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1 Variability and change in the west Antarctic Peninsula marine system: research priorities and  
2 opportunities

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39 Abstract

40 The west Antarctic Peninsula (WAP) region has undergone significant changes in temperature and  
41 seasonal ice dynamics since the mid-twentieth century, with strong impacts on the regional  
42 ecosystem, ocean chemistry and hydrographic properties. Changes to these long-term trends of  
43 warming and sea ice decline have been observed in the 21<sup>st</sup> century, but their consequences for  
44 ocean physics, chemistry and the ecology of the high-productivity shelf ecosystem are yet to be fully  
45 established. The WAP shelf is important for regional krill stocks and higher trophic levels, whilst the  
46 degree of variability and change in the physical environment and documented biological and  
47 biogeochemical responses make this a model system for how climate and sea ice changes might  
48 restructure high-latitude ecosystems. Although this region is arguably the best-measured and best-  
49 understood shelf region around Antarctica, significant gaps remain in spatial and temporal data  
50 capable of resolving the atmosphere-ice-ocean-ecosystem feedbacks that control the dynamics and  
51 evolution of this complex polar system. Here we summarise the current state of knowledge  
52 regarding the key mechanisms and interactions regulating the physical, biogeochemical and  
53 biological processes at work, the ways in which the shelf environment is changing, and the  
54 ecosystem response to the changes underway. We outline the overarching cross-disciplinary  
55 priorities for future research, as well as the most important discipline-specific objectives.  
56 Underpinning these priorities and objectives is the need to better-define the causes, magnitude and  
57 timescales of variability and change at all levels of the system. A combination of traditional and  
58 innovative approaches will be critical to addressing these priorities and developing a co-ordinated  
59 observing system for the WAP shelf, which is required to detect and elucidate change into the  
60 future.

61

62 Introduction

63 The west Antarctic Peninsula (WAP) continental shelf hosts a productive marine ecosystem, which is  
64 regionally important for krill stocks over the shelf and downstream in the Southern Ocean circulation  
65 system (e.g. Atkinson et al. 2004; Quetin et al. 1996), and for larger marine organisms as a breeding  
66 and/or feeding ground for migratory and year-round species (e.g. Costa and Crocker 1996; Ducklow  
67 et al. 2007; Friedlaender et al. 2006). From a climatic and biogeochemical perspective, the WAP is  
68 important because the southern flank of the Antarctic circumpolar current (ACC) flows particularly  
69 close to the shelf edge in this region (Orsi et al. 1995). As such, circumpolar deep water (CDW) from  
70 its mid-depths incurs directly on to the shelf in a less modified form than elsewhere around  
71 Antarctica, facilitating greater connectivity and exchange of physical and biogeochemical properties  
72 between these intermediate water masses and the atmosphere and surface ocean (Hofmann et al.  
73 1996; Klinck 1998). Significant variability in the physical environment, modulated by strong coupling  
74 to climate processes over interannual and decadal timescales, is having a strong impact on regional  
75 biogeochemistry and all levels of the shelf ecosystem, making the WAP an important model region in  
76 which to understand the impacts of climate on polar marine systems.

77 Temperature records for the WAP have shown the largest average atmospheric warming in the  
78 southern hemisphere during the twentieth century, with particularly pronounced warming during  
79 winter (King et al. 2003; Vaughan et al. 2003). This has been accompanied by a significant decadal  
80 warming of surface and deeper waters and changes in salinity over large parts of the WAP shelf  
81 (Meredith and King 2005). Significant warming and salinification of the deeper waters over the  
82 southern and central WAP shelf resulted from shoaling of the thermocline along the slope and  
83 increased transport of warm upper circumpolar deep water (UCDW) onto the shelf, as well as  
84 increased heat content of the UCDW layers themselves (Martinson et al. 2008; Schmidtke et al.

85 2014). Significant surface freshening has been observed closer to coastal glacial meltwater sources,  
86 whilst upper layer salinification has occurred further offshore (Bers et al. 2013; Meredith and King  
87 2005; Schloss et al. 2012).

88 Atmospheric and oceanic warming trends have been accompanied by strong changes in ice dynamics  
89 along the WAP, with the regional extent and duration of sea ice cover declining significantly since  
90 the late 1970s (Stammerjohn et al. 2012). Climate change appears more advanced in the northern  
91 region of the WAP as the warmer maritime climate moves southwards displacing the colder drier  
92 continental climate that dominated previously (Ducklow et al. 2007; Montes-Hugo et al. 2009).  
93 Substantial and widespread glacial retreat along the WAP has been attributed primarily to increasing  
94 ocean temperatures (Cook et al. 2016; Padman et al. 2012), with an important role for atmospheric  
95 forcing in the northern WAP (Falk and Sala 2015).

96 Whilst the regional warming and sea ice declines have been particularly rapid since the mid-  
97 twentieth century, these trends have slowed and plateaued since the late 1990s (Figure 1), with an  
98 absence of statistically significant atmospheric warming and sea ice losses between 1999 and 2014  
99 (Turner et al. 2016). Statistically significant increases in sea ice extent have been observed in the  
100 northern WAP since the late 1990s (Turner et al. 2016), and an increase in both the extent and  
101 duration of sea ice cover, and its interannual variability, have been observed in the coastal WAP  
102 since the late 2000s (Figure 1; Schofield et al. 2017). These recent short-term reversals and the  
103 plateauing of longer-term trends reflect significant natural internal variability in the regional climate  
104 superimposed on longer-term trends, which leads to substantial short-term variation in sea ice  
105 dynamics (Hobbs et al. 2016; Stammerjohn and Maksym 2017; Turner et al. 2016). Whilst the  
106 plateauing of temperature and sea ice trends has weakened the magnitude of the longer-term  
107 trends, the overall warming and sea ice losses are still statistically significant (Figure 1).

108 Large-scale atmospheric circulation patterns and in particular the Amundsen Sea Low (ASL) exert a  
109 strong control on the observed climatic variability and change at the WAP (Raphael et al. 2016). The  
110 ASL is a persistent low pressure region between the Ross Sea and the Bellingshausen Sea/WAP  
111 sector, which is strongly influenced by the Southern Annular Mode (SAM) and also by the El Niño  
112 Southern Oscillation (ENSO) (Lachlan-Cope et al. 2001; Raphael et al. 2016; Turner et al. 2013).  
113 Changes in the ASL affect the strength and direction of winds over the WAP, which act as a key  
114 control on the amount and meridional extent of sea ice (Turner et al. 2013). A deepening ASL over  
115 the second half of the twentieth century, associated with positive SAM and more persistent La Niña  
116 phases, generated stronger north-to-northwesterly winds that advect warm moisture-laden air from  
117 the north and drive sea ice to the south, creating warm, low-ice conditions over the WAP and  
118 increasing precipitation (Turner et al. 1997). The recent plateauing of temperature and sea ice  
119 trends is associated with periods of more neutral to negative SAM phases, or positive SAM offset by  
120 El Niño, that promote cyclonic to anticyclonic conditions east to west of the peninsula, respectively,  
121 leading to more frequent cold east-to-southeasterly winds over the WAP and increased ice extent  
122 (Meredith et al. 2016; Stammerjohn et al. 2008; Turner et al. 2016). The combination of short-term  
123 internal variability and longer-term changes in atmospheric and ocean circulation patterns  
124 responding to global climate change complicates future projections of Antarctic sea ice, both at WAP  
125 and circumpolar scales (Turner and Comiso 2017). Understanding the extent to which the long-term  
126 trend of atmospheric warming and declining sea ice will continue in future, and the timescales over  
127 which different forcings are relevant, are leading-order challenges for the WAP scientific community.

128 The pronounced variability and change observed in atmospheric forcing, sea ice dynamics, glacial  
129 retreat, freshwater distribution and ocean physics along the WAP have a strong impact on primary  
130 production, community composition, ecosystem functioning, ocean chemistry and ocean-  
131 atmosphere exchanges of heat and dissolved gases (e.g. Ducklow et al. 2013; Meredith et al. 2017;

132 Venables and Meredith 2014). Improving our understanding of this dynamic system is of high  
133 scientific priority as a result of significant variability and change in the physical environment,  
134 important biological and biogeochemical consequences, and documented sensitivity to – and  
135 feedbacks on – climate change. The documented responses of ocean chemistry and biology to  
136 changes in climate and ocean physics make the WAP shelf region a unique model system for  
137 assessing how changes in climate might restructure ecosystems here and in other polar regions  
138 where sea ice changes are underway or expected in future. This importance is one of the key  
139 reasons why the WAP shelf region is the focus of a large international research effort, with a number  
140 of long-term records and spatially-extensive studies that are unparalleled around Antarctica. There  
141 are over thirty research stations along the WAP, either permanent or summer only, and a number of  
142 research ships that frequent the region, predominantly during summer.

143 Figure 2 shows the major sustained research efforts along the WAP, delineation of the northern,  
144 central and southern sub-regions referred to in this paper, and the major circulation and  
145 bathymetric features of the shelf system. The US Palmer Antarctica Long-Term Ecological Research  
146 (LTER) project has been in operation since 1990, and consists of spring/summer time-series sampling  
147 adjacent to Palmer Station, Anvers Island, and an annual summer cruise occupying a grid of stations  
148 over the WAP shelf between Anvers and Charcot Islands. The US National Oceanic and Atmospheric  
149 Administration Antarctic Marine Living Resources (AMLR) program has been active around the South  
150 Shetland Islands in the northern WAP since 1986, conducting annual research surveys and land-  
151 based field measurements with a focus on ecosystem-based management of fisheries, primarily krill.  
152 Since 1997, the Rothera Time Series (RaTS) of the British Antarctic Survey, located in Ryder Bay,  
153 northern Marguerite Bay adjacent to Rothera Research Station on Adelaide Island, has made year-  
154 round quasi-weekly measurements of physical and biogeochemical oceanographic parameters,  
155 benthic ecology and sea ice cover, with a large number of linked and complementary studies  
156 conducted by UK and international partners. The establishment of additional laboratories at Rothera  
157 by the Netherlands Organisation for Scientific Research (NWO) in 2012 increased the Dutch research  
158 effort in the WAP region substantially. The Argentinian Antarctic Program consists of time-series and  
159 process studies at a number of research stations along the WAP, as well as ship-based campaigns  
160 across the shelf. Year-round time-series monitoring of hydrographic and biological variables in Potter  
161 Cove, King George Island/ Isla 25 de Mayo, South Shetland Islands, has been conducted fortnightly-  
162 monthly since 1991, based at Carlini Station, which has been in operation since 1982. A joint  
163 Argentinian-German research program at Dallmann Laboratory on Carlini Station focusing on Potter  
164 Cove started in 1994, and forms an important part of the German research efforts in the WAP  
165 region, coordinated by the Alfred Wegener Institute (AWI). The Chilean Antarctic Institute (INACH)  
166 conducts scientific research programs at four bases along the WAP, supported by the Armed Forces.  
167 Chilean base Yelcho on Doumer Island was reopened in 2015 and there are plans to reopen Base  
168 Carvajal on Adelaide Island to complete a latitudinal transect from King George Island to Adelaide  
169 Island, as well as developing a long-term monitoring program. The Peruvian National Antarctic  
170 Program comprises summertime studies at Machu Picchu Research Station on King George Island,  
171 which was established in 1989, and oceanographic cruises. Spanish research programs centre on  
172 Juan Carlos I and Gabriel de Castilla Stations in the South Shetland Islands, which were opened in the  
173 late 1980s, as well as ship-based research. Brazilian research efforts have been underway in the  
174 northern WAP since the 1980s, with dedicated ship-based monitoring programs conducted through  
175 a number of initiatives coordinated by the Brazilian Antarctic Program since 2000. Chinese  
176 monitoring programs at Great Wall Station on King George Island have been in operation as part of  
177 the Chinese National Antarctic Program since the base was established in 1985. The Korea Polar  
178 Research Institute (KOPRI) runs a year-round marine ecosystem monitoring program in operation  
179 since 1996 at King Sejong Station on King George Island, which was inaugurated in 1988.

180 The Southern Ocean Observing System (SOOS) is an international organisation supported by the  
181 Scientific Committees on Antarctic Research (SCAR) and Oceanic Research (SCOR), which aims to co-  
182 ordinate Southern Ocean research, disseminate key findings and identify future directions and  
183 priorities (Meredith et al. 2013). The WAP working group of SOOS aims to bring together the  
184 different national programs, initiatives and projects working in the Peninsula region to maximise the  
185 science output across the spectrum of WAP marine research activities, to improve coordination and  
186 collaboration amongst ongoing research efforts, and to instigate and promote future developments  
187 and progress by identifying key gaps and opportunities to be addressed by future research. In this  
188 paper, we summarise the current state of knowledge under two high-priority overarching questions  
189 in WAP marine science:

190 1) What are the key mechanisms and interactions regulating ecosystem functioning and ocean-  
191 atmosphere coupling along the WAP shelf?

192 2) How is the WAP shelf environment changing and what are the ecosystem responses to and ocean-  
193 climate feedbacks on the changes underway?

194 We take a whole ecosystem approach and consider the full range of dynamics and interactions from  
195 sea ice and water properties and circulation through phytoplankton dynamics and ocean  
196 biogeochemistry to pelagic, benthic and microbial food webs. We then discuss the most significant  
197 challenges and key overarching priorities for the international scientific community within the  
198 framework of these two questions, and present a model for an observing system for the WAP based  
199 on sustained observations of key variables and detailed process studies that will allow us to address  
200 these priorities. Figure 3 summarises the current state of knowledge of the key components of the  
201 WAP marine system and the most important mechanisms and interactions in the context of the two  
202 overarching questions outlined above, as well as the major priorities and approaches for future  
203 marine research at the WAP.

204

205 1) What are the key mechanisms and interactions regulating ecosystem functioning and ocean-  
206 atmosphere coupling along the WAP shelf?

207 1.1. Physical oceanography

208 The hydrography and circulation of the WAP shelf are influenced by intrusions of oceanic water from  
209 the ACC, inflow around the tip of the Peninsula from the Weddell Sea, and coupling with the  
210 atmosphere, cryosphere and land (Klinck et al. 2004; Martinson et al. 2008). Modulated by shelf  
211 dynamics, these processes lead to significant spatial and temporal property gradients in this region.  
212 Large seasonal variability occurs in surface waters, driven by strong heat loss and ice growth and  
213 advection in autumn and winter that leads to the formation of a deep winter mixed layer, and ice  
214 melting and partial restratification during spring and summer (Klinck et al. 2004; Meredith et al.  
215 2008). Precipitation, glacial melt and sea ice melt modulate the freshwater content and stratification  
216 of the surface layer, with significant variability driven by ENSO and SAM over interannual timescales  
217 (Meredith et al. 2010; Meredith et al. 2017). A main feature of the surface circulation is the Antarctic  
218 Peninsula Coastal Current (APCC), a seasonal buoyancy- and wind-forced surface current, which  
219 flows southwestwards along the coast south of Anvers Island and west of Adelaide and Alexander  
220 Islands during summer and autumn with a cyclonic circulation inferred within Marguerite Bay  
221 (Beardsley et al. 2004; Moffat et al. 2008; Savidge and Amft 2009).

