present at concentrations approaching 1,000 µg l^{-1} on the underside of sea ice during the spring and summer (Thomas and Dieckmann 2002), variation in sea ice conditions—extent, thickness, opacity, permanence, snow cover—can impact under-ice algal production and the amount and freshness of detrital algal material raining down on the benthic habitats below (Dayton and others 1986; Cattaneo-Vietti and others 1999; Rysgaard and others 2001; Arrigo and Thomas 2004; Norkko and others 2007; Thrush and Cummings 2011; Wing and others 2012; Arrigo and others 2012).

Ice-covered coastal marine ecosystems in Antarctica share some key characteristics with those in the high Arctic, with low levels of primary production for the majority of the year and a pulse of production associated with sea ice breakout during summer (Rysgaard and others 1999; Glud and others 2002; Rysgaard and Nielsen 2006). Even the functional types of organisms dominating benthic communities can be similar (Sejr and others 2000). In the Arctic, the summertime production pulse is followed by a rapid response of the benthos to the settling material. This includes increased sediment oxygen demand, nitrate and ammonium efflux, and denitrification (Rysgaard and others 1998), despite almost no seasonal variation in bottom water temperature or salinity (Rysgaard and others 1999). This provides a framework for general predictions about how Antarctic systems are likely to respond to climate-related shifts in sea ice characteristics.

Like the Arctic (Kinnard and others 2011; Arrigo and others 2012), significant declines in sea ice extent and persistence have already occurred in the western Antarctic Peninsula and southern Bellingshausen Sea (Stammerjohn and others 2008). This represents a potential precedent for change in the Ross Sea over the next 100 years. Although there is substantial uncertainty about future sea ice conditions at specific Ross Sea sites (as winds, snowfall and current patterns may all change with Southern Ocean warming; Fyfe and others 2007; Vaughan and Doake 1996; Thrush and Cummings 2011), we expect alterations in sea ice conditions to have significant impacts on marine ecosystem functioning, specifically the manner and rate at which organic detritus is remineralized in benthic soft-sediment habitats (Rysgaard and others 1998).

We addressed this hypothesis by measuring benthic processes linked to organic matter remineralization at two coastal Ross Sea sites: Granite Harbour (GH) and New Harbour (NH) (Figure 1). The two study sites were selected based on contrasting sea ice conditions that we predicted would drive differences in the amount of detrital algal organic material present in the sediment (Table 1). GH generally experiences a period of open water during the summer each year (annual sea ice breakout) and a brief but intense phytoplankton bloom. Although the thickness of the sea ice at GH in spring generally exceeds 2 m, the surface of the sea ice is smooth and has a minimal amount of snow coverage. Sufficient light penetrates through the ice so that its under-surface is covered by luxuriant microalgal growth prior to the summertime ice breakout.

NH has been covered by sea ice continuously for more than a decade (11 years prior to the commencement of our study). The seawater beneath this multiyear sea ice has low concentrations of