222 The deep circulation and properties, particularly in the southern and central WAP, are strongly  
223 influenced by the proximity of the ACC to the shelf break, and by shelf topography and vertical  
224 mixing with the upper layers (Klinck 1998; Klinck et al. 2004; Martinson et al. 2008; Orsi et al. 1995).  
225 The CDW that resides in the mid-depths of the ACC is the main source of heat, salt, macronutrients  
226 and carbon for the subsurface shelf waters. Observational studies have revealed that CDW intrusions  
227 move across the shelf as small (~5 km wide) subsurface eddies, and are transported preferentially in  
228 deep, glacially-scoured submarine troughs that cross-cut the shelf (Couto et al. 2017; Martinson and  
229 McKee 2012; Moffat et al. 2009). Numerical models of the region have recently become eddy-  
230 resolving and revealed that shoreward transport can be expected via several of these troughs  
231 (Graham et al. 2016). The available observational evidence points to only weak seasonal variability in  
232 deep water properties, with synoptic-scale intrusion of eddies and other intraseasonal variability  
233 dominating instead (Martinson and McKee 2012; Moffat et al. 2009). The intruding waters cool and  
234 freshen on the shelf due to mixing with overlying waters and heat loss to the surface layer and  
235 atmosphere. Although the drivers of modification and vertical ventilation of CDW remain poorly  
236 understood, recent observations suggest that flow-topography interactions along the deep troughs  
237 constitute a key mechanism for vertical mixing (Venables et al. 2017). Mean upward heat fluxes from  
238 modified CDW to the surface layer are small (on average  $\sim 1 \text{ W/m}^2$ ), with stronger fluxes observed in  
239 early spring shortly after the first seasonal retreat of sea ice, but before the upper layer is strongly  
240 restratified (Brearley et al. 2017). Both of these processes highlight the importance of small-scale  
241 spatial (<1 km) and temporal (days to weeks) variability in controlling mixing rates and water  
242 modification at the WAP.

243 Bransfield Strait in the northern WAP differs markedly from the shelf to the south, with deep  
244 properties being modulated by colder, fresher waters originating in the Weddell Sea (Gordon and  
245 Nowlin 1978; Hofmann et al. 1996; van Caspel et al. 2018). The circulation in Bransfield Strait is  
246 generally cyclonic, with southward flow along the WAP coast and then turning towards the South  
247 Shetland Islands (Sangra et al. 2011; Zhou et al. 2002). A significant temperature gradient exists  
248 across Bransfield Strait, with warmer waters around the South Shetland Islands than along the  
249 mainland. The strong contrast in deep properties between Bransfield Strait and the shelf to the  
250 south suggests that deep water exchange between these two basins is limited (Hofmann et al. 1996),  
251 although its magnitude, temporal evolution, and dynamics are not fully described and understood.

## 252 1.2. Phytoplankton community dynamics

### 253 1.2.1. Pelagic primary production

254 The WAP shelf is a productive marine ecosystem, where primary production varies significantly in  
255 time and space, due to its regulation by upper ocean physics, light availability and the supply of  
256 macro- and micronutrients. As well as the role of phytoplankton in taking up nutrients and carbon  
257 dioxide, thus mediating air-sea gas exchange and larger-scale biogeochemical cycling, these primary  
258 producers constitute a critical food source for the entire WAP shelf ecosystem. High-biomass  
259 phytoplankton blooms occur during spring and summer (Hart 1942; Nelson and Smith 1991; Prézelin  
260 et al. 2000; Smith et al. 2008), when solar illumination increases and sea ice has retreated leaving an  
261 exposed ocean surface (Moline and Prézelin 1996; Smith and Stammerjohn 2001). There is a strong  
262 productivity gradient with high productivity ( $\sim 1000 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) inshore compared with offshore  
263 waters ( $\sim 100 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) (Vernet et al. 2008). Seasonal satellite studies and in situ measurements  
264 show that net community production peaks first offshore and follows the inshore retreat of the sea  
265 ice (Arrigo et al. 2017; Li et al. 2016). The magnitude of primary productivity on an annual basis is  
266 linked to climate modes such as ENSO and SAM, and their effect on the ASL, which influence the  
267 amount of sea ice present in the winter (Stammerjohn et al. 2008a), and this in turn affects primary  
268 productivity in the following spring and summer seasons (Saba et al. 2014). The duration of winter

269 sea ice and the extent of winter wind-driven mixing, combined with the timing of ice retreat and  
270 mixing during spring, has been shown to control upper ocean stability during spring and summer,  
271 thus preconditioning the water column for phytoplankton growth (Venables et al. 2013; Saba et al.  
272 2014; Schofield et al. 2017; Rozema et al. 2017a). In high-ice years, less wind-induced mixing over  
273 winter and a subsequent strong seasonal melt results in a more stable water column that retains  
274 phytoplankton in a shallower surface layer, where light conditions are favourable for growth (Moline  
275 1998; Vernet et al. 2008; Carvalho et al. 2016). In low-ice years, enhanced wind-driven mixing and  
276 subsequently deeper mixed layers, combined with a smaller input of meltwater to restabilise the  
277 upper ocean, result in phytoplankton cells being mixed over a greater depth interval, experiencing  
278 lower light levels overall, such that primary productivity is reduced (Figure 4). Superimposed on the  
279 seasonal bloom dynamics are shorter-lived phytoplankton blooms (days-week) facilitated by periods  
280 of low wind that lead to increased water column stability (Moline 1998; Vernet et al. 2008; Carvalho  
281 et al. 2016). High primary productivity supports a productive food web that is tightly coupled to the  
282 seasonal phytoplankton dynamics, suggesting strong bottom-up control of the ecosystem (Saba et  
283 al. 2014).

284 While WAP phytoplankton communities are often dominated by diatoms, other taxa are increasingly  
285 recognised as important components of the food web. The importance of nanoplankton (<20 µm)  
286 and picoplankton (<2 µm) has been documented, with cryptophytes being the dominant nano-  
287 flagellate over much of the region (e.g. Krebs 1983; Buma et al. 1991; Kopczynska 1992; Garibotti et  
288 al. 2003; Varela et al. 2002; Rodriguez et al. 2002). Other major phytoplankton taxa include mixed  
289 flagellates and haptophytes, with haptophytes (e.g. the prymnesiophyte *Phaeocystis antarctica*)  
290 being more prominent than cryptophytes in Marguerite Bay (Garibotti et al. 2003; Kozlowski et al.  
291 2011; Rozema et al. 2017a; Stefels et al. 2018). *P. antarctica* dominated the phytoplankton  
292 community during spring 2014 in the central WAP prior to the peak of the diatom bloom (Arrigo et  
293 al. 2017). During high-chlorophyll years, the late-spring/summer phytoplankton community is  
294 dominated by larger cells, primarily diatoms, with only a minor contribution from smaller size  
295 classes, primarily haptophytes and cryptophytes (Moline et al. 2004; Rozema et al. 2017a; Schofield  
296 et al. 2017; Schloss et al. 2014). In low-ice low-chlorophyll years, the haptophyte and cryptophyte  
297 contributions increase, whilst the diatom contribution is reduced. Cryptophyte abundance increases  
298 when a shallow meltwater lens, probably of glacial origin, overlies a well-mixed upper water column  
299 (Mura et al. 1995; Moline et al. 2004). Cryptophytes take up less CO<sub>2</sub> per unit chlorophyll than  
300 diatoms, such that a greater cryptophyte contribution may lead to reduced carbon uptake compared  
301 to diatom-dominated assemblages (Schofield et al. 2017).

302 Whilst the factors influencing phytoplankton community composition remain poorly understood, it is  
303 possible to segregate the presence and abundance of cryptophytes and diatoms at Palmer Station in  
304 temperature-salinity phase space (Figure 5a) (Schofield et al. 2017). Diatoms were observed over the  
305 full range of observed salinities and temperatures, with their abundance being significantly lower in  
306 colder and lower-salinity waters. Conversely, cryptophytes were most abundant in lower-salinity  
307 colder waters (-1 to 1° C), and absent at higher temperatures and salinities. The segregation of major  
308 phytoplankton taxa based on water mass properties at Palmer Station is not robust at the wider  
309 shelf scale (Figure 5b), since ship-based surveys indicate a range of cryptophyte species across the  
310 WAP that can occupy a range of hydrographic niches.

### 311 1.2.2. Coupling between sea ice and pelagic ecosystems

312 As well as regulating phytoplankton productivity through its control on upper ocean physics, sea ice  
313 can also play an important role in seeding the pelagic community. Primary production rates in  
314 Antarctic sea ice are highly variable, ranging from 0.5 to 1250 mg C m<sup>-2</sup> d<sup>-1</sup> (Arrigo 2017), and  
315 reaching maxima in spring and summer, when ice algae can contribute up to 50-60 % of total



316 primary production in a given area (e.g. McMinn et al. 2010). The direct coupling between sea ice  
317 and pelagic ecosystems varies seasonally, according to ice extent and its productivity compared to  
318 underlying waters. When ice melts in spring, release of algal cells into the water column can initiate  
319 under-ice algal blooms (Lizotte 2001), although differences in species composition between sea ice  
320 and water column communities have been documented (e.g. Riaux-Gobin et al. 2011). The timing  
321 and pulse size of release act as strong controls on the fate of sympagic (ice-associated) algae (Selz et  
322 al. 2018), with a rapid early release contributing substantially to pelagic production, and a later  
323 release being more likely to be consumed by pelagic zooplankton or benthic communities (e.g.  
324 Riebesell et al. 1991).

325 Antarctic sympagic algae are an important food source for zooplankton, such as juvenile krill  
326 (Kohlbach et al. 2017) and various life stages of copepods (Bluhm et al. 2017). This is especially the  
327 case during winter, when chlorophyll concentrations in bottom sea-ice layers close to the ice-water  
328 interface can be 10 to 100-fold higher than in the underlying seawater. At the WAP, bottom-ice  
329 chlorophyll increased from  $\sim 5 \mu\text{g L}^{-1}$  to  $\sim 500 \mu\text{g L}^{-1}$  from September to December 2014 in land-fast  
330 ice adjacent to Rothera Station (Meiners et al. *in press*).

331 Export of ice-associated organic carbon, that is not remineralised in the sea ice or surface waters, to  
332 benthic ecosystems occurs at rates determined by its composition (Riebesell et al. 1991) and the  
333 dynamics of ice retreat (e.g. Norkko et al. 2007; Wing et al. 2012). Whilst organic carbon fluxes  
334 during ice-covered seasons are small compared to summertime fluxes along the WAP, sea ice algae  
335 are most relevant for local and episodic inputs preceding pelagic blooms, and in providing source  
336 material that is remineralised in winter to support detritus feeders (Mincks et al. 2005). Biogenic  
337 particle fluxes beneath land-fast sea ice were  $\sim 0.2 \text{ g m}^{-2} \text{ d}^{-1}$  during winter at King George Island/ Isla  
338 25 de Mayo (Khim et al. 2007), and would be expected to increase dramatically during ice melt in  
339 spring. In the Ross Sea, tracer analysis shows that sea ice organic carbon fluxes can contribute  $>50\%$   
340 of the total diet of Antarctic benthic organisms (Wing et al. 2012).

### 341 1.3. Nutrient biogeochemistry

342 The supply and cycling of inorganic and organic macro- and micronutrients along the WAP is  
343 regulated by physical and biological processes, and influences the spatial and temporal variation in  
344 production and ecosystem structure. Inorganic macronutrients are supplied to WAP shelf  
345 ecosystems primarily by CDW intruding onto the shelf from the ACC (Klinck et al. 2004; Prezelin et al.  
346 2000). Cross-shelf transport of CDW in deep glacially-scoured canyons increases the supply of  
347 nutrients to biota in overlying waters, as well as increasing heat flux and reducing sea ice coverage,  
348 such that phytoplankton biomass is higher and more diatom-dominated over the canyons compared  
349 with adjacent shelf areas (Kavanaugh et al. 2015). The supply of inorganic nitrogen and silicic acid  
350 from sea ice is small compared to CDW, and dominated by regenerated nutrients (Fripiat et al. 2015;  
351 Henley et al. 2017). Phosphate accumulates in sea ice (Fripiat et al. 2017), but its effect on water  
352 column phosphate and micronutrient inventories remains unclear (Hendry et al. 2010). A glacial  
353 source of silicic acid in basal meltwater has been demonstrated around Greenland (Hawkings et al.  
354 2017), and warrants investigation along the WAP.

355 Vertical nutrient fluxes from the modified CDW source into the surface ocean vary substantially in  
356 space and time. Vertical nitrate fluxes during summer in Marguerite Bay and along Marguerite  
357 Trough were estimated as  $0.18 \pm 0.17 \text{ mmol NO}_3 \text{ m}^{-2} \text{ d}^{-1}$  with a maximum of  $0.56 \text{ mmol NO}_3 \text{ m}^{-2} \text{ d}^{-1}$   
358 (Henley et al. 2018). The mean summertime vertical nitrate flux for the Palmer LTER grid for 1998-  
359 2007 was estimated as  $1.36 \pm 1.79 \text{ mmol NO}_3 \text{ m}^{-2} \text{ d}^{-1}$  (Pedulli et al. 2014), although the latter study  
360 used a uniform value for the vertical eddy diffusivity ( $K_z$ ) that is likely to overestimate fluxes.  
361 Seasonal variability is poorly constrained, although vertical nutrient fluxes are expected to be

362 greatest following the initial retreat of sea ice, in agreement with heat fluxes (Brearley et al. 2017).  
363 Whilst macronutrients are normally replete in WAP surface waters, intense biological drawdown by  
364 phytoplankton can lead to transient nutrient limitation in coastal areas during some summers  
365 (Henley et al. 2017). Interannual variability in CDW-derived nutrient supply is attributed to the  
366 degree of wintertime mixing at Palmer Station (Kim et al. 2016), but this cannot fully account for the  
367 observed variability at Rothera (Henley et al. 2017).

368 The degree of summertime surface ocean macronutrient depletion shows an onshore-offshore  
369 gradient driven by higher primary production in inshore regions (Pedulli et al. 2014). Seasonal  
370 nutrient drawdown during summer follows interannual variability in chlorophyll, sea ice and upper  
371 ocean conditions, such that high-ice, high-chlorophyll years lead to greater nutrient drawdown than  
372 lower-chlorophyll years (Figure 4) (Henley et al. 2017; Kim et al. 2016), with the potential to  
373 influence WAP shelf nutrient budgets and exports. In the coastal regions, the summer N/P uptake  
374 ratio varies between  $\sim 13$ , indicative of diatom-dominated phytoplankton communities under bloom  
375 conditions, and  $\sim 21$ , indicative of communities dominated by non-diatom phytoplankton and/or  
376 lower productivity conditions (Clarke et al. 2008; Henley et al. 2017; Kim et al. 2016). The summer  
377 Si/N uptake ratio is usually  $\geq 1$  in the Rothera and Palmer time series, indicating diatom-dominated  
378 production in these coastal regions (Henley et al. 2017; Kim et al. 2016). Nutrient uptake varies  
379 significantly within a season, due to changes in water column structure, sea ice and phytoplankton  
380 communities (Hendry et al. 2009). For example, time-series analyses of the stable silicon isotope  
381 composition ( $\delta^{30}\text{Si}$ ) of silicic acid from northern Marguerite Bay show strong silicic acid drawdown by  
382 diatoms, interspersed with wind-driven mixing events that replenish the silicic acid reservoir from  
383 underlying waters (Cassarino et al. 2017).

384 Nitrate, phosphate and inorganic carbon are progressively enriched in subsurface waters as CDW  
385 moves across the shelf, and the stable nitrogen ( $\delta^{15}\text{N}$ ) and oxygen ( $\delta^{18}\text{O}$ ) isotope composition of  
386 nitrate (Figure 6) and nutrient stoichiometry show that this is driven by local remineralisation of  
387 organic matter and nutrient recycling in the upper water column ( $\leq 200$  m) (Henley et al. 2017, 2018).  
388 Nitrification (regeneration of nitrate via ammonium oxidation) occurs in the deeper darker part of  
389 the euphotic layer, making the regenerated nitrate contribution to surface ocean primary production  
390 sensitive to whether the base of the euphotic layer resides within the mixed layer. Nitrate and  
391 phosphate regenerated in subsurface shelf waters, as opposed to that supplied from the CDW  
392 source, can account for up to one third of the surface ocean nutrient pools during summer, with  
393 implications for new production, net  $\text{CO}_2$  uptake and organic matter export. Silicic acid is also  
394 enriched across the shelf, with maximum enrichment at depth (Henley et al. 2018). This indicates  
395 biogenic silica dissolution occurring deeper in the water column than organic matter  
396 remineralisation, and potentially in sediment porewaters, driving a return flux of silicic acid to the  
397 water column. New porewater silicon isotope data provide evidence for down-core changes in silicic  
398 acid being driven by dissolution of diatom frustules and potentially reverse weathering reactions  
399 (Cassarino et al. *in prep*).

400 Our understanding of organic nutrient budgets and cycling is more limited. Dissolved organic carbon  
401 (DOC) and nitrogen (DON) concentrations are low in the Southern Ocean compared to other ocean  
402 regions, with a labile to semi-labile pool in the upper ocean and a large refractory pool in CDW  
403 (Hansell et al. 2009; Kirchman et al. 2009; Ogawa et al. 1999). Low DOC concentrations and low  
404 bacterial production rates and biomass along the WAP suggest that bacterial production may be  
405 limited by the availability of dissolved organic matter (DOM) (Ducklow et al. 2012a; Kim et al. 2016),  
406 but this is yet to be fully understood.

407 The essential micronutrient iron is supplied to the WAP surface ocean primarily from glacial  
408 meltwater and shallow sedimentary sources (Annett et al. 2015; Annett et al. 2017; Bown et al.

409 2018; Monien et al. 2017; Sherrell et al. 2018). Iron concentrations are replete in inshore regions,  
410 but can be drawn down by phytoplankton blooms to limiting levels further offshore. Micronutrients  
411 other than iron show temporal and spatial variability, although their roles in regulating primary  
412 productivity along the WAP are yet to be determined (Bown et al. 2017; Hendry et al. 2008).

#### 413 1.4. Climate-active gases

##### 414 1.4.1. Marine carbonate chemistry and air-sea CO<sub>2</sub> fluxes

415 Carbonate chemistry and air-sea CO<sub>2</sub> fluxes along the WAP are influenced strongly by ocean physics  
416 and biological processes. Year-round measurements of dissolved inorganic carbon (DIC) and total  
417 alkalinity (TA) taken at the Rothera Time Series since 2010 show that all carbonate chemistry  
418 parameters have a strong, asymmetric seasonal cycle in surface waters with some year-to-year  
419 variation (Figure 7; Legge et al. 2015, 2017; Jones et al. 2017). Concurrent with the late spring/early  
420 summer phytoplankton bloom, DIC, TA and the fugacity of carbon dioxide ( $f\text{CO}_2$ ) decrease sharply,  
421 while pH and the saturation state ( $\Omega$ ) of the calcium carbonate minerals calcite and aragonite  
422 increase sharply. Values for all parameters then gradually return to winter values. Aragonite  
423 saturation state shows notably low wintertime values, just above 1, a critical boundary below which  
424 aragonitic organisms can become susceptible to growth impairment and dissolution (Jones et al.  
425 2017). Photosynthesis and respiration dominate these seasonal changes in surface water carbonate  
426 chemistry, with biological uptake driving the substantial reductions in DIC during spring and summer  
427 (Carrillo et al. 2004; Legge et al. 2017; Tortell et al. 2014). Upwelling and vertical mixing of carbon-  
428 rich deep water increase upper ocean DIC, especially during winter, whilst sea ice reduces CO<sub>2</sub>  
429 outgassing. Ryder Bay is a net sink for atmospheric CO<sub>2</sub> of 0.90-1.39 mol C m<sup>-2</sup> yr<sup>-1</sup> (Legge et al. 2015).  
430 It remains unclear whether the WAP shelf as a whole is a net annual sink or source for atmospheric  
431 CO<sub>2</sub>.

432 Across the WAP shelf, carbonate system parameters show strong onshore-offshore gradients in the  
433 upper ocean during summer, with low DIC and  $f\text{CO}_2$  and high pH and aragonite saturation state in  
434 near-shore waters, due to strong biological carbon uptake, especially in the southern WAP sub-  
435 region (Figure 8) (Carrillo et al. 2004; Hauri et al. 2015; Ruiz-Halpern et al. 2014). The degree of  
436 summertime DIC and  $f\text{CO}_2$  drawdown is closely related to phytoplankton biomass and primary  
437 production (Moreau et al. 2012), which are regulated by winter sea ice coverage and wind patterns  
438 during spring (Montes-Hugo et al. 2010). In the central WAP, dilution by meltwater inputs reduces  
439 TA and DIC in near-shore waters (Hauri et al. 2015). Most of the WAP shelf exhibited  $f\text{CO}_2$   
440 undersaturation and net CO<sub>2</sub> uptake during summers between 2005 and 2009, although there was a  
441 region of  $f\text{CO}_2$  supersaturation and net CO<sub>2</sub> release in the outer shelf region to the north of Anvers  
442 Island (Ruiz-Halpern et al. 2014). Air-sea CO<sub>2</sub> fluxes in Bransfield Strait are highly variable, with  
443 surface waters switching between sink and source behaviour in consecutive summer seasons (Ito et  
444 al. 2018).

##### 445 1.4.2. Halogens

446 Halogen gases can be released from phytoplankton and ice algal communities along the WAP, with  
447 consequences for atmospheric chemistry and regional climate. The halogens play an important role  
448 in the Antarctic atmospheric boundary layer, being involved in the cycling of O<sub>3</sub>, HO<sub>x</sub>, NO<sub>x</sub>, Hg, CH<sub>4</sub>  
449 and the formation of precursor molecules to cloud condensation nuclei (CCN) (reviewed by Saiz-  
450 Lopez and von Glasow 2012). Destruction by bromine radicals is thought to be the primary driver for  
451 ozone depletion events, during which Antarctic boundary layer O<sub>3</sub> can decrease from around 30 ppb  
452 to below instrumental detection (1-2 ppb) for up to a few days (e.g. Jones et al. 2013). Additionally,  
453 modelling studies suggest that some halogen oxides are involved in controlling CCN formation

454 through oxidation of the semi-volatile organic sulphur compound dimethyl sulphide by bromine  
455 monoxide (Breider et al. 2015) and possibly new particle formation involving iodine oxides (e.g. Saiz-  
456 Lopez et al. 2008; Roscoe et al. 2015).

457 Biotic and abiotic sources of halogens to the Antarctic atmospheric boundary layer have been  
458 identified. The 'explosive' emission of bromine needed to initiate ozone depletion events is driven by  
459 catalytic liberation from condensed-phase sea-salt bromide present on airborne particulates, and  
460 snow and sea ice surfaces (reviewed by von Glasow and Hughes 2015). Sea salt aerosol (Legrand et  
461 al. 2016) and blowing saline snow (Yang et al. 2008, 2010; Lieb-Lappen and Obbard 2015) are also  
462 thought to be important sources of gaseous inorganic bromine in Antarctica. Whilst these abiotic  
463 sources are thought to dominate, Hughes et al. (2009, 2012) show that high rates of biogenic  
464 bromoform ( $\text{CHBr}_3$ ) flux from diatom blooms in the seasonal ice zone of the WAP could also  
465 contribute significantly to gaseous inorganic bromine during certain times of year. Similar to the  
466 uptake of macronutrients being reduced during relatively low-productivity spring/summer seasons  
467 following winter periods with reduced fast-ice duration (Henley et al. 2017), biogenic bromoform  
468 ( $\text{CHBr}_3$ ) emissions are also reduced in low-ice low-productivity years (Hughes et al. 2012).

469 Whilst iodine emissions to the Antarctic atmosphere have also been linked to abiotic reactions on  
470 the snowpack (Saiz-Lopez et al. 2008; Freiss et al. 2010), additional biological sources have been  
471 proposed for coastal regions at the WAP and elsewhere. These include iodocarbon (e.g.  $\text{CH}_2\text{I}_2$ ,  $\text{CH}_3\text{I}$ )  
472 emissions from surface waters and sea ice (Chance et al. 2010; Granfors et al. 2013), and microalgal-  
473 mediated inorganic iodine flux from sea ice brine channels (Saiz-Lopez et al. 2015).

#### 474 1.4.3. Organic sulphur compounds

475 Dimethyl sulphide (DMS) is the most important natural sulphur source to the atmosphere, where it  
476 is oxidised to form sulphate aerosols, which act as CCNs and exert a cooling effect through albedo  
477 feedbacks. DMS can also be released from phytoplankton and ice algal communities along the WAP,  
478 resulting in a direct feedback between the ecosystem and regional climate. Climatologies of DMS  
479 concentrations and fluxes show that the Southern Ocean as a whole is a global hotspot of DMS  
480 production, and its modelled contribution to atmospheric sulphate is especially high (Gondwe et al.  
481 2003; Lana et al. 2011). The Southern Ocean also exhibits the highest temporal variability in DMS  
482 concentrations, and the highest concentrations in the marginal ice zone. The latest Southern Ocean  
483 climatology indicates that the WAP is not a particular hotspot of DMS production (Jarníková and  
484 Tortell 2016), although this may reflect a shortage of published datasets, particularly from the  
485 marginal ice zone. Two time series from the Palmer LTER show highest DMS concentrations in  
486 January between 5 and 15 nM (Asher et al. 2017; Herrmann et al. 2012), which compare well with  
487 the climatological mean for January of  $10.8 \pm 6.9$  (SD) nM for the whole Austral Polar province (Lana  
488 et al. 2011). A recent continuous 5-year time series at Rothera shows large seasonal fluctuations in  
489 northern Marguerite Bay, with considerably higher concentrations in January, reaching an average of  
490  $24 \pm 35$  (SD) nM and a maximum of 160 nM in January 2015 (Webb et al. *in review*). This new time  
491 series documents a 3-fold higher flux of DMS to the atmosphere than previously calculated. High  
492 concentrations were also observed throughout Marguerite Bay and out to the shelf edge in January  
493 2015, and are likely associated with the location of the marginal ice zone (Figure 9; Stefels et al.  
494 2018).

495 The role of sea ice in the sulphur cycle is complex and the processes involved are poorly quantified.  
496 Large phytoplankton blooms and spikes of DMS have been linked to melting sea ice (Trevena and  
497 Jones 2006), potentially caused by the release of large amounts of ice algae that produce the DMS  
498 precursor, dimethylsulphoniopropionate (DMSP) (Stefels et al. 2018). This is supported by extremely  
499 high DMSP concentrations common in sea ice, 2-3 orders of magnitude higher than in underlying

500 surface waters. However, release from sea ice does not necessarily result in high DMS  
501 concentrations (Tison et al. 2010). The efficiency of DMSP conversion to DMS depends strongly on  
502 phytoplankton community structure, as *Phaeocystis* and dinoflagellates readily convert DMSP into  
503 DMS whilst diatoms do not, on bacterial processes, which often demethylate DMSP rather than  
504 producing DMS, and on abiotic factors (Stefels et al. 2007). With particular relevance to Antarctic ice  
505 and surface waters, high levels of UV radiation can photo-oxidise DMS to dimethylsulphoxide  
506 (DMSO), as well as inhibiting algal and bacterial activity (Toole and Siegel 2004; Zemmeling et al.  
507 2008a). Whilst high DMS fluxes have been found above sea ice, it remains unclear how much is  
508 derived from surface ice communities, which are often dominated by the well-known DMS producer  
509 *Phaeocystis*, and/or from leads between ice floes, where surface-microlayer concentrations of DMS  
510 can be an order of magnitude higher than in the underlying water column (Zemmeling et al. 2008a,  
511 b). Ice-derived DMS fluxes are likely to be largest during early spring, when surface ice communities  
512 are developing and surface ice and snow layers become permeable due to rising temperatures. Sea  
513 ice dynamics also impact on pelagic DMSP production, both directly via DMSP release from ice algae  
514 input to surface waters, and indirectly by shaping the conditions for pelagic blooms that produce  
515 DMSP (Stefels et al. 2018; Webb et al. *in review*).

## 516 1.5. Microbial processes

517 Bacterioplankton (free-floating and particle-attached archaea and bacteria) community dynamics  
518 are closely coupled to phytoplankton dynamics in the upper ocean, and strongly influenced by  
519 environmental characteristics, such as sea ice, salinity, temperature, stratification and nutrient  
520 availability (e.g. Ghiglione and Murray 2012; Luria et al. 2016, 2017; Piquet et al. 2011; Rozema et al.  
521 2017b; Signori et al. 2014; Obryk et al. 2016). These microbial communities play a key role in  
522 biogeochemical cycling. Close coupling between bacterial and phytoplankton dynamics along the  
523 WAP has been emphasised by microbial studies conducted as part of the Palmer LTER (2002-  
524 ongoing) and earlier RACER (1987-1989) projects. Variability in abundance and productivity of  
525 bacterioplankton is governed largely by the availability of phytoplankton-derived DOM, as terrestrial  
526 input of organic carbon is negligible (Ducklow et al. 2012a) – in great contrast to the Arctic.  
527 Bacterioplankton abundance varies across the WAP shelf, being higher further south and towards  
528 the inshore regions, in broad agreement with phytoplankton distributions (Figure 10). Pronounced  
529 temporal variability is evident as abundance increases from winter minima of  $2.0 \pm 0.8 \times 10^8$  cells L<sup>-1</sup>  
530 to a maximum of  $\sim 2\text{-}3 \times 10^9$  cells L<sup>-1</sup> during summers with high phytoplankton biomass (Ducklow et  
531 al. 2012a; Evans et al. 2017). Hotspots of bacterial production and abundance do not necessarily  
532 overlap, as production per bacterium can vary by up to an order of magnitude between years, in  
533 addition to spatial differences (Figure 10). Multi-year and spatially-extensive studies have suggested  
534 a low ratio ( $\sim 4\%$ ) of bacterial to primary production (Ducklow et al. 2012a; Kim and Ducklow 2016),  
535 which is unique to the Southern Ocean and the cause remains unknown (Kirchman et al. 2009).  
536 Seasonal-scale studies that have addressed phytoplankton bloom dynamics and bacterioplankton  
537 diversity simultaneously suggest that time-lagged responses are important in the coupling between  
538 phytoplankton and bacteria, leading to increased heterogeneity in the microbial community (Luria et  
539 al. 2014; Moreno-Pino et al. 2016; Piquet et al. 2011; Rozema et al. 2017b; Bowman et al. 2017;  
540 Bowman et al. 2016). A stronger relationship between summertime bacterial production and  
541 phytoplankton biomass estimated from chlorophyll than with primary production suggests that  
542 bacteria preferentially utilise DOM derived from grazing, sloppy feeding and viral lysis, rather than  
543 DOM excreted by phytoplankton (Ducklow et al. 2012a; Kim and Ducklow 2016; Ruiz-Halpern et al.  
544 2011). Bacterioplankton itself could be an underestimated source of DOM through grazing by  
545 zooplankton and mixotrophic algae, or by viral lysis; an important loss factor for Antarctic  
546 bacterioplankton (Brum et al. 2015; Evans et al. 2017; Evans and Brussaard 2012; Vaqué et al. 2017).  
547 Although studies of DOM origin, speciation and bioavailability are rare in this region, one winter

548 survey revealed that ~35 % of dissolved amino acids, and thus potentially a large proportion of the  
549 DOM pool, was of bacterial origin (Shen et al. 2017).