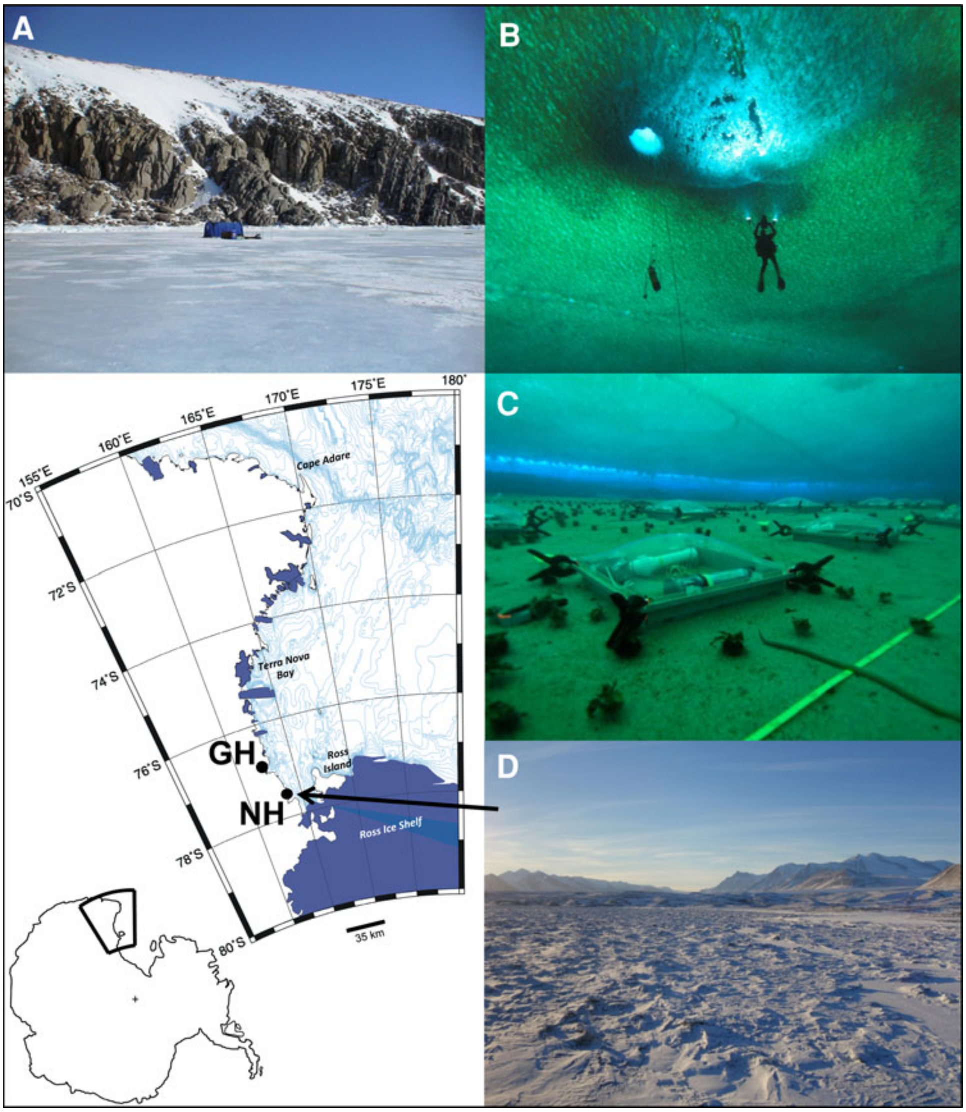

Figure 1. Study site locations Granite Harbour (GH) and New Harbour (NH) are shown along with the surface (**A**) and under-surface (**B**) of the smooth, snow-free, annual fast ice at GH. **C** shows benthic incubation chambers (0.25 m^2 area) deployed to the soft-sediment habitat 15 m beneath the sea ice at GH. The chambers were used to assess fluxes of oxygen and nutrients across the sediment–water interface at both sites. **D** shows the buckled, snow-covered, multi-year ice at NH. Photo credits: D. Lohrer (**A**), R. Budd (**B**, **C**), P. Notman (**D**).

phytoplankton, because it flows to the site after circulating beneath the Ross Ice Shelf (no light, deep, extremely cold; Dayton and Oliver 1977; Barry and Dayton 1988; Bergamasco and Carniel 2000; Reddy and others 2010). At NH in November 2009, the surface of the sea ice was buckled and uneven with thick snow drifts. The thickness of the ice was greater than 4 m. Drill holes through the ice at NH revealed layers of wind-blown terrigenous dust/gravel and, on the underside of the ice, ice algae was absent. Conditions were noticeably darker underneath the ice at NH ($\ll$0.1% of incident above-ice PAR) than they were at GH.

The objective of our study was to elucidate fundamental marine ecosystem processes including detritus decomposition and nutrient regeneration by (1) assessing the quantity and quality of algal detritus in sediments at both study sites in early November when coastal sea ice in the southwestern Ross Sea is at its maximum thickness, (2) comparing associated fluxes of oxygen and nutrients across the sediment–water interface in these contrasting ice-covered benthic habitats and (3) accounting for the potential interactive effects of a large detritus-feeding epibenthic species common to both sites.

METHODS

GH and NH are located in the southwestern Ross Sea (GH, 77°00.957S, 162°52.581E; NH, 77°34.573′S, 163°32.608′E). We investigated marine soft-sediment habitats at GH and NH in November of 2008 and 2009, respectively. Both study sites were 15-m deep and seafloor sediments were dominated by moderately- to well-sorted sands. The grain size of the sands was medium-to-coarse at GH (80% > 250 μm) and predominantly fine at NH

Table 1. Sea Ice Characteristics at the Two Ross Sea Study Sites

	GH 77°00.957S, 162°52.581E	NH 77°34.573′S, 163°32.608′E
Persistence	Ice breaks apart each year, open water exists during the height of summer each year	Coastal zone has remained covered by sea ice since 1998 (the most recent breakout)
Surface smoothness	Smooth flat sea ice (due to being annually formed)	Rough, buckled sea ice (due to surface freezing and thawing and ablation over multiple seasons and years)
Snow cover	Predominantly snow free, presumably due to regular sweeping by catabatic winds, with irregular patches of snow 0- to 5-cm thick	Snow drifts accumulating in depressions and against ridges can be 30- to 50-cm thick or more
Opacity	Sea ice matrix contains no large particles of any sort. Solid blue ice	Sea ice matrix contains layers of terrigenous sand/gravel blown in from adjacent dry valley. Shells and other marine life have been lifted into the sea ice matrix from below due to anchor ice formation. Evidence of layering in the ice matrix due to freezing/thawing/snow
Thickness	2.1 m in November 2007 and 2008	4.1 m in November 2009

(70% between 125 and 250 µm). The epifaunal brittle star *Ophionotus victoriae* was abundant at both sites. The infaunal bivalve *Laternula elliptica* was common at GH but absent at NH. Like several of the other species we observed, these are large benthic species with circumpolar distributions that often attain extremely high densities (for example, *Laternula* 170 m^{-2}, Cummings and others 2011).

Benthic incubation chambers were used to measure fluxes of oxygen and nutrients across the sediment–water interface. Fluxes were measured at each site in ambient light and in total darkness (that is, with and without photosynthesis possible, sensu Lohrer and others 2004). In addition, treatments with differing densities of *O. victoriae* were applied to better understand the contributions of this species to the sediment's oxygen and nutrient dynamics. The omnivorous diet of *O. victoriae* includes detrital algal material (Kellogg and Kellogg 1982; Norkko and others 2007), which it accesses by deposit feeding from the sediment surface (Fratt and Dearborn 1984).

Experimental design and sampling protocols were identical at each site, although the sites had to be sampled in back-to-back years for logistical reasons. We are confident that our findings would not have changed had we sampled NH first and GH second, as day length, sea ice conditions, and seawater temperatures are consistent in November at these sites between years (24 h d^{-1}, covered by sea ice, and −1.92°C, respectively). Sea ice thickness at GH was 2.1 m November 2007 and November 2008, typical of the thickness of first year ice that develops in this region by this time of year. Sea ice thickness at NH was 4.1 m in November 2009, reflecting the continual development and ablation of new ice at this site over the previous decade (S. Bowser, personal communication). The normal pattern for the southwestern Ross Sea is a massive bloom of phytoplankton during summer, the timing of which is highly predictable (Smith and others 2000; Arrigo and van Dijken 2004; Thrush and Cummings 2011), although there is always very little phytoplankton in the water at each site during November.