550 Whilst low *in situ* temperatures could be co-limiting bacterial production along the WAP (Pomeroy  
551 and Wiebe 2001), no significant relationship between bacterial production and temperature was  
552 observed for half of the summers since 2002, and for the other summers, only weakly-to-moderately  
553 significant relationships were found over seasonal timescales (Kim and Ducklow 2016). Temperature  
554 may affect bacterial production indirectly, due to its influence on phytoplankton production, grazer  
555 activity and diversity, and viral infection (Ducklow et al. 2012b; Kim and Ducklow 2016; Maat et al.  
556 2017; Vaqué et al. 2017).

557 Stark contrasts exist between surface and deep (>100 m) community composition along the WAP,  
558 with diversity being more stable over time and space at depth than in surface waters (Luria et al.  
559 2014). Metabolic structure also varies seasonally and with depth, and can be used to segment  
560 bacterioplankton communities along the WAP (Bowman and Ducklow 2015; Bowman et al. 2017).  
561 Microbial communities can be transported by ocean currents and winds, increasing connectivity  
562 amongst populations (Bowman and Deming 2017; Wilkins et al. 2013). As in the wider Southern  
563 Ocean, the dominant phyla are Alpha- and Gamma- Proteobacteria, Actinobacteria and  
564 Bacteroidetes (the Cytophaga-Flavobacterium-Bacteroides group) (Abell and Bowman 2005;  
565 Delmont et al. 2014; Gentile et al. 2006; Landa et al. 2016).

566 The pelagic archaeal community along the WAP is dominated by ammonia-oxidising  
567 *Thaumarchaeota* (previously Marine Group I *Crenarchaeota*) (Abele et al. 2017; Grzymski et al. 2012;  
568 Hernández et al. 2015; Luria et al. 2014; Signori et al. 2014). *Thaumarchaeota* were also found to  
569 dominate sea ice and benthic archaeal communities (Cowie et al. 2011; Learman et al. 2016). The  
570 widespread distribution of *Thaumarchaeota* suggests an important ecological function involved in  
571 nitrogen recycling (Tolar et al. 2016), particularly in winter when bacterioplankton communities are  
572 enriched in archaea compared with summer communities (Church et al. 2003; Grzymski et al. 2012;  
573 Hernández et al. 2015; Murray et al. 1998; Murray and Grzymski 2007), and nitrogen recycling  
574 pathways have been identified in proteomic data (Williams et al. 2012).

575 High functional diversity is suggested by studies of species composition using the 16S rRNA gene,  
576 and confirmed by metagenomics and metaproteomics approaches, which provide a mechanistic  
577 understanding of the microbial processes at work. Bacterioplankton are involved in  
578 chemoheterotrophy, photoheterotrophy or aerobic anoxygenic photosynthesis during summer,  
579 whilst chemolithoautotrophic pathways dominate during winter (Grzymski et al. 2012; Williams et al.  
580 2012). Abundant Flavobacteria have been shown to bind and exploit polymeric substrates, including  
581 carbohydrates, polypeptides, and lipids, thereby providing a crucial function in microbial  
582 decomposition (Williams et al. 2013). 16S rRNA sequencing data from King George Island have also  
583 revealed a previously unknown clade of Archaea potentially capable of oxidising ferrous iron (Abele  
584 et al. 2017; Hernández et al. 2015).

## 585 1.6. Zooplankton dynamics

586 Zooplankton abundance, distribution and species assemblages along the WAP are influenced  
587 strongly by the availability and composition of their phytoplankton food source, as well as the  
588 physical structure of the water column, and play a pivotal role in food web interactions and carbon  
589 and nutrient cycling. The major taxa comprising meso- and macrozooplankton (>200 µm, hereafter  
590 macrozooplankton) assemblage composition along the WAP are well known, with the Antarctic krill,  
591 *Euphausia superba*, being well-established as a keystone species in the regional food web (e.g.  
592 Quetin and Ross 2003). The WAP is an important spawning and nursery area for *E. superba*, where

593 spawning success, larval survival over winter and recruitment the following summer are largely  
594 dependent on winter sea ice coverage through provision of the ice algal food source and by setting  
595 favourable conditions for summer phytoplankton blooms (Atkinson et al. 2004; Saba et al. 2014).  
596 Krill spawning and recruitment along the WAP plays a key role in supporting large krill biomass  
597 across the southwest Atlantic (Atkinson et al. 2004). The important roles of other taxa, such as the  
598 salp *Salpa thompsoni* and the pteropod *Limacina helicina*, in WAP food web dynamics and  
599 biogeochemical cycling are increasingly being recognised (e.g. Bernard et al. 2012). In Potter Cove,  
600 South Shetland Islands, inshore macrozooplankton assemblages are numerically dominated by the  
601 small copepod *Oithona similis*, whereas large copepods such as *Rhincalanus gigas* and *Calanus*  
602 *propinquus* tend to dominate in terms of biomass (Garcia et al. 2016).

603 WAP microzooplankton (<200 µm) assemblages are dominated by aloricate ciliates and athecate  
604 dinoflagellates (Calbet et al. 2005; Garzio and Steinberg 2013), with tintinnids associated with sea ice  
605 (Alder and Boltovskoy 1991). In summer, aloricate ciliate and tintinnid biomass increases with  
606 increasing latitude, with high microzooplankton biomass hot spots in productive inner-shelf areas to  
607 the south, such as Marguerite Bay (Garzio and Steinberg 2013). Microzooplankton biomass is  
608 positively correlated with chlorophyll *a* and particulate organic carbon (POC) concentrations (Garzio  
609 and Steinberg 2013).

610 Consistent with most ocean regions, microzooplankton are the dominant grazers during summer,  
611 consuming 55-85 % of primary production per day, whilst macrozooplankton (copepods, krill, salps,  
612 pteropods) consume on average ~1 % (Bernard et al. 2012; Garzio et al. 2013; Saille et al. 2013;  
613 Gleiber et al. 2015). However, aggregations of krill, salps or copepods common in the WAP result in  
614 higher localized macrozooplankton grazing contributions (Bernard et al. 2012; Gleiber et al. 2015). In  
615 summer, the impact of macrozooplankton grazing on phytoplankton increases significantly when  
616 salps are present, due to high ingestion rates (Bernard et al. 2012). Krill and pteropods are the major  
617 macrozooplankton grazers near the coast and over the shelf, whilst salps dominate in offshore slope  
618 waters (Bernard et al. 2012). Ingestion rates of copepods in summer are up to 70 times greater in  
619 productive coastal waters than offshore (Gleiber et al. 2015). Daily phytoplankton carbon rations for  
620 WAP macrozooplankton are often similar to, or even below, those needed to satisfy their metabolic  
621 needs and fuel reproduction, indicating that protozoans and other zooplankton are an important  
622 food source even during the productive summer period (Bernard et al. 2012; Gleiber et al. 2015).  
623 Macrozooplankton have been shown to feed on smaller zooplankton prey in the WAP (e.g. Atkinson  
624 and Snyder 1997; Calbet et al. 2006; Atkinson et al. 2012), although potential trophic cascades that  
625 could result have not been investigated. There are also regional differences in zooplankton prey  
626 quality that could affect top predators, indicated by lower lipid content of *E. superba* in the central  
627 WAP compared to the southern sub-region (Ruck et al. 2014).

628 A year-round time-series sediment trap located over the WAP shelf indicates that zooplankton fecal  
629 pellets (mostly from krill) dominate export, comprising on average 67 % of the total POC flux over  
630 170 m (Gleiber et al. 2012). By comparing copepod fecal pellet flux from the same sediment trap and  
631 copepod egestion rates from experiments, Gleiber et al. (2015) estimate on average 58 % retention  
632 of copepod fecal pellets in the upper 170 m, such that copepod pellets are likely recycled in surface  
633 waters to a greater extent than those from krill. *Salpa thompsoni* along the WAP produce large fecal  
634 pellets that sink on average 700 m per day, and have defecation rates that can exceed those of krill  
635 (Phillips et al. 2009). Changes in zooplankton species composition can therefore have a significant  
636 effect on POC fluxes, biogeochemical cycling, benthic food supply and the biological carbon pump  
637 (Gleiber et al. 2012; Steinberg and Landry 2017). *E. superba* is known to forage on the benthos,  
638 which has further implications for benthic-pelagic coupling, including the vertical transfer of  
639 particulate iron ingested at depth into surface waters where it is subsequently metabolised and  
640 made bioavailable to phytoplankton (Schmidt et al. 2011; Schmidt et al. 2016).

641 1.7. Higher trophic levels

642 The WAP ecosystem comprises diverse assemblages and high biomass of top predators that  
643 represent both Antarctic and sub-Antarctic habitats, supported by the large and persistent biomass  
644 of krill predominantly in the central and southern WAP and the pack ice zone (Costa and Crocker  
645 1996; Ducklow et al. 2007; Friedlaender et al. 2011; Kock and Shimadzu 1994; Nowacek et al. 2011).  
646 Along the northern slope and in oceanic waters where copepods dominate, mesopelagic fish and  
647 squid act as intermediate consumers. Predator hotspots develop in areas where bathymetric troughs  
648 facilitate intrusions of nutrient-rich CDW onto the continental shelf (Dinniman et al. 2011;  
649 Friedlaender et al. 2011; Friedlaender et al. 2006; Kavanaugh et al. 2015). More ephemeral predator  
650 hotspots are found along fronts and filaments that aggregate and concentrate prey (Bost et al. 2009;  
651 Cotté et al. 2015; Dragon et al. 2010; Scheffer et al. 2010; Warren et al. 2009). The biophysical  
652 coupling by which predators use and rely on mesoscale features that can aggregate their prey, and  
653 the dive behaviours that determine the decisions predators make in response to prey availability  
654 (Friedlaender et al. 2016), are critical to how top predators partition their habitat.

655 While top predators exist in similar regions and often share the same prey, they have different life  
656 history patterns and habitat preferences that likely alleviate some of the potential for competition.  
657 During the summer, penguins, flying seabirds and fur seals forage along the shelf break and the  
658 southern boundary of the ACC, periodically returning to their breeding colonies (Ribic et al. 2011). In  
659 winter, seabirds are found near the ice edge, along the shelf break and around the Polar Front to the  
660 north (Chapman et al. 2004). While gentoo penguins (*Pygoscelis papua*) remain near their breeding  
661 colonies throughout the year (Cimino et al. 2016; Miller et al. 2009), Adélie (*P. adeliae*) and chinstrap  
662 (*P. antarcticus*) penguins move far away from their colonies in winter, with Adélie penguins  
663 preferring winter sea ice, and chinstrap penguins preferring open water (Hinke et al. 2015;  
664 Trivelpiece et al. 2007). Adélie penguins forage in shallow (<200 m) waters near land and in deeper  
665 waters (200–500 m) near the edge of deep troughs cross-cutting the shelf (Erdmann et al. 2011).  
666 Crabeater (*Lobodon carcinophagus*), Weddell (*Leptonychotes weddellii*) and leopard (*Hydrurga*  
667 *leptonyx*) seals remain in the WAP year-round, maintaining access to ice or land to haul out and  
668 reproduce (Figure 11) (Costa et al. 2010). While Weddell seals remain in the fjords, crabeater seals  
669 move extensively along the shelf, staying closer to the coast in regions with greatest change in  
670 bathymetry, and deep within the pack ice throughout the winter (Burns et al. 2004). The short  
671 breeding season of southern elephant seals (*Mirounga leonina*) enables them to spend months at  
672 sea moving into the pack ice, along the outer shelf and offshore into pelagic waters (Costa et al.  
673 2010). Seals partition their habitat by foraging depth and duration, with the longest and deepest  
674 dives by elephant seals (Hindell et al. 2016). Fur seals show significant seasonal variability in their  
675 distribution, remaining within a few hundred kilometres of their breeding colonies during summer  
676 and dispersing widely during winter (Figure 11). Humpback whales (*Megaptera novaeangliae*) forage  
677 broadly across the WAP shelf during summer, moving inshore in autumn, with their density and  
678 distribution controlled by those of their krill prey and their preference for ice-free conditions and  
679 dense aggregations of larger, older krill (Friedlaender et al. 2006; Johnston et al. 2012; Murphy et al.  
680 2007; Weinstein and Friedlaender 2017; Weinstein et al. 2017). Humpback whales forage in a  
681 manner consistent with optimal foraging theory to maximize their energetic gains (Friedlaender et  
682 al. 2013; Friedlaender et al. 2016; Tyson et al. 2016) and remain in significant numbers in ice-free  
683 areas until the beginning of winter. Minke whales (*Balaenoptera bonaerensis*) avoid competition with  
684 humpback whales by foraging on deeper krill aggregations (Friedlaender et al. 2009) and, being  
685 smaller and more manoeuvrable, they can forage under the ice, their preferred habitat (Friedlaender  
686 et al. 2014). Recent work found long-term preferences of minke whales for ice edge regions during  
687 summer (Williams et al. 2014) and throughout the foraging season (Lee et al. 2017). While they are  
688 known to be the only endemic cetacean species, present year-round, evidence suggests that some  
689 portion of the population migrates to sub-tropical latitudes in winter (Lee et al. 2017). Blue



690 (*Balaenoptera musculus*) and right (*Eubalena glacialis*) whales are also seasonally present and  
691 similarly feed on krill. Different ecotypes of killer whales (*Orcinus orca*) are seasonally present in the  
692 WAP following the distribution of their prey (e.g. seals, whales or fish) (Pitman and Ensor 2003).

693 As well as providing top-down control on the ecosystem, top predators can also influence  
694 biogeochemical cycling by transporting macro- and micronutrients vertically and horizontally  
695 (Doughty et al. 2016; Ratnarajah et al. 2016; Roman et al. 2014).