To deploy the chambers, square aluminium bases (50 × 50 cm, walls 15 cm high) were pressed 7.5-cm deep into the sediment by SCUBA divers. Any large organisms found on the sediment surface within the bases were removed. *O. victoriae* were then added at densities of 0, 5, 10 or 15 per chamber. These four density treatments were randomly interspersed throughout the experimental array, with two ($n = 2$) replicates per treatment. Note that the highest density treatment of 15 individuals per chamber was roughly equivalent to the maximum observed densities of *Ophionotus* at GH and NH.

Clear acrylic lids were fitted to each aluminium base and secured with clamps immediately after *Ophionotus* addition, isolating approximately 25 l of seawater. To prevent water stagnation and associated artefacts inside the chambers, all chambers were fitted with non-directional water stirrers that mixed chamber waters for 5 s every 5 min throughout the incubation period (Lohrer and others 2004; Needham and others 2011). Although chamber lids eliminate the potential influence of waves and currents on solute fluxes in permeable sediments (Huettel and Gust 1992), chambers have many advantages over other methods (for example, microelectrodes) particularly for incorporating the effects of large fauna. Moreover, we consider possible flow artifacts to be of minimal concern at GH and NH because these sites were capped by ice (no waves) and had practically no current (≤ 3.3 cm s^{-1}).

An initial ($T = 0$) water sample was collected from each chamber moments after each lid was affixed (by connecting a syringe to a sampling port), and water samples were collected every morning and afternoon thereafter for an incubation duration of more than 48 h. Dissolved oxygen (DO) concentrations were determined from each sample using an optical DO probe (Yellow Springs Instruments ProODO Professional Series model). Samples were then immediately filtered (GF/C Millipore filters), and the water frozen and stored in the dark until later analysis to determine dissolved inorganic nutrient concentrations (ammonium nitrogen, nitrate + nitrite nitrogen, reactive phosphorus) using standard methods for seawater (Lohrer and others 2004; Needham and others 2011).

The experiments consisted of a light and a dark phase, using clear lids and black lids, respectively, to allow or prevent photosynthetic reactions. Although the light phase at GH and the light and dark phases at NH were able to be completed as planned, the dark phase of the experiment at GH failed for reasons beyond our control. Light and dark fluxes of DO and nutrients were calculated for each chamber by plotting oxygen and nutrient concentrations over time (all available data between $T = 0$ and $T = \text{end}$). Flux values were determined by the signs and magnitudes of the slopes of the regression lines fitted through the data points (Needham and others 2011). Negative flux values indicated a movement of material into the sediment (influx, consumption), whereas positive flux values indicated release from the sediments (efflux, production). At the end of the experiment at each site, the *Ophionotus* and *Laternula* present in the chambers were enumerated and photographed (for later size assessment).

Ambient seawater and sediment characteristics were assessed from samples collected outside of the chambers at each site. A sample of ambient bottom water was collected with a syringe every time the chambers were sampled and analyzed in the same way as described above. Five small cores of ambient sediment (2 cm internal diam., 2-cm deep) were collected and sub-sampled to determine sediment particle size distribution, pigment concentrations and organic matter content. Samples were frozen and stored in the dark until analysis using previously described standard methodologies (Cummings and others 2006; Thrush and Cummings 2011).

To enable us to calculate the expected proportions of oxygen and nutrient fluxes that were directly attributable to *Ophionotus*, we quantified the per capita respiration and nutrient excretion rates of *Ophionotus* in ambient seawater at NH, in the dark, without sediment. By accounting for the effects of *Ophionutus* in isolation, and subtracting those values from the fluxes measured in the chambers, we were able to compare the relative contributions of *Ophionotus* versus the rest of the sediment system (the bacteria, microphytes, meio- and macrofauna present inside the chambers). One adult *Ophionotus* was carefully placed at depth into each of 11 individual, opaque, sealed containers (700-ml volume) with ambient bottom water. Seven identical control containers were filled with bottom water only. The containers were secured 0.5 m above the seafloor for 28.6 h. An additional four control containers filled with bottom water were brought to the surface immediately for an assessment of initial conditions (DO and dissolved inorganic nutrient concentrations). At the end of the incubation, characteristics of the *Ophionotus* individuals in each container (size, weight), and DO and nutrient concentrations of the container water were assessed as described above. There were no mortalities or signs of stress in the *Ophionotus* used; all were active and behaving normally at the end of the incubation period.

We calculated the average rate of DO consumption by *Ophionotus* in bottom water (µmol O_2 h^{-1}) based on rates of change of DO in the 11 *Ophionotus* containers. We multiplied the average rate of DO consumption by *Ophionotus* in bottom water by 5, 10 or 15 to predict the amount of oxygen that would be consumed during dark chamber incubations with 5, 10 and 15 *Ophionotus* enclosed. This assumed that the per capita rate of oxygen consumption was independent of density, which was likely the case, as we have never observed any changes in *Ophionotus* behaviour (for example, increased agonistic interactions) with increased density. The effect of bottom water itself inside the chambers was predicted using the average rate of change of DO in containers without *Ophionotus*.

The same procedures were used to predict fluxes of ammonium, nitrate + nitrite and phosphate in chambers with 0, 5, 10 or 15 *Ophionotus*. At GH, where we found an average of 3–4 large infaunal bivalves (*L. elliptica*) per chamber, we assumed that their per capita contributions to oxygen and nutrient flux were one to two times those of *Ophionotus*. We verified this assumption using oxygen respiration data for *Laternula* collected from GH in 2008 (Cummings and others 2011).

Data were analyzed using two-way ANOVA with site (GH, NH) and *Ophionotus* density (0, 5, 10 and 15) as fixed factors, applying data transformations when necessary to satisfy assumptions of normality and homogeneity of variance. One-way ANOVA's were used to analyze the response to the *Ophionotus* treatment within sites. When main effects were significant at $\alpha = 0.05$, pairwise comparisons were made using Student–Newman–Keuls (SNK) post-hoc tests.

RESULTS

Sediments at GH had 14 times more chlorophyll *a* (chl*a*) and three times more phaeophytin than the sediments at NH (Table 2). Sediment phaeophytin content (phae) was higher than chl*a* content at both study sites (Table 2). The ratio of fresh to degraded material (chl*a*:phae) was more than five times higher at GH (0.67) than at NH (0.12).

Fluxes of DO were negative at both sites and in all treatments, indicating a net consumption of oxygen by the benthos. A two-way ANOVA revealed effects of site ($p = 0.0011$) and *Ophionotus* density ($p = 0.0600$) on light DO flux (Table 3). Rates of benthic oxygen consumption were significantly greater at GH than they were at NH (Figure 2A, B), and generally increased with increasing *Ophionotus* density. Although the site * treatment interaction was not significant in the two-way ANOVA model for DO flux in light chambers ($p = 0.4979$), increased oxygen consumption with increasing *Ophionotus* density was significant in the one-way ANOVA model at NH, and SNK tests revealed significant differences among all the *Ophionotus* treatments at NH (Table 3). Differences among the *Ophionotus* treatments were not significant at GH.

At NH, the average DO flux in dark chambers without *Ophionotus* was -21.15 µmol O_2 m^{-2} h^{-1} (Figure 3A). In corresponding light chambers, DO flux was -8.67 µmol O_2 m^{-2} h^{-1}. The average DO flux in dark chambers with 15 *Ophionotus* was -100.27 µmol O_2 m^{-2} h^{-1}, whilst DO flux averaged -74.96 µmol O_2 m^{-2} h^{-1} in the corresponding light chambers. Across all of the *Ophionotus* density treatments at NH, average DO flux values were consistently higher (less negative) in the light chambers than they were in the dark (by 16 µmol O_2 m^{-2} h^{-1}, on average).

The average DO flux in light chambers at GH without *Ophionotus* was -104.40 µmol O_2 m^{-2} h^{-1}. In the chambers with 15 *Ophionotus*, average light DO flux was -227.16 µmol O_2 m^{-2} h^{-1}, which was more than two times lower than the lowest DO flux values observed at NH (Figure 3A). Although dark DO flux values were not available at GH, it is assumed that dark DO flux values would have been less than (more negative) or equal to the light DO fluxes, given that no oxygen production can occur in dark chambers.

Table 4 provides estimates of expected fluxes in dark benthic chambers based solely on the densities of large fauna present in those chambers at the end

Table 2. Bio-physical Habitat Characteristics at the Two Ross Sea Study Sites

	GH	NH
Water temperature (°C)	−1.9	−1.9
Thickness of sea ice (m)	2.1	4.1
PAR available at 15 m depth (% of incident)	<0.01	≪ 0.01
DO (µmol O_2 l^{-1})[1]	305 ± 2.5	316 ± 4.5
Ammonium (µmol N L^{-1})[1]	0.12 ± 0.02	0.04 ± 0.00
Nitrate + nitrite (µmol N L^{-1})[1]	28.8 ± 0.32	31.3 ± 0.17
Phosphate (µmol P L^{-1})[1]	2.09 ± 0.02	2.08 ± 0.02
Sediment chlorophyll *a* content (µg g^{-1} sediment)	1.56 ± 0.17	0.11 ± 0.02
Sediment phaeophytin content (µg g^{-1} sediment)	2.71 ± 0.48	0.97 ± 0.08
Ratio of sediment chlorophyll *a* to sediment phaeophytin (Chl*a*:phae)	0.67 ± 0.16	0.12 ± 0.02

Measurements made at GH and NH in November 2008 and 2009, respectively; data towards the bottom of the table are mean ± 1 standard error.

[1] *Average concentration measured in ambient seawater samples collected 0.5 m above the seafloor (15 m depth) next to the chambers at each site.*

Table 3. Results of Statistical Analyses: ANOVA and Post-hoc Tests

Response variable	Two-way ANOVA (source of variation)	*P* value	SNK post hoc tests among treatments 0, 5, 10, 15
(a)			
DO flux Light	Full model	0.0145	
	Site	0.0011	
	Treatment	0.06	a, ab, ab, b
	Site * treatment	0.4979	
Log NH_4^+ flux light	Full model	0.0058	
	Site	0.0022	
	Treatment	0.0129	a, b, b, b
	Site * treatment	0.0652	
Log NO_X flux light	Full model	0.2127	
	Site	0.0375	
	Treatment	0.4499	a, a, a, a
	Site * treatment	0.3808	
Log DRP flux light	Full model	0.0092	
	Site	0.2022	
	Treatment	0.0019	a, b, b, b
	Site * treatment	0.4274	