## 696 1.8. Benthic ecosystems

697 Benthic organisms and processes play a critical role in whole-ecosystem structure and functioning  
698 along the WAP, as well as biogeochemical cycling and sequestration of carbon from the overlying  
699 water column. WAP benthic ecosystems are characterised by a rich diversity of macro- and  
700 megafauna including echinoderms such as brittle stars, holothurians, sea urchins, asteroids and  
701 crinoids, as well as abundant sponges, ascidians, polychaetes, bivalves, gastropods, brachiopods,  
702 bryozoans and sipunculan worms (e.g. Clarke et al. 2007; Gutt 2007; Peck 2018; Piepenburg et al.  
703 2002; Sahade et al. 1998; Smith et al. 2012). Hard-substrate communities are widespread in the  
704 region around Palmer Station and further north to the South Shetland Islands, and are dominated by  
705 large perennial brown macroalgae in shallow waters, with red macroalgae dominating the  
706 understory (Wiencke and Amsler 2012; Deregibus et al. 2016; Ducklow et al. 2013). These  
707 macroalgae and their epiphytes form important year-round carbon sources in coastal and near-  
708 shore systems (Dunton, 2001; Gillies et al. 2012; Jacob et al. 2006; Pasotti et al. 2015), and support  
709 rich assemblages of benthic invertebrates, including amphipods, gastropods and echinoderms  
710 (Huang et al. 2007; White et al. 2012). South of the Palmer Station region, benthic communities at  
711 depths >50 m are dominated by sessile invertebrates including sponges, soft corals, bryozoans and  
712 tunicates (Ducklow et al., 2013), whilst mobile scavengers such as starfish, brittle stars and urchins  
713 are abundant in shallower waters (Clarke and Johnston 2003). Fjordic systems along the WAP have  
714 been shown to exhibit higher abundance and diversity than adjacent shelf areas (Grange and Smith  
715 2013).

716 In general, benthic organisms in the WAP region are characterised by very slow growth and  
717 development rates, which are slowed beyond the expected effects of temperature compared to  
718 temperate and tropical species (Figure 12) (Peck 2016, 2018). Rates of activity and other processes  
719 including routine oxygen consumption are not similarly slowed, indicating that the limitations on  
720 growth and development are likely caused by restricted protein manufacture at low temperatures  
721 (Fraser et al. 2004, 2007; Peck 2016). The slow growth rates result in extended longevity and  
722 deferred maturity (longer generation times), which has been demonstrated in amphipods (Johnson  
723 et al. 2001), the bivalve *Adacnara nitens* (Higgs et al. 2009), and a range of other molluscs,  
724 brachiopods and echinoderms (Peck 2018). High-latitude Southern Ocean benthic organisms, such as  
725 fish (Leis et al. 2013), hyppolytid shrimps (Clarke 1985) and several starfish (Bosch and Pearse 1990),  
726 also produce fewer larger eggs, with egg diameters generally 2-5 times greater than those of lower-  
727 latitude species (Arntz et al. 1994; Peck 2018).

728 Benthic organisms assimilate carbon fixed by primary producers in the overlying water column  
729 and/or sea ice, and can store carbon more efficiently and over longer periods than pelagic organisms  
730 (Barnes 2017; Peck et al. 2010). The degree and timescale of carbon sequestration is dependent on  
731 sea ice dynamics and the duration of the ice algal and phytoplankton blooms, local oceanographic  
732 conditions such as current speeds and nutrient supply, organisms' lifespans and behaviours, and the  
733 frequency of ice scour, which has a major role in structuring benthic ecosystems (Barnes et al. 2018).  
734 The contribution of benthic processes to pelagic productivity via nutrient supply at the WAP is a  
735 current area of debate. Nutrient release from sediments and porewaters by diffusion, physical

736 disturbance and bioturbation by burrowing organisms, such as polychaetes, echinoderms and  
737 bivalve molluscs (Poigner et al. 2013), has the potential to act as a significant source of nutrients to  
738 water column biota. Physical disturbance by iceberg scour can expose buried sediments from water  
739 depths exceeding 300 m, and can produce sediment scours over 10 m deep (Lien et al. 1989),  
740 releasing large quantities of sediment-derived nutrients. Currents entrained by moving icebergs can  
741 redistribute sediment several metres up into the water column for short periods and across many  
742 metres of the seabed (Bigg 2016; Peck et al. 2005). Icebergs can also distribute sediments over  
743 considerable distances and through the water column as ice melts, and act as a dispersal mechanism  
744 for some benthic species (Peck 2018). Mixing of the upper water column by icebergs, winds and  
745 currents will regulate the extent to which sediment-derived nutrients reach the surface ocean and  
746 influence pelagic primary productivity.

747

748 2) How is the WAP shelf environment changing and what are the ecosystem responses to and ocean-  
749 climate feedbacks on the changes underway?

750 Our knowledge of the key mechanisms and interactions regulating ecosystem functioning and  
751 ocean-atmosphere coupling along the WAP shelf, and in particular the interdependence between  
752 physical, biogeochemical and biological processes, paves the way for understanding the ongoing  
753 changes in ice dynamics, ocean physics, biogeochemistry, air-sea exchange, and pelagic, benthic and  
754 microbial food webs.

755 2.1. Physical oceanography and ice dynamics

756 The long-term change in atmospheric and oceanic properties along the WAP has been a strong focus  
757 of scientific efforts given its large magnitude, and its observed and potential impact on the regional  
758 ecosystem (Constable et al. 2014a, b; Ducklow et al. 2013; Martinson et al. 2008; Meredith et al.  
759 2017; Schofield et al. 2017; Venables et al. 2013). The evolution of sea ice cover on timescales from  
760 seasonal to inter-decadal is a key modulator of physical and biogeochemical processes on the shelf.  
761 For example, sea ice extent and its growth and retreat modulate vertical mixing, air-sea fluxes, light  
762 penetration, and the salt and heat content of the surface ocean. On average, sea ice extent in the  
763 WAP region varies between 1 and  $6 \times 10^5$  km<sup>2</sup> over the annual cycle (Meredith et al. 2017). Alongside  
764 substantial warming of the atmosphere and ocean, the period of seasonal sea ice cover has  
765 shortened by more than three months since the late 1970s, with autumn advance being delayed by  
766 two months and spring retreat occurring more than one month earlier (Stammerjohn et al. 2012;  
767 Stammerjohn et al. 2008a). Strong correspondence between retreat and subsequent advance  
768 suggests a strong feedback in ocean thermal properties in autumn in response to changes in the  
769 timing of retreat in spring. The trend is less clear in the northern WAP (Schloss et al. 2012) where  
770 substantial sea ice declines have already occurred, although Bers et al. (2013) showed the strong  
771 effect of climatic forcing even in inshore waters of King George Island.

772 The warming trends and salinity changes documented in the surface and deep water layers across  
773 much of the WAP shelf have not been observed in Bransfield Strait, likely because of the modulation  
774 by Weddell Sea inflow around the northern tip of the Peninsula (Bers et al. 2013; Meredith and King  
775 2005; Schloss et al. 2012; Schmidtke et al. 2014). This highlights strong gradients along the shelf in  
776 the processes controlling long-term property trends, as well as the mean properties themselves. The  
777 alongshore structure of mid-depth (>100 m) ocean temperature plays a pivotal role in glacier retreat  
778 rates along the WAP, with warmer subsurface waters in the southern and central WAP (south of  
779 Bransfield Strait) acting as the primary driver of substantial glacial retreat along the adjacent coast  
780 (Cook et al. 2016; Padman et al. 2012). In contrast, glaciers along Bransfield Strait terminate in

781 colder Weddell-modulated waters and are retreating at slower rates, with some even advancing. In  
782 cases where glaciers in the northern WAP are experiencing high melt rates and retreat, for example  
783 at King George Island, atmospheric forcing is thought to be the primary driver (Falk and Sala 2015).

784 The observation that the long-term trends of atmospheric warming and sea ice declines have  
785 plateaued since the late 1990s (Figure 1), with recent increases in sea ice extent and duration  
786 recorded in some places (Schofield et al. 2017; Turner et al. 2016), reflects substantial natural  
787 internal variability that is likely to have broad-scale impacts on ocean properties and circulation of  
788 the WAP shelf. The nature and importance of these interactions superimposed onto the long-term  
789 trends is still to be determined. In contrast, there is no evidence for a slow-down or reversal in the  
790 trends of oceanic warming over the southern and central WAP shelf, or glacial retreat along much of  
791 the WAP coast (Cook et al. 2016).

## 792 2.2. Phytoplankton and microbial community dynamics

793 The documented sea ice declines since the late 1970s have led to overall reductions in  
794 phytoplankton biomass, with regional differences along the WAP in the response of phytoplankton  
795 dynamics to the climatic and oceanic changes observed (Montes-Hugo et al. 2009). These changes in  
796 phytoplankton dynamics are attributed to changes in sea ice and upper ocean conditions, rather  
797 than any long-term trend in CDW incursion and/or nutrient supply. Satellite analyses suggest that  
798 the shelf sub-region to the north of Anvers Island experienced decadal declines in summer  
799 chlorophyll levels between the early 1980s and early 2000s concurrent with declining sea ice extent  
800 and duration (Montes-Hugo et al. 2009; Stammerjohn et al. 2008a, b). Low sea ice cover during  
801 winter and early spring leads to low chlorophyll in summer due to increased wind-driven mixing and  
802 potentially increased cloud cover, and consequently a less favourable light environment for  
803 phytoplankton growth (Montes-Hugo et al. 2009; Saba et al. 2014; Venables et al. 2013). In contrast,  
804 satellite-derived chlorophyll increased in the central and southern sub-regions over the same period,  
805 attributed to longer periods of open water (Montes-Hugo et al. 2009) resulting from the seasonal  
806 declines in sea ice (Stammerjohn et al. 2008a, b). However, strong decreases in chlorophyll in the  
807 northern sub-region outweighed the increases further south, leading to an overall reduction in  
808 phytoplankton biomass along the WAP (Montes-Hugo et al. 2009). More recently, the increase in sea  
809 ice duration since the late 2000s has led to higher chlorophyll levels in WAP coastal regions  
810 (Schofield et al. 2017).

811 Coastal time-series data from Potter Cove at King George Island/ Isla 25 de Mayo (Schloss et al.  
812 2012) and Palmer Station at Anvers Island (Schofield et al. 2017) suggest that the observed declines  
813 in phytoplankton biomass reversed around 2010. In Potter Cove, chlorophyll concentrations were  
814 typically low between 1991 and 2009, with maximum values ( $\sim 4 \text{ mg m}^{-3}$ ) during short-lived episodic  
815 events, when phytoplankton assemblages were dominated by large diatoms from several genera  
816 (*Corethron criophilum*, *Odontella weissflogii*, *Eucampia antarctica*, *Thalassiosira sp.*, *Porosira sp.*)  
817 (Schloss et al. 1997). Nutrients were not limiting, and low phytoplankton biomass was attributed to  
818 adverse physical conditions, with intense turbulent mixing and sediment-rich meltwater inputs  
819 limiting light conditions for phytoplankton growth and preventing bloom formation (Schloss et al.  
820 2002; Kim et al. 2018). A first high-chlorophyll bloom ( $\sim 14 \text{ mg m}^{-3}$ ) lasted approximately two weeks  
821 in January 2010 and was followed by several subsequent high-chlorophyll seasons, with the same  
822 genera present as earlier in the time series (Schloss et al. 2014; Kim et al. 2018). Whilst a  
823 combination of low air temperatures, which delayed the melting of the surrounding Fourcade  
824 glacier, and low wind intensities can explain the bloom duration in January 2010, different  
825 mechanisms are behind increased productivity in more recent years. Experimental work has shown  
826 that smaller diatoms (e.g. *Navicula*, *Nitzschia*, etc.) have greater tolerance to low salinities than large  
827 diatoms (Hernando et al. 2015), such that the phytoplankton response to glacial meltwater inputs

828 may differ depending on community composition and the timing of inputs relative to bloom  
829 progression.

830 Chlorophyll concentrations have also increased since the late 2000s at Palmer Station, ~400  
831 kilometres to the south, concurrent with an increase in the number of days of sea ice cover each  
832 year and shallower spring/summer mixed layers, which have led to larger phytoplankton blooms  
833 dominated primarily by diatoms (Schofield et al. 2017). This is in contrast to much of the duration of  
834 the Palmer time series, where a statistically significant decline in sea ice duration was observed. At  
835 the Rothera Time Series (RaTS) in northern Marguerite Bay, ~400 kilometres south of Palmer Station,  
836 short-lived winter sea ice cover led to a substantial reduction in summertime chlorophyll levels  
837 between 2007 and 2010 (Venables et al. 2013). Since 2010, sea ice duration and chlorophyll have  
838 increased again, with sea ice persisting into December and large phytoplankton blooms (chlorophyll  
839  $>15 \text{ mg m}^{-3}$ ) in the most recent years. A recent synthesis of chlorophyll and physical oceanographic  
840 time-series data from Potter Cove, Palmer and Rothera demonstrates that whilst large-scale climate  
841 forcing influences all three sites, local processes such as ice melt and mixing superpose distinct  
842 interannual patterns and trends (Kim et al. 2018). Longer-term changes in primary production and  
843 community structure over the WAP shelf will depend on the interaction of long-term climatic  
844 warming trends and large natural internal variability in regulating seasonal sea ice dynamics over  
845 interannual-to-decadal timescales.

846 Projected increases in glacial meltwater input (Meredith et al. 2010) are likely to modify  
847 phytoplankton dynamics by promoting upper ocean stability and altering nutrient availability.  
848 Combined with long-term reductions in sea ice cover and persistence of deeper mixed layers,  
849 increased surface stratification would potentially favour cryptophytes and smaller diatoms over  
850 larger diatoms, with shifting phytoplankton community structure as a result (Moline et al. 2004;  
851 Schofield et al. 2017).

852 There has been significantly less focus on the consequences of sea ice and physical oceanographic  
853 changes for the direct coupling between sea ice and pelagic ecosystems, through ice-ocean  
854 exchange and sea ice algal inputs to the water column. Changes in the timing of sea ice retreat may  
855 lead to phenological changes, and earlier or later ice algal and/or phytoplankton blooms may result  
856 in trophic mismatches as pelagic herbivores become less able to synchronize with the blooms, with  
857 negative reproductive consequences and the potential for cascading effects through the entire food  
858 web (e.g. Søreide et al. 2010).

859 Relatively little is known about the response of microbial communities to ongoing changes in the  
860 physical environment and phytoplankton dynamics. However, response time to changing  
861 environmental conditions is known to vary spatially and between phytoplankton and  
862 bacterioplankton (Moreno-Pino et al. 2016; Rozema et al. 2017b), likely increasing spatial patchiness  
863 in the microbial community (Figure 10) and functional diversity, thus affecting ecosystem resilience.  
864 The strong dependence of microbial processes on other rapidly changing ecosystem components,  
865 e.g. phytoplankton (Bertrand et al. 2015), zooplankton, benthic organisms, seeding from  
866 macrofaunal microbiomes (Bik et al. 2016) or terrestrial systems (Cavicchioli 2015), and the  
867 bioavailability of DOM substrate, suggests that continual and pronounced changes in microbial  
868 community composition and functioning are likely.

### 869 2.3. Biogeochemical changes and air-sea exchange

870 Physical and biological changes along the WAP are closely related to changes in ocean chemistry and  
871 biogeochemistry, in particular the budgets and cycling of macro- and micronutrients, and the  
872 production and air-sea exchange of climate-active gases, with the potential for larger-scale

873 consequences and feedbacks. For example, continued glacial retreat can be expected to increase the  
874 supply of iron and other micronutrients (Zn, Cd, Co etc.) from glacial and shallow sediment sources,  
875 and potentially their availability to phytoplankton (Annett et al. 2015; Annett et al. 2017; Bown et al.  
876 2017, 2018; Hendry et al. 2008; Monien et al. 2017). Seasonal biological uptake of nutrients and  
877 carbon will be determined by the documented variability and ongoing changes in seasonal  
878 phytoplankton dynamics driven by changes in sea ice and upper ocean conditions (Henley et al.  
879 2017; Legge et al. 2015; Kim et al. 2016).