	One-way ANOVA (treatment)	NH	GH
(b)			
DO flux light	*P* value	0.029	0.2772
	SNK results:	a, ab, b, b	a, a, a, a
NH_4^+ flux light	Treatment	0.0007	0.5304
	SNK	a, b, c, d	a, a, a, a
NO_X flux light	Treatment	0.7137	0.5265
	SNK	a, a, a, a	a, a, a, a
DRP flux light	Treatment	0.0398	0.2166
	SNK	a, ab, ab, b	a, a, a, a
DO flux dark	Treatment	0.1066	
	SNK	a, a, a, a	
Log NH_4^+ flux dark	Treatment	0.079	
	SNK	a, a, a, a	
NO_X_flux dark	Treatment	0.9575	
	SNK	a, a, a, a	
Log DRP flux dark	Treatment	0.1296	
	SNK	a, a, a, a	

*Statistical results showing (a), the effects of site (two levels: GH, NH) and treatment (four levels: 0, 5, 10 or 15 O. victoriae per chamber) in two-way analyses of variance (ANOVA). SNK post-hoc tests were used to determine the significance of differences among treatments. Log transformations were necessary to satisfy assumptions of ANOVA in some cases. Because the effects of site were significant for three of the four flux variables assessed, and because there was a site * treatment interaction for* NH_4^+ *flux light, data from the two sites were also analyzed separately, (b) using one-way ANOVA to understand the effects of the Ophionotus treatment.*

of the experiment. The table indicates the combined effects of the *Ophionotus* added to chambers at both sites—based on the empirically measured per capita respiration and excretion rates of this species (see also Obermüller and others 2010)—plus the effects of the *Laternula* that we could not remove from the chambers at GH without disrupting the sediment system. Figure 2 indicates how these estimates matched up to the empirically measured fluxes. Doubling the estimates of per capita respiration and excretion by *Laternula* altered the predictions slightly (that is, Table 4), but not the conclusions of the study.

Fluxes of ammonium nitrogen (μmol N m^{-2} h^{-1}) were generally positive at both study sites, indicating the net movement of ammonium away from sediments and to the overlying water (Figure 2C, D). Fluxes of ammonium in light chambers differed by site ($p = 0.0022$) and treatment ($p = 0.0129$), with indications of a site * treatment interaction ($p = 0.0652$; Table 2). The site * treatment interaction emerged because of a significant *Ophionotus* density effect at NH ($p = 0.0007$, SNK test: $0 < 5 < 10 < 15$), but not at GH ($p = 0.5304$). The magnitude and variability of light ammonium flux was substantially higher at GH, across all treatments, than it was at NH (Figure 2): ammonium flux in the 0 *Ophionotus* chambers was 5.88 μmol N m^{-2} h^{-1} at GH, compared with 0.04 at NH, whilst the flux in the 15 *Ophionotus* chambers was 15.31 μmol N m^{-2} h^{-1} at GH, relative to 4.46 at NH.

Patterns of nitrate + nitrite flux (μmol N m^{-2} h^{-1}) differed at the two study sites (Figure 2). At NH, positive flux values were observed, indicating an efflux of nitrate + nitrite out of the sediment to the overlying water. At GH, in contrast, negative flux values were observed, signalling a removal of nitrate + nitrite from the overlying water (influx, uptake by the sediment). Although site was significant in our analysis of light flux values ($p = 0.0375$), the effects of treatment and site * treatment were not ($p = 0.4499$ and 0.3808, respectively). The values ranged from 1.3 to 4.3 μmol N m^{-2} h^{-1} at NH, and from 0.1 to −3.0 μmol N m^{-2} h^{-1} at GH (Figure 2E, F).

Fluxes of phosphate (μmol P m^{-2} h^{-1}) were generally positive at both study sites (Figure 2G, H). The only exceptions came from chambers at NH without *Ophionotus* (Figure 3D). Phosphate fluxes measured in the light chambers did not differ by site ($p = 0.2022$), whereas the effect of treatment was significant ($p = 0.0019$), driven by elevated phosphate fluxes in chambers containing *Ophionotus* (SNK test: $0 < 5 = 10 = 15$; Table 2). Phosphate fluxes were less than 0.80 in all cases, including in the dark chambers at NH (Figure 3D). The patterns observed in the dark chambers were somewhat similar to the light chambers, although