880 Changes in the properties, transport and circulation of CDW across the shelf, particularly in the  
881 southern and central WAP regions to the south of Bransfield Strait (Martinson et al. 2008; Schmidtko  
882 et al. 2014), are likely to increase the supply of macronutrients and CO<sub>2</sub> to subsurface shelf waters.  
883 The extent to which this affects surface ocean nutrient and carbon budgets will depend on the  
884 evolution of mixing processes in response to sea ice and atmospheric forcing. Carbonate system  
885 parameters (DIC, TA, pCO<sub>2</sub>) on the Palmer LTER grid do not show statistically significant trends  
886 during summer seasons between 1993 and 2012 (Hauri et al. 2015). However, a continuation of the  
887 long-term reduction in seasonal sea ice cover and continued strengthening and southward shifting of  
888 westerly winds (Le Quéré et al. 2007; Stammerjohn et al. 2008b; Landschützer et al. 2015) may  
889 increase upwelling of DIC-rich water and CO<sub>2</sub> outgassing in winter, as well as altering the  
890 phytoplankton community and potentially reducing biological CO<sub>2</sub> uptake in summer (Legge et al.  
891 2015; Saba et al. 2014). The resultant reduction in net annual CO<sub>2</sub> uptake along the WAP is unlikely,  
892 in itself, to make a significant difference to the functioning of the Southern Ocean CO<sub>2</sub> sink, due to  
893 the small size of the WAP shelf region. However, if the changes anticipated at the WAP are manifest  
894 across larger areas of the Southern Ocean in the coming decades, the detailed knowledge of the  
895 physical and biological mechanisms regulating CO<sub>2</sub> fluxes obtained in the WAP system will be useful  
896 in projecting change at the wider scale, which could be significant terms in the global carbon budget.

897 Given that sea-to-air emissions of halogens and DMS are directly linked to sea ice dynamics (von  
898 Glasow and Hughes 2015) or are derived from the ecosystems that exist within or around sea ice  
899 (Hughes et al. 2013; Stefels et al. 2018), it is likely that the sea ice changes and variability observed  
900 along the WAP in recent decades will alter the fluxes of these gases to the atmosphere over  
901 interannual and longer timescales. This will be important for climate (through aerosol and CCN  
902 formation) and atmospheric chemistry (via tropospheric ozone destruction) locally and regionally.

#### 903 2.4. The WAP pelagic food web

904 Interannual variability in phytoplankton biomass has strong implications for the productivity of the  
905 entire food web, with low chlorophyll years leading to less successful recruitment of the keystone  
906 species Antarctic krill (*Euphausia superba*) (Atkinson et al. 2004; Saba et al. 2014). As such, low sea  
907 ice conditions are likely to hold negative consequences for higher trophic levels such as penguins,  
908 flying sea birds, seals and whales (Constable et al. 2014a, b; Costa et al. 2010; Trivelpiece et al.  
909 2011). Conversely, the recent increases in chlorophyll are likely to be beneficial for zooplankton and  
910 their pelagic and benthic consumers (Saba et al. 2014).

911 Seasonal changes in WAP macrozooplankton abundance are driven by a combination of long-term  
912 trends linked to warming and sea ice declines, sub-decadal shifts attributed to oscillations in  
913 atmospheric forcing, such as SAM and ENSO, which affect sea ice dynamics and sea surface  
914 temperature, and local and regional changes in primary production, all of which have strong  
915 interdependences (Figure 13; Steinberg et al. 2015). For example, a decrease in krill density between  
916 the 1970s and early 2000s in the WAP and southwest Atlantic sector of the Southern Ocean was  
917 attributed to long-term warming and sea ice declines, which reduce the availability of the ice algal  
918 food source required to promote larval survival and recruitment, as well as driving the overall

919 decline in the summer phytoplankton food source (Atkinson et al. 2004; Montes-Hugo et al. 2009). It  
920 has been contested that this decline in krill resulted from a period in the decadal-scale population  
921 variability of unusually high krill abundance in the late 1970s, rather than being driven by climate  
922 change over subsequent decades (Loeb and Santora 2015). However, more recent evidence has  
923 shown a southward contraction of krill distribution throughout the sector over the last 90 years,  
924 with a concomitant reduction in juvenile recruitment linked to reduced food availability, and a  
925 concentration of the population over the WAP shelf (Atkinson et al. 2019). Since the early 1990s, krill  
926 abundance on the Palmer LTER grid (central and southern WAP) has shown a stable 5-year cycle that  
927 reflects variability in reproductive and recruitment success linked to ENSO cycles and their influence  
928 on sea ice dynamics (Loeb et al. 2009; Quetin and Ross 2003; Ross et al. 2014; Steinberg et al. 2015),  
929 in broad agreement with findings from the northern WAP around the South Shetland Islands (Loeb  
930 and Santora 2015; Richerson et al. 2017). Accordingly, both *E. superba* and *Thysanoessa macrura* are  
931 positively correlated to regional primary production two years prior (Figure 13; Steinberg et al.  
932 2015). Local effects can also be pronounced, for instance high krill mortality in Potter Cove in recent  
933 years is attributed to unfavourable conditions caused by high meltwater-sourced particle loads from  
934 a retreating glacier (Fuentes et al. 2016). In contrast to krill, abundance of the major copepod taxa  
935 showed a regional long-term increase between 1993 and 2013 (Gleiber 2015). Variability in *Salpa*  
936 *thompsoni* over the shelf is influenced by both ENSO (Loeb and Santora 2012) and SAM (Figure 13;  
937 Steinberg et al. 2015), whilst long-term increases throughout the southwest Atlantic sector have  
938 accompanied the declines in krill (Atkinson et al. 2004). Variability in abundance of the pteropod  
939 *Limacina helicina* along the WAP is also linked to ENSO cycles (Figure 13; Loeb et al. 2009; Loeb and  
940 Santora 2013; Ross et al. 2014; Steinberg et al. 2015). Shifts in phytoplankton community structure  
941 can also affect the abundance of krill relative to other major zooplankton taxa, because the grazing  
942 efficiency of *E. superba* is reduced significantly on particles <20 µm, such that diatom-dominated  
943 communities are likely to favour krill, whilst communities dominated by cryptophytes and/or  
944 haptophytes are likely to favour salps and other taxa (Haberman et al. 2003; Meyer and El-Sayed  
945 1983; Moline et al. 2004). Shifts in the dominance of krill compared to other taxa have major  
946 consequences for higher trophic levels that rely on krill as their primary food source, as well as for  
947 carbon export and nutrient recycling, and may lead to substantial reorganisations of the pelagic food  
948 web (e.g. Atkinson et al. 2004, 2019; Quetin and Ross 2003).

949 The distribution and abundance of a number of krill-dependent pelagic consumers are changing in  
950 concert with changes in the physical environment and the availability of krill (Constable et al. 2014a,  
951 b). Winter sea ice conditions along the WAP are particularly important for krill predators, because  
952 they regulate krill availability and therefore foraging conditions, which are a key determinant of  
953 recruitment and overwinter survival of adult and juvenile animals (Hinke et al. 2017b). Sea ice-driven  
954 changes in phenology can also lead to trophic mismatches between predator foraging needs and  
955 prey availability, with major demographic consequences (Youngflesh et al. 2017). Populations of ice-  
956 dependent Adélie and chinstrap penguins have declined significantly (e.g. Figure 14; Ducklow et al.  
957 2013; Hinke et al. 2017a; Juarez et al. 2015; Trivelpiece et al. 2011) and the only Emperor penguin  
958 colony at the WAP has been lost due to changes in seasonal sea ice duration (Trathan et al. 2011).  
959 Southward shifts of the maritime climate, displacing the Antarctic climate, have also increased  
960 precipitation and snow accumulation, which reduces the survival of Adélie penguin chicks (Carlini et  
961 al. 2009; Chapman et al. 2011). In the northern WAP in particular, the shift to a more maritime  
962 climate is likely to shift southward the distributions of ice- and krill-dependent species, such as  
963 Weddell and crabeater seals, minke whales and Adélie penguins, leading to local declines as their  
964 habitat contracts with diminishing sea ice (Ducklow et al. 2013; Huckstadt et al. 2012a; Siniff et al.  
965 2008). In contrast, ice-tolerant species such as fur seals (*Arctocephalus gazella*), humpback whales  
966 and gentoo penguins and those less dependent on krill, such as elephant seals, have increased in  
967 number (Costa et al. 2010; Ducklow et al. 2013) and in the length of time they remain feeding locally  
968 (e.g. Friedlaender et al. 2016; Weinstein and Friedlaender 2017). The decline in Adélie penguin

969 numbers slowed down in the mid-2000s and the total number of penguins stabilised, although this  
970 was a consequence of increasing gentoo penguin numbers (Figure 14). Some krill predators exhibit  
971 trophic plasticity and can increase their consumption of fish in years of lower krill availability (e.g.  
972 crabeater seals; Huckstadt et al. 2012a), although the extent to which this plasticity can relieve the  
973 dependence on krill remains unknown. Sub-Antarctic King penguins (*Aptenodytes patagonicus*) have  
974 extended their distribution southwards, recently being recorded for the first time at King George  
975 Island (Juarez et al. 2017). Increasing westerly wind intensity has benefitted wandering albatrosses  
976 (*Diomedea exulans*), by increasing their foraging speeds and reducing trip length, thus enhancing  
977 their foraging efficiency and breeding success (Weimerskirch et al. 2012).

## 978 2.5. The WAP benthic food web

979 Benthic communities along the WAP are sensitive to variability in physical and biogeochemical  
980 forcing, because many organisms are sessile and therefore unable to migrate. Benthic responses to  
981 ocean warming depend on organisms' abilities to adapt or acclimate to altered conditions. Antarctic  
982 benthos have a reduced capacity to adapt compared to lower-latitude populations, due to their low  
983 production rates of novel genetic material that enhance survival, which arise from longer generation  
984 times and production of fewer larger eggs without an increase in mutation rate or population size  
985 (Arntz et al. 1994; Higgs et al. 2009; Johnson et al. 2001; Peck 2018). Geneflow between Antarctic  
986 populations is also slower than for temperate or tropical populations due to relatively high levels of  
987 protected development and proportionally fewer species using pelagic larval dispersal (Arntz et al.  
988 1994; Peck 2018; Hoffman et al. 2011, 2012). For species that do use pelagic dispersal, rising ocean  
989 temperatures increase larval development rates, thus shortening the larval phase substantially (Peck  
990 2016, 2018). This reduces dispersal distances and increases isolation between populations, as well as  
991 altering the timings of reproductive cycles in relation to key environmental events (Bowden et al.  
992 2009), such that larval success may decline significantly due to phenological mismatches as warming  
993 proceeds.

994 Given limited rates of adaptation, Antarctic benthos need sufficient phenotypic plasticity to  
995 acclimate to altered conditions and survive the projected climate change in coming decades (Peck  
996 2011). Antarctic fish (Bilyk and DeVries 2011) and invertebrates (Morley et al. 2016; Peck 2018; Peck  
997 et al. 2009, 2014) have very limited tolerance to warming in laboratory-based experiments,  
998 indicating that acclimation to elevated temperature is poor in Antarctic species (Peck et al. 2014).  
999 Thermal tolerances are influenced by a number of different species-specific factors (Clark et al.  
1000 2017), including heat shock responses to warming (Clark and Peck 2009; Clark et al. 2008), and upper  
1001 temperature limits being set by accumulation of toxic metabolic end-products (Heise et al. 2007),  
1002 limitation of energy reserves (Peck 2018; Peck et al. 2014), and temperature sensitivity of critical  
1003 enzymes (Clark et al. 2016). In general, the rate of oxygen supply to tissues (Pörtner and Farrell  
1004 2008; Pörtner et al. 2012) does not exert a major limitation on thermal tolerance (e.g. Devor et al.  
1005 2016). The first *in situ* warming experiment in the Southern Ocean, conducted at Rothera, showed  
1006 that growth of biofouling species was significantly faster at 1°C above ambient than at ambient  
1007 (Figure 15) and this was attributed to factors including more efficient protein synthesis and faster  
1008 processing of food allowing greater nutrient intake in a summer season (Ashton et al. 2017). Mixed  
1009 results from +2°C treatments likely indicate that growth of some species was restricted by their  
1010 temperature limits.

1011 Benthic community structure is strongly influenced by ice dynamics along the WAP. Whereas sea ice  
1012 organic fluxes are an important food source for the benthos, solid ice can have a devastating effect  
1013 by removing a significant proportion of macro- and meiofauna from the seabed (Peck et al. 1999;  
1014 Lee et al. 2001). Iceberg impacts can be very frequent in shallow waters along the WAP (Brown et al.  
1015 2004), and ongoing increases in iceberg scour driven by glacial retreat, receding ice shelves and an

1016 overall decline in fast ice have caused a marked drop in biomass of shallow benthic fauna in Ryder  
1017 Bay, Adelaide Island (Barnes and Souster 2011). This is expected to continue, and potentially  
1018 intensify in the coming decades (Barnes 2015; Smale et al. 2008). In Potter Cove, South Shetland  
1019 Islands, increased sedimentation from a retreating glacier was the most important factor driving  
1020 sudden shifts in nearby benthic assemblage composition with unexpectedly rapid loss of diversity  
1021 and biomass (Sahade et al. 2015; Torre et al. 2017). Contrary to the adverse effects of ice scour and  
1022 ice-derived sedimentation, the retreat of coastal glaciers and disintegration of ice shelves along the  
1023 WAP has opened up new ocean areas for pelagic productivity and benthic ecosystem development  
1024 (Peck et al. 2010). The loss of benthic carbon storage caused by increased iceberg scour during  
1025 glacial retreat and ice shelf disintegration is significantly outweighed by the increase in carbon  
1026 storage resulting from increased primary production and benthic biomass, such that these ice losses  
1027 lead to a substantial net increase in carbon drawdown to the seabed (Barnes 2015, 2017; Barnes et  
1028 al. 2018). Glacial retreat has also opened up newly ice-free areas in Potter Cove, including a new  
1029 island, which have been colonised by communities exhibiting high diversity, biomass and a complex  
1030 structure at rates far exceeding previously observed or predicted rates in Antarctic benthos (Lagger  
1031 et al. 2017a, b). Macroalgal forests can colonise recently ice-free hard substrates (Campana et al.  
1032 2018; Quartino et al. 2013), and may expand further in the northern WAP in future as more frequent  
1033 ice-free winters and early spring fast-ice disintegration are expected to increase the annual light  
1034 budget (Deregibus et al. 2016). Bacterial groups that dominate in sediments enriched with  
1035 macroalgal detritus (e.g. Proteobacteria, Bacteroidetes, Planctomycetes and Verrucomicrobia) would  
1036 also become increasingly important with continued macroalgal expansion (Abele et al. 2017; Pasotti  
1037 et al. 2015). The net effect of ongoing ice changes for benthic communities along the WAP will  
1038 depend on water depth and proximity to glaciers and/or ice shelves, and their effect on iceberg  
1039 scour, sedimentation and light availability. Results from Potter Cove show that benthic ecosystem  
1040 responses may be non-linear and particularly rapid, intense and heterogeneous in fjordic systems.  
1041 Throughout the coastal WAP, longer-term losses of glaciers and ice shelves may reduce ice scour and  
1042 sedimentation significantly, increasing benthic carbon drawdown substantially, but the timing of  
1043 these changes is unknown.