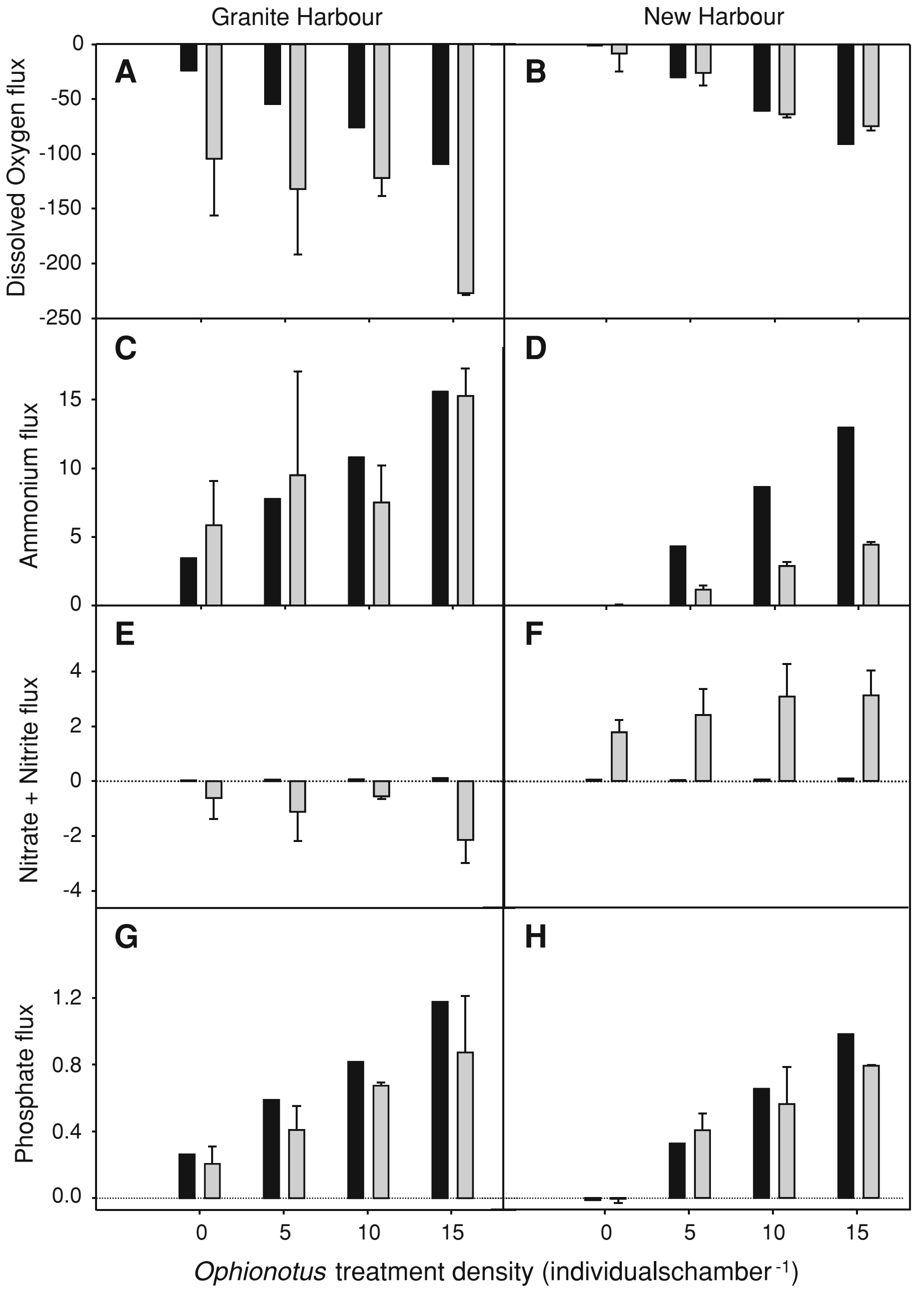

Figure 2. Fluxes (μmol m^{-2} h^{-1}) of DO (**A**, **B**), inorganic nitrogen (ammonium **C**, **D**; nitrate + nitrite **E**, **F**) and reactive phosphorus (**G**, **H**) in light chambers deployed to the seafloor at two sites in Antarctica (*grey bars* mean + 1 SE). Data from GH are on the left (**A**, **C**, **E**, **G**); data from NH are on the right (**B**, **D**, **F**, **H**). *Black bars* The predicted fluxes of DO and inorganic nitrogen in dark benthic chambers based solely on the contributions of animal respiration and excretion (due to *O. victoriae* and *L. elliptica* at GH, and *Ophionotus* only at NH; see Table 4 for more information on these estimates).

treatment was not significant in this instance ($p = 0.1296$).

DISCUSSION

The differences in sea ice thickness and permanence at our two study sites had a profound influence on the quantity and quality of algal detritus in the sediment. Sediments at both sites contained a preponderance of degraded algal material (phaeophytin), relative to fresh algae (chl*a*), consistent with low in situ production and seasonally pulsed phytoplankton input. However, the total amount of chl*a* and the ratio of fresh to degraded material was significantly greater at GH (>5×), where algal material is more easily advected from open water and can settle to the seafloor from the under-surface of the ice above. Furthermore, the ice breaks out from the coast at GH each year, stimulating local benthic and water column primary production. Thus, GH appears to receive greater and more regular inputs of labile organic material than NH, which has been dark and ice-covered for more than a decade.

It is well recognized that changes in sea ice conditions will alter coastal production (Dayton

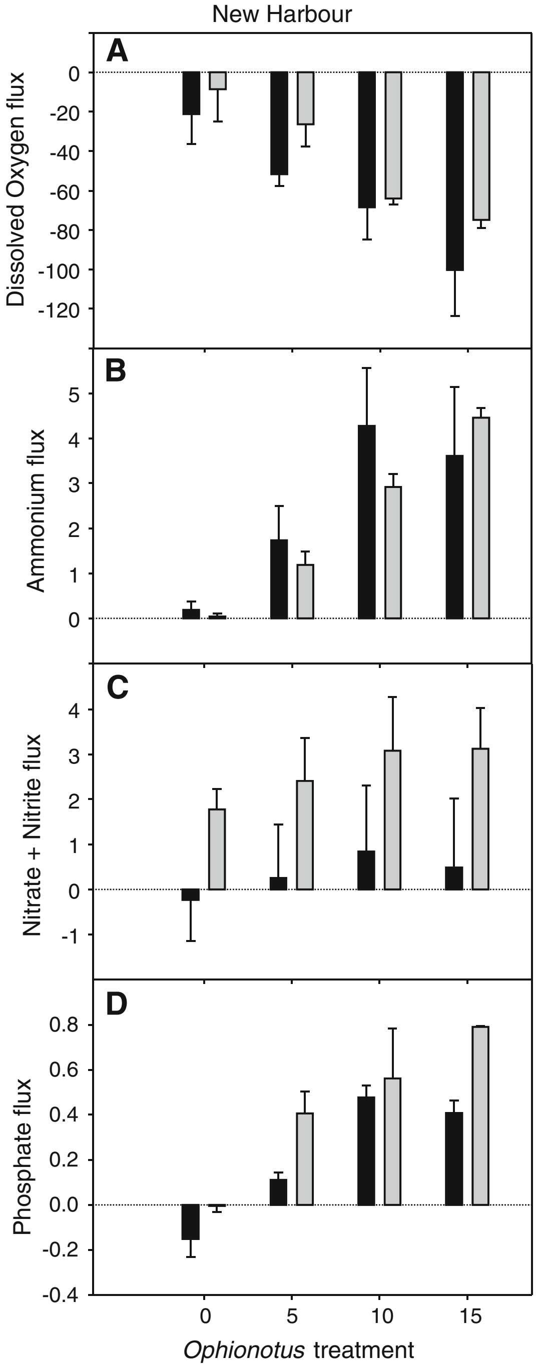

Figure 3. Fluxes (μmol m^{-2} h^{-1}) of DO (**A**), ammonium (**B**), nitrate + nitrite (**C**) and reactive phosphorus (**D**) in dark and light chambers deployed at NH (*black bars* dark chambers, *grey bars* light chambers). Data are mean with 1 SE.

and others 1986; Glud and others 2002; Rysgaard and Nielsen 2006), and recent studies in the Arctic suggest that substantial changes may be happening much more rapidly than first predicted (Kinnard and others 2011; Arrigo and others 2012). Also consistent with Arctic research (Rysgaard and others 1998), our study provides evidence of a tangible link between sea ice conditions and benthic ecosystem functioning. Our results suggest that changes in sea ice will not only alter coastal productivity, but may also include shifts in the dominant modes of nutrient regeneration. We also illustrated the potential for climate change to greatly influence ecosystem processes in coastal Antarctica in a context dependent manner, given that changes in food quality and quantity are linked to local coastal sea ice characteristics and relative connectivity to primary production in open waters.

Benthic oxygen consumption is commonly used as an indicator of variability in the supply and metabolism of organic carbon on the sea floor (Grebmeier and McRoy 1989; Vopel and others 2003). In our investigation, the sediments at both GH and NH were net consumers of oxygen (negative DO flux in light chambers), with a significantly larger total benthic oxygen demand at GH. Across treatments, after accounting for the effects of animal respiration (Table 4), total benthic oxygen demand at GH averaged 60 μmol O_2 m^{-2} h^{-1}, compared to 15 μmol O_2 m^{-2} h^{-1} at NH. As the remineralization of labile organic matter by bacteria is an oxygen-consuming process, the 5- to 10-fold difference in the quality and quantity of detrital algal material between the two sites likely contributed to the difference in benthic oxygen demand. Sediment oxygen consumption at GH was about 3 times lower than rates reported for the Arctic during periods of ice cover (Rysgaard and others 1998 and references therein), although GH likely had substantially less organic matter in the sediment also (compared to sediment chl*a* concentrations and accumulation rates reported by Rysgaard and others (1998), Glud and others (2002) and Rysgaard and Nielsen (2006)).

Ice conditions (thickness, permanency, snow cover, opacity) likely influenced the amount and quality of benthic detrital material at our sites, which in turn affected the fluxes of DO and nutrients and the coupling between nitrification and denitrification. In sediments, the remineralization of organic material by bacteria elevates the concentration of ammonium in sediment pore water (Blackburn and others 1996; Farías and others 2004). Efflux of ammonium from the sediment to the water column can then occur as a result of diffusion across the concentration gradient. Macrofauna contribute to nutrient flux by mixing sediment and advecting pore water (which is many times faster than diffusion) (Aller 1978;

Table 4. Large Benthic Fauna: Effects on Fluxes of Oxygen, Nitrogen and Phosphorus

Site	Treatment (+*Laternula*)	DO	NH_4^+	NO_X	DRP
NH	0 *Ophionotus*	0.00	0.01	0.05	−0.01
NH	5 *Ophionotus*	−30.4	4.34	0.03	0.33
NH	10 *Ophionotus*	−60.8	8.67	0.06	0.65
NH	15 *Ophionotus*	−91.2	13.01	0.09	0.98
GH	0 *Ophionotus* (+4 *Laternula*)	−24.3	3.47	0.03	0.26
GH	5 *Ophionotus* (+4 *Laternula*)	−54.7	7.80	0.06	0.59
GH	10 *Ophionotus* (+2.5 *Laternula*)	−76.0	10.84	0.08	0.82
GH	15 *Ophionotus* (+3 *Laternula*)	−109.4	15.61	0.11	1.17

Average wet weight of Ophionotus was 11 g (0.77 g AFDW); per capita DO respiration rate was 1.97 µmol O_2 consumed h^{-1} g^{-1} AFDW; per capita NH_4^+ excretion rate was 0.286 µmol N produced h^{-1} g^{-1} AFDW, per capita NO_X excretion rate was 0.0021 µmol N produced h^{-1} g^{-1} AFDW, per capita DRP excretion rate was 0.026 µmol P produced h^{-1} g^{-1} AFDW. Predicted fluxes of dissolved oxygen (DO), ammonium (NH_4^+), nitrate + nitrite (NO_X) and reactive phosphorus (DRP) in dark benthic chambers based solely on the contributions of animal respiration and excretion. Estimates are based on average per capita respiration and excretion rates of Ophionotus measured at the NH site and correspond to the four treatments (0, 5, 10 or 15 Ophionotus per chamber) applied at each site. At GH, large infaunal bivalves L. elliptica also likely contributed to DO and nutrient fluxes, as an average of 3–4 Laternula were found in each chamber. The per capita respiration and excretion rates of Laternula were estimated to be equivalent to those of Ophionotus (see ''Methods''). All data have units of µmol m^{-2} h^{-1}.