1044 Invasive species occur on the WAP shelf as a result of larval dispersal and anthropogenic vectors  
1045 such as ship ballast water and hull biofouling (Clayton et al. 1997; Hughes and Ashton 2017; Lee and  
1046 Chown 2009). The long-term warming and sea ice trends are altering the natural barriers to species  
1047 invasions along the WAP, by dampening the effect of sea ice cover in reducing dispersal and killing  
1048 potential invasives, by increasing the coverage of year-round ice-free shallow benthic habitats, and  
1049 by weakening the temperature limitation of biological processes in warmer-water species. These  
1050 trends combined with increasing ship traffic are likely to promote the import and success of  
1051 invasives along the WAP, with potential for major ecosystem disruption, although the timing,  
1052 magnitude and impact of these invasions is not known.

## 1053 2.6. Ecosystem responses to ocean acidification

1054 Ocean acidification is expected to be particularly pronounced and to occur earlier in the Southern  
1055 Ocean, which absorbs more than 40 % of global anthropogenic CO<sub>2</sub> (Fletcher et al. 2006; Orr et al.  
1056 2001), than in other ocean regions (Feely et al. 2009; McNeil and Matear 2008; Orr et al. 2005).  
1057 Whilst statistically significant trends in inorganic carbon and pH have not yet been detected at the  
1058 WAP (Hauri et al. 2015), aragonite  $\Omega$  close to 1 has recently been documented in the coastal WAP  
1059 during winter (Jones et al. 2017), making aragonitic organisms susceptible to small changes in pH.  
1060 Decadal enrichment in inorganic carbon and acidification have been documented in the Drake  
1061 Passage to the north (Hauri et al. 2015; Takahashi et al. 2014), suggesting that this mechanism may  
1062 have significant ecosystem consequences along the WAP in future.



1063 Ocean acidification has the potential to impact on WAP phytoplankton communities, as experiments  
1064 from the Ross Sea have shown a shift from the small haptophyte *Phaeocystis antarctica* or pennate  
1065 diatoms at low CO<sub>2</sub> to large centric chain-forming *Chaetoceros* diatoms at elevated CO<sub>2</sub> levels (Tortell  
1066 et al. 2008; Feng et al. 2010). These findings were supported by laboratory studies that suggest  
1067 diatoms may have a competitive advantage over other taxa at elevated CO<sub>2</sub> (Chen and Gao 2004;  
1068 Sobrino et al. 2008; Wu et al. 2010). An acidification-driven shift towards larger diatoms would act  
1069 against the proposed shift towards smaller diatoms, haptophytes and cryptophytes driven by  
1070 changing ice distributions and freshwater inputs (e.g. Hernando et al. 2015; Rozema et al. 2017a;  
1071 Schofield et al. 2017). As such, the phytoplankton response to competing physical and biological  
1072 forcings along the WAP could vary significantly over time and space, compounding variability in the  
1073 forcings themselves. Shifts in phytoplankton species composition could have significant  
1074 consequences throughout the food web due to different feeding preferences of the major  
1075 zooplankton taxa and their consumers.

1076 The effects of ongoing atmospheric CO<sub>2</sub> uptake and ocean acidification on polar zooplankton are not  
1077 well understood. To the north of the WAP in the Scotia Sea, live pteropods (*L. helicina*) showed signs  
1078 of shell dissolution in a region undersaturated with aragonite (Bednaršek et al. 2012). Conversely,  
1079 recent evidence for *L. helicina* from the Arctic repairing their shells after mechanical and dissolution  
1080 damage suggests that these pteropods may be more resilient to ocean acidification than previously  
1081 thought (Peck et al. 2018). *E. superba* in the WAP region have been shown to increase their feeding  
1082 and excretion rates under high CO<sub>2</sub> conditions, especially in the case of pregnant krill (Saba et al.  
1083 2012).

1084 Antarctic benthos are thought to be vulnerable to current and future ocean acidification, because  
1085 many have calcified skeletons that use up a greater proportion of the organism's energy budget than  
1086 lower-latitude species (Watson et al. 2017), as well as low physiological rates and a limited ability to  
1087 resist environmental change in general. Research on the capacity of Antarctic benthos to acclimate  
1088 to lowered pH is conflicting, with some studies showing poor capacities in certain organisms (e.g.  
1089 Schram et al. 2016), whilst most studies demonstrate little effect of lowered pH, even on early  
1090 stages (e.g. Catarino et al. 2012), and several studies demonstrate greater effects of temperature  
1091 than pH (Byrne et al. 2013; Cross et al. 2015; Kapsenberg and Hofmann 2014). Recent studies show  
1092 that although long acclimation periods are required, Antarctic benthos can acclimate to altered pH,  
1093 at least to end-century conditions, and acclimated organisms exhibit physiological and reproductive  
1094 performance similar to those in controls (Cross et al. 2015; Suckling et al. 2015; Morley et al. 2016).

### 1095 3. Overarching priorities and approaches for future work

1096 Whilst significant progress has been made in recent decades in understanding the functioning of the  
1097 WAP shelf ecosystem, its physical and biogeochemical drivers, the coupling between the ocean and  
1098 atmosphere, and how these interactions are changing over time, critical knowledge gaps remain.  
1099 Further elucidation is required regarding the relative importance of the different controlling  
1100 mechanisms and the interactions between these mechanisms, in order to develop a whole-system  
1101 understanding of the WAP shelf ecosystem and its response to ongoing changes in climate and the  
1102 physical environment over seasonal-to-decadal timescales. As sea ice dynamics exert such an  
1103 important control on ocean physics, chemistry and ecosystem functioning, a fundamental challenge  
1104 for the observational and modelling communities is to unravel the importance of long-term climate-  
1105 driven trends compared with large natural internal variability, and consequently the extent to which  
1106 the recent slow-down in warming and sea ice losses will persist against the background long-term  
1107 trend. This challenge is a highly active area of research for the international community (Reid and  
1108 Massom 2015; Reid et al. 2018), but will ultimately require longer time series of satellite and in situ  
1109 ocean and sea ice measurements, and an improvement in the performance of IPCC-class models for

1110 the forthcoming Coupled Model Intercomparison Project Phase 6 (CMIP6). Regional models can be  
1111 used to elucidate the important local-scale ice-ocean-atmosphere feedbacks modulated by relatively  
1112 small-scale processes (e.g. ocean eddies with scales of a few kilometers). However, given the known  
1113 dependence of WAP climate on remote processes (e.g. ENSO, and its interaction with the SAM),  
1114 these models would need to take reliable boundary conditions from global climate/Earth System  
1115 models that reproduce both the low-latitude modes and their propagation to high latitudes. Such a  
1116 framework would allow us to increase the reliability of the relevant signals in the IPCC-class models  
1117 and improve our ability to project future changes in ice coverage and duration.

1118 Table 1 outlines the important discipline-specific research objectives in WAP marine science over the  
1119 next 2-10 years, and Table 2 outlines the key approaches and innovations required to address these  
1120 objectives. One of the major findings over the last three decades has been the importance of  
1121 physical oceanographic processes in modulating biological and biogeochemical processes, from  
1122 nutrient supply and phytoplankton dynamics to zooplankton distributions and foraging behaviour of  
1123 pelagic consumers. This degree and multilateral nature of physical control makes defining the  
1124 processes of oceanic water mass transport onshore, and its modification and vertical ventilation on  
1125 the shelf, a key priority. The importance of ice-ocean interactions necessitates full characterisation  
1126 of sea ice dynamics, glacial meltwater and other freshwater inputs, and their modulation of these  
1127 physical processes. Quantifying these physical dynamics will pave the way for projecting their  
1128 impacts on biogeochemical and biological processes throughout the entire food web. Pronounced  
1129 spatial heterogeneity and temporal variability on timescales of several days to decades necessitates  
1130 longer time series capturing the complete annual cycle and increased temporal and spatial  
1131 resolution of observations across the shelf, including under the sea ice. This increased resolution and  
1132 capability can be achieved by developing an observing system for the WAP shelf combining  
1133 traditional ship- and station-based approaches with novel technologies based on gliders,  
1134 autonomous underwater vehicles (AUVs), and mooring and high-frequency (HF) radar networks.

1135 HF radar measures ocean surface (upper 1 m) current velocities over hundreds of square miles  
1136 simultaneously. A shore-based three-site HF radar network deployed recently at the WAP provides  
1137 hourly surface current data over the entire Palmer Station region (Figure 16), and has been used  
1138 with penguin foraging data to identify the selection of foraging locations relative to mapped  
1139 convergent features over the Palmer Deep canyon (Kohut et al. 2014). These systems have proven to  
1140 be robust and cost-effective with many applications, and a significant opportunity exists to develop a  
1141 shelf-wide integrated system to define the regional surface ocean circulation, which is currently one  
1142 of the least understood aspects of the shelf circulation.

1143 Moorings have been deployed routinely along the WAP, providing high-frequency time-series  
1144 measurements year-round for over a decade. These moorings have been critical in documenting the  
1145 frequency and mechanisms of subsurface intrusions of modified CDW onto the continental shelf  
1146 (Martinson and McKee 2012; Moffat et al. 2009). A key limitation of moorings is that they are  
1147 typically unable to collect data near the surface, due to the presence of seasonal ice and icebergs  
1148 (Savidge and Amft 2009), and their spatial coverage is limited.

1149 Autonomous gliders (Sherman et al. 2001; Eriksen et al. 2001; Webb et al. 2001) are complementing  
1150 mooring measurements by providing high-resolution spatial measurements over the full shelf depth  
1151 (Carvalho et al. 2016; Carvalho et al. 2017; Couto et al. 2017; Brearley et al. 2017). These gliders are  
1152 capable of sampling over thousands of kilometres and spending months at sea, making them ideal  
1153 for maintaining a sustained presence and filling critical observational gaps between ship-board  
1154 surveys, research stations and mooring arrays, and at smaller spatial scales than are captured by  
1155 shipboard sampling (Venables et al. 2017). These systems are cost-effective, capable of carrying a

1156 range of sensors, and have been proven to be effective tools to leverage data collection across a  
1157 broad range of applications and ocean regions (Schofield et al. 2015).

1158 Powered AUVs have been used in the Southern Ocean for bathymetric, physical oceanographic and  
1159 biological surveys under and in the vicinity of sea ice (e.g. Brierley et al. 2002). Expanding the use of  
1160 such AUVs in the WAP region has the potential to provide a wealth of water column data from  
1161 under-ice environments. Most under-ice powered AUV missions to date have been conducted by  
1162 large complex platforms capable of under-ice navigation and advanced autonomous decision-  
1163 making, requiring ship support and making deployments expensive. Transitioning to smaller, less  
1164 complex and less expensive systems capable of sustained missions would increase the number and  
1165 scope of deployments at the WAP and elsewhere.

1166 Using autonomous technologies will be of particular value in improving observational coverage  
1167 during ice formation in autumn, the ice-covered winter period and the springtime transition from  
1168 winter into the ice-free phytoplankton growing season. These times of year are critically important  
1169 in regulating phytoplankton bloom dynamics, and other key ecosystem processes, yet remain  
1170 severely undersampled across all disciplines of WAP marine science. In future, real-time sampling  
1171 and data transfer using these technologies has the potential to inform predictions of key ecosystem  
1172 processes at the seasonal scale, e.g. phytoplankton bloom timing, magnitude and distribution based  
1173 on mooring- and glider-derived measurements/parameterisations of mixed layer depth and stability.  
1174 Upscaling the use of gliders and powered AUVs in the seasonally ice-covered WAP shelf environment  
1175 would require a robust and well-integrated system for under-ice navigation, using compact accurate  
1176 inertial navigation systems and/or acoustic telemetry networks that allow AUVs to triangulate their  
1177 position. Such systems would facilitate major innovations in future observational studies, for  
1178 example in elucidating the role of small- and meso-scale processes under the ice, the transports they  
1179 produce, and their effect on the larger-scale circulation, under-ice ecosystems and biogeochemical  
1180 cycles. Alongside technological developments in observational approaches, improvements in the  
1181 resolution of regional ocean circulation models and incorporation of realistic bottom topography are  
1182 required to fully resolve the most important physical drivers of the shelf ecosystem.

1183 Utilising the WAP shelf region as a natural laboratory or model system to understand the impacts of  
1184 climate and sea ice changes and the resultant physical oceanographic changes here and in other  
1185 marginal ice zone settings on phytoplankton dynamics, carbon and nutrient cycling, air-sea fluxes of  
1186 climate-active gases, and pelagic, benthic and microbial food webs requires an integrated approach.  
1187 Novel process-based experimental, technological and modelling approaches should be combined  
1188 with the long-running time-series and spatial measurements that form the backbone of our  
1189 knowledge of variability and change in the WAP marine system. Given pronounced heterogeneity  
1190 across the shelf, quantifying the importance of biological hotspots for the regional ecosystem and  
1191 biogeochemical cycling is a high priority. Detailed process studies and repeat sampling of these  
1192 hotspots, including along the sea ice edge and in the high-productivity fjords, will improve our  
1193 understanding of the conditions required to create these hotspots and their change over time.

1194 In such a highly coupled system, it is imperative to cross-cut disciplinary boundaries and characterise  
1195 the interactions between different system components, e.g. phytoplankton, zooplankton and  
1196 microbial dynamics in regulating biogeochemical cycling and the biological carbon pump, bottom-up  
1197 versus top-down predation control of zooplankton distributions, benthic faunal composition and  
1198 behaviours and benthic-pelagic nutrient fluxes. For example, further application of genomics,  
1199 transcriptomics and proteomics approaches have the potential to revolutionise our understanding of  
1200 microbial processes and interactions, and marine ecosystem functioning in general, by revealing vital  
1201 functions of phytoplankton and bacterioplankton, and identifying the many viruses infecting a range  
1202 of hosts. Combining a range of methodologies relevant to different processes, interactions and

1203 timescales will also be critical to making progress. Adopting such an interdisciplinary whole-system  
1204 approach offers perhaps the most promising opportunity for driving a step-change in our  
1205 understanding of the functioning of the WAP marine ecosystem and its response to, and role in,  
1206 ongoing climatic and environmental changes, making this a clear overarching priority for the  
1207 international community.