Hines and others 1982; Lohrer and others 2004; Needham and others 2011), and also by excreting ammonium as a metabolic waste. Ammonium can also be converted to nitrate by aerobic bacteria (nitrification), although the nitrate produced is sometimes immediately utilized by anaerobic bacteria that convert it to N_2 gas (denitrification). Nitrification and denitrification can be tightly coupled, particularly at oxic–anoxic interfaces in organic rich sediments where aerobic and anaerobic bacteria live in close proximity (Blackburn and Blackburn 1993; Caffrey and others 1993; Blackburn and others 1996; Rysgaard and others 1998).

At GH, no nitrate + nitrite efflux was observed—the sediments at GH actually took up a small amount of nitrate + nitrite from the overlying water—and ammonium efflux was roughly proportional to our predictions based on the densities of large benthic animals present in the chambers (*Ophionotus* and *Laternula*; Figure 2C). The higher availability of fresh labile organic material and the greater benthic O_2 demand at GH, relative to NH, are consistent with these findings. Ammonium generated by microbial remineralization of organic matter in the sediments at GH was probably first converted to nitrate (nitrification) and subsequently converted to nitrogen gas (denitrification). The denitrification step requires an anoxic layer within the sediment column and a supply of labile carbon. Using a standard equation for oxygen penetration depth developed by Cai and Sayles (1996) based on the porosity of the well-sorted sands (Curry and others 2004), the diffusivity of DO in −2°C seawater (Table 2 of Gypens and others 2008), empirically measured concentrations of DO in bottom water and rates of sediment oxygen consumption quantified in the chambers, we estimated the anoxic interface to be less than 1 cm beneath the sediment surface at GH. Sediment pigment data indicated a ready supply of fresh labile algal detrital matter present at the depth of the anoxic interface, suggesting that suitable conditions for tightly coupled nitrification–denitrification existed at this site during November 2008. Thus, where there was greater food quantity and quality, the large fauna regenerated much more utilizable inorganic nitrogen to the water column than sediment biogeochemical processes did, mainly because of tight coupling between nitrification and denitrification in the sediments.

At NH, in contrast, there was an unexpectedly large efflux of nitrate + nitrite from the sediment (Figure 2F), with about half of the expected production of ammonium by benthic animals missing (Figure 2D). A combination of factors related to low sediment organic content suggests that nitrification is the dominant process at this site. First, nitrification does not depend on the presence of organic carbon substrates (only on ammonium, oxygen and carbon dioxide). Although the lack of fresh algal detritus in the sediments at NH may have limited the stock of ammonium in the pore water, the ammonium excreted by *Ophionotus* would have been available to the nitrifying bacteria. Furthermore, the potential for denitrification to remove nitrate + nitrite would have been limited at NH, given the presence of oxygen to a depth greater than 10 cm and the paucity of organic carbon in the sediments at this site [according to the standard equation of Cai and Sayles (1996) and empirically measured sediment pigment data, respectively]. These circumstances explain both the lower than expected efflux of ammonium and the enhanced efflux of nitrate + nitrite across the sediment–water interface at NH.

The low levels of PAR under the ice in the southwestern Ross Sea mean that nutrients excreted by large invertebrates or released from sediments are likely to be underutilized, although they may contribute to a bloom of production later in the year when light becomes available (that is, during summertime break-out at GH). When no break-out occurs for many years (for example, NH), and the opacity of the ice becomes greater with each passing year, there is little possibility of significant new local production to replenish stocks of labile organic material in the sediment to refuel the system. Indications are that NH receives only small amounts of advected food (Dayton and Oliver 1977; Barry and Dayton 1988; Dayton and others 1986; Thrush and others 2006; Reddy and others 2010) and that the stocks of labile organic detritus are becoming depleted (Norkko and others 2007; Cummings and others 2006, compare our Table 2).

Our in situ experiments at two contrasting study locations with extremely different sea ice conditions provided insights into the context dependency of key ecosystem functions at coastal sites in the southwestern Ross Sea. The manner and rate at which algal food resources are remineralized may play an important role in overall system functioning as climate variation drives changes in coastal ice dynamics. If sea ice becomes thicker and more persistent in the high Antarctic due to changing climatic conditions or due to massive icebergs trapping ice near the coast, we would expect to see a slow degradation in benthic community metabolism and lower rates of nitrogen regeneration from the benthos. In contrast, thinner ice and longer periods of ice-free open water at the coast will fuel benthic food webs (Rysgaard and Nielsen 2006; Arrigo and others 2012) and, as our study suggests, elevate the importance of excretion by large benthic fauna in regenerating inorganic nitrogen to the water column. Substantial increases in local food resources may help to offset the negative effects of ocean acidification on benthic fauna (for example, Cummings and others 2011; Ericson and others 2011) and nitrifying microbes (Hutchins and others 2009). In sum, although the complexity of these interactions is not yet fully resolved, our study highlights how climate related shifts in productivity in coastal Antarctica are likely to influence detrital food webs and the pathways and rates of nutrient resupply from sediments to the water column. Large benthic organisms such as the mobile epifauna we studied are expected to have an expanded role in mediating the effects of elevated coastal productivity and detrital rain on ecosystem dynamics.

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