1208 Temporal and spatial coverage of data illuminating these physical-biological-biogeochemical  
1209 interactions can be augmented by maintaining and strategically enhancing the existing programs of  
1210 sustained observations, by adopting the essential ocean variables (EOVs; Constable et al. 2016; A  
1211 Framework for Ocean Observing, 2012) as a framework for an observing system for the WAP, and by  
1212 employing technological innovations to fill data gaps and increase resolution in time and space. In  
1213 addition to the discipline-specific approaches and innovations outlined in Table 2 and the physics-  
1214 based technologies detailed above, a number of sensor-based innovations can be employed across  
1215 disciplines and provide a more integrated perspective. For example, the utility of AUVs, gliders and  
1216 moorings can be expanded substantially by increasing the number and reliability of sensors capable  
1217 of measuring a range of physical, biological and chemical parameters (e.g. turbulence, fluorescence,  
1218 pCO<sub>2</sub>, nitrate). Equipping seals with small CTD tags has provided the extensive hydrographic MEOP  
1219 (Marine Mammals Exploring the Oceans from Pole to pole) dataset alongside complementary animal  
1220 behaviour data (Treasure et al. 2017), with significantly greater coverage than otherwise available.  
1221 Developing and deploying a greater range of sensors (e.g. fluorescence, dissolved oxygen etc.) would  
1222 facilitate more detailed sampling in ice-covered regions, near-shore embayments and over larger  
1223 spatial scales than ship-based efforts. Systematic deployment of multi-frequency acoustics on ships,  
1224 moorings and AUVs would allow us to estimate krill biomass and distribution, and the movement  
1225 and foraging behaviour of their pelagic predators, with unprecedented accuracy and coverage across  
1226 the shelf, including in the data-sparse southern region and under ice.

1227 In the context of physical controls on ecosystem structure and functioning, a major question to be  
1228 addressed is the extent to which organisms at all trophic levels can acclimate, adapt, migrate, and/or  
1229 change their behaviours, and the rates at which these processes can occur. Process studies and  
1230 manipulation experiments are required, focusing on the physiological profiles of the major species of  
1231 phytoplankton, bacterioplankton, viruses, zooplankton and benthic organisms across current and  
1232 future physical (temperature, salinity, mixing), chemical (macro- and micronutrients, pCO<sub>2</sub> and Ω)  
1233 and ecological (grazing pressure, viral infection) conditions, and therefore their ability to acclimate.  
1234 Rates of geneflow within and between populations are needed to quantify the capacity of benthic  
1235 and pelagic communities to adapt to altered environments. Top predators can be used as sentinels  
1236 of ecosystem change as their abundance and distributions reflect those of their prey. Reproductive  
1237 studies targeting major zooplankton taxa and higher trophic level organisms and in-depth studies of  
1238 the growth, diet and behaviours of juveniles would inform our assessments of recruitment success  
1239 and population dynamics of key species, and their responses to different conditions. Understanding  
1240 organisms' abilities to acclimate, adapt, migrate and/or change behaviours, and over what  
1241 timescales, will shed light on the resilience and sensitivity of different ecosystem components in the  
1242 face of pronounced environmental variability and change, and their response to multiple natural and  
1243 anthropogenic stressors.

1244 Direct human pressure on regional krill stocks is increasing as a result of expanding commercial  
1245 fishing activity, particularly in the northern WAP and adjacent open ocean, potentially reducing food  
1246 availability for krill predators (Trivelpiece et al. 2011). Management of this fishery by the Convention  
1247 on Conservation of Antarctic Marine Living Resources (CCAMLR) must be informed by our knowledge  
1248 of the foraging behaviour of krill predators, for instance using satellite tags and motion-sensing tags  
1249 to determine the critical locations and times of year for their feeding (Weinstein et al. 2017), so that  
1250 any overlap and potential competition with fishing activity can be minimised (Hinke et al. 2017b).

1251 Enhancements of our observational capacity and coverage across the WAP shelf must be  
1252 accompanied by continued development of modelling frameworks and capabilities to reveal the  
1253 most important mechanisms behind variability and change at all levels of the ecosystem. Improving  
1254 the resolution and scope of regional physical, biogeochemical and habitat or ecosystem models is a  
1255 particular priority, given large heterogeneity spatially and over daily to decadal timescales. Better-  
1256 constraining the rates of key processes, such as onshelf CDW transport, meltwater inputs, algal  
1257 growth and organic matter remineralisation, and the major fluxes of heat, nutrients, gases and  
1258 particles based on coherent high-quality observational data is needed for optimisation of model  
1259 input parameters and boundary conditions. Ongoing development of regional system models will  
1260 allow us to test the relative importance of different processes, elucidate the combined and/or  
1261 competing effects of multiple stressors, and explore the feedbacks between the drivers and  
1262 consequences of change amongst the different system components over a range of timescales.  
1263 Further, only once we can represent accurately the key processes and interactions at work in  
1264 modelling frameworks can we be confident in our projections of future changes in upper ocean  
1265 mixing, nutrient supply, primary production, ecosystem functioning and resilience, and air-sea  
1266 exchange of climate-active gases as the changes in sea ice extent, duration and atmospheric forcing  
1267 continue to evolve. Ultimately, better quantification of the processes and feedbacks at the WAP, and  
1268 their interactions with systems up- and down-stream in regional atmospheric and oceanic circulation  
1269 systems, will enable us to better-represent this Southern Ocean region in global climate models and  
1270 understand its role in contemporary global change.

#### 1271 4. Closing remarks

1272 We have demonstrated the importance of the WAP marine system due to pronounced variability  
1273 and change in the physical environment and ocean-climate interactions, strong biological and  
1274 biogeochemical consequences locally and regionally, and its utility as a natural laboratory for  
1275 examining how climate and sea ice changes might restructure ecosystems here and elsewhere. We  
1276 have summarised the state of knowledge regarding the key mechanisms and interactions regulating  
1277 ecosystem functioning and ocean-atmosphere coupling, as well as the changes underway and the  
1278 ecosystem responses and ocean-climate feedbacks. We also highlight the overarching priorities and  
1279 discipline-specific objectives for future research and present a vision for an observing system  
1280 capable of addressing these priorities and objectives. Working towards this vision will require further  
1281 improvements in integration, collaboration and co-ordination across national programs, projects and  
1282 initiatives, including sharing of expertise, standardisation of field, experimental and analytical  
1283 techniques, and optimisation of ship-time, station infrastructure and other resources. To this end,  
1284 SOOS has recently launched the Due South online database of ship- and station-based fieldwork  
1285 programs in the Southern Ocean (<https://data.aad.gov.au/duesouth/>), as well as establishing  
1286 regional working groups for the WAP and other regions. More effective engagement with other  
1287 research communities, such as the climate science, meteorology, glaciology, terrestrial  
1288 biogeochemistry and paleoclimate communities will be critical in defining the most important  
1289 external controls on the WAP marine environment, the key fluxes into and out of the system, and  
1290 the longer-term context of the changes underway.

1291 Improvements in data accessibility across disciplines and national programs is also called for,  
1292 following the examples of the Palmer LTER project (<http://pal.lternet.edu/data>), the KRILLBASE  
1293 database for zooplankton survey data (Atkinson et al. 2017) and the Surface Ocean CO<sub>2</sub> Atlas (Bakker  
1294 et al. 2016). Widespread adoption of similar data policies and practices across the international  
1295 community, and efficient linking of existing publicly available databases, for example using the  
1296 SOOSmap online data portal (<http://www.soos.aq/data/soosmap>), would be of significant benefit.  
1297 Co-ordinating and opening up all data sources is recommended as a significant scientific opportunity  
1298 for the international community working across multiple disciplines in the WAP region and beyond.

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1313 and MPM instigated and oversaw the project, and contributed substantially to the writing of the  
1314 manuscript. IRS, DKS, CM, LSP, DPC, DEB, CH, PDR, HWD, DA, JS, MAVL, CPDB, AGJB, JK, RS, ASF, SES  
1315 and HJV contributed significantly to the writing of the manuscript and the production of figures. All  
1316 authors have approved the version for submission.

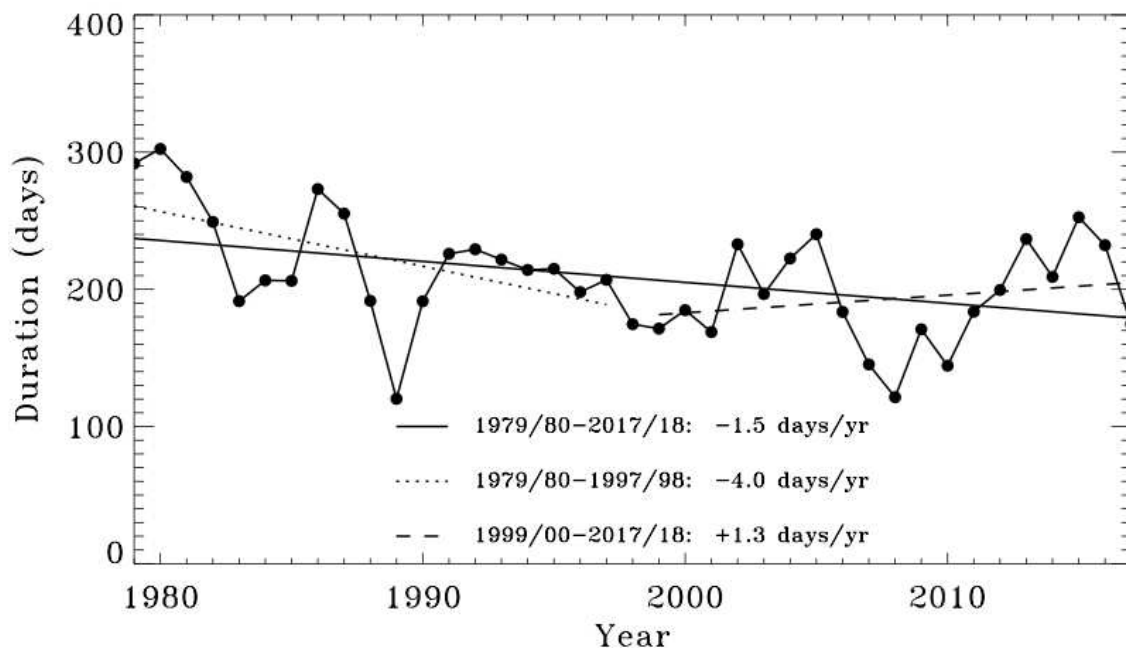
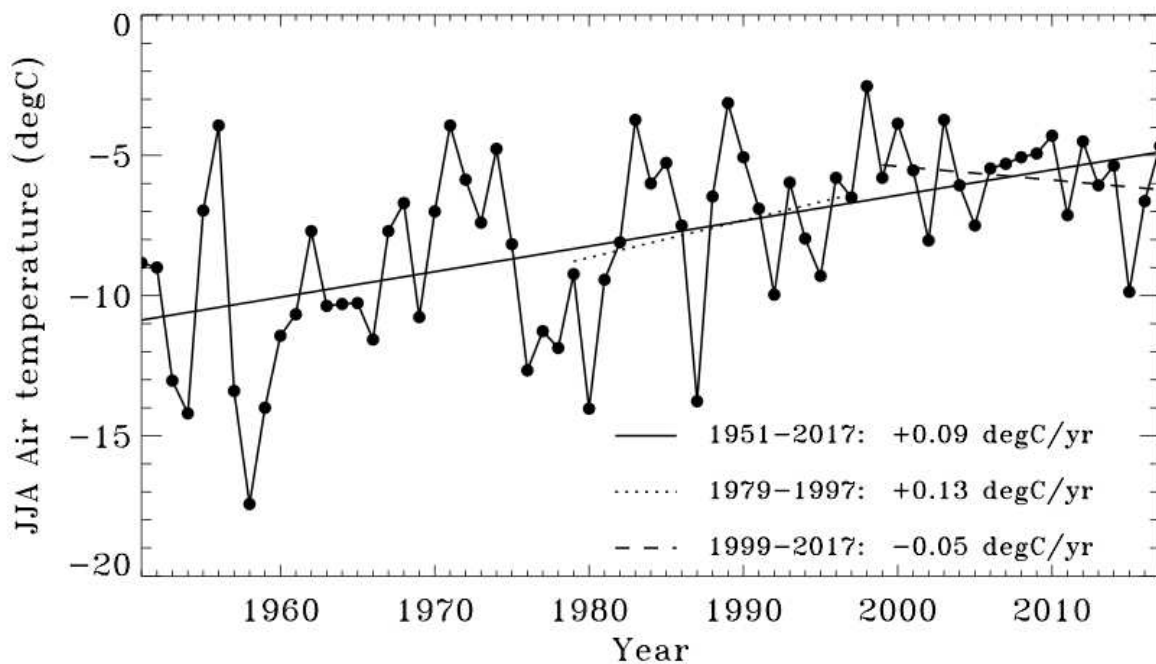
1317 Competing interests: There are no competing interests associated with this work.

1318 Declaration of interests: none

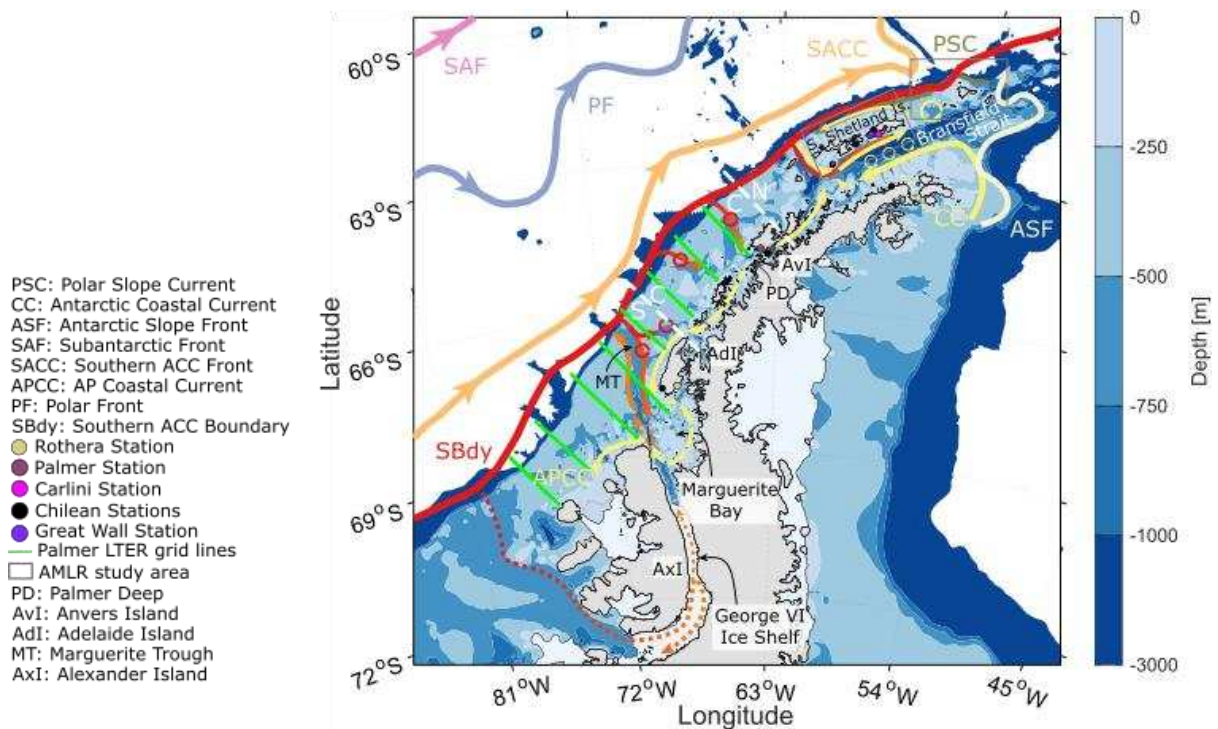
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1320 Figures

1321 Note: Figures 2-11 and 13-16 should be published in colour; Figures 1 and 12 should be black and  
1322 white.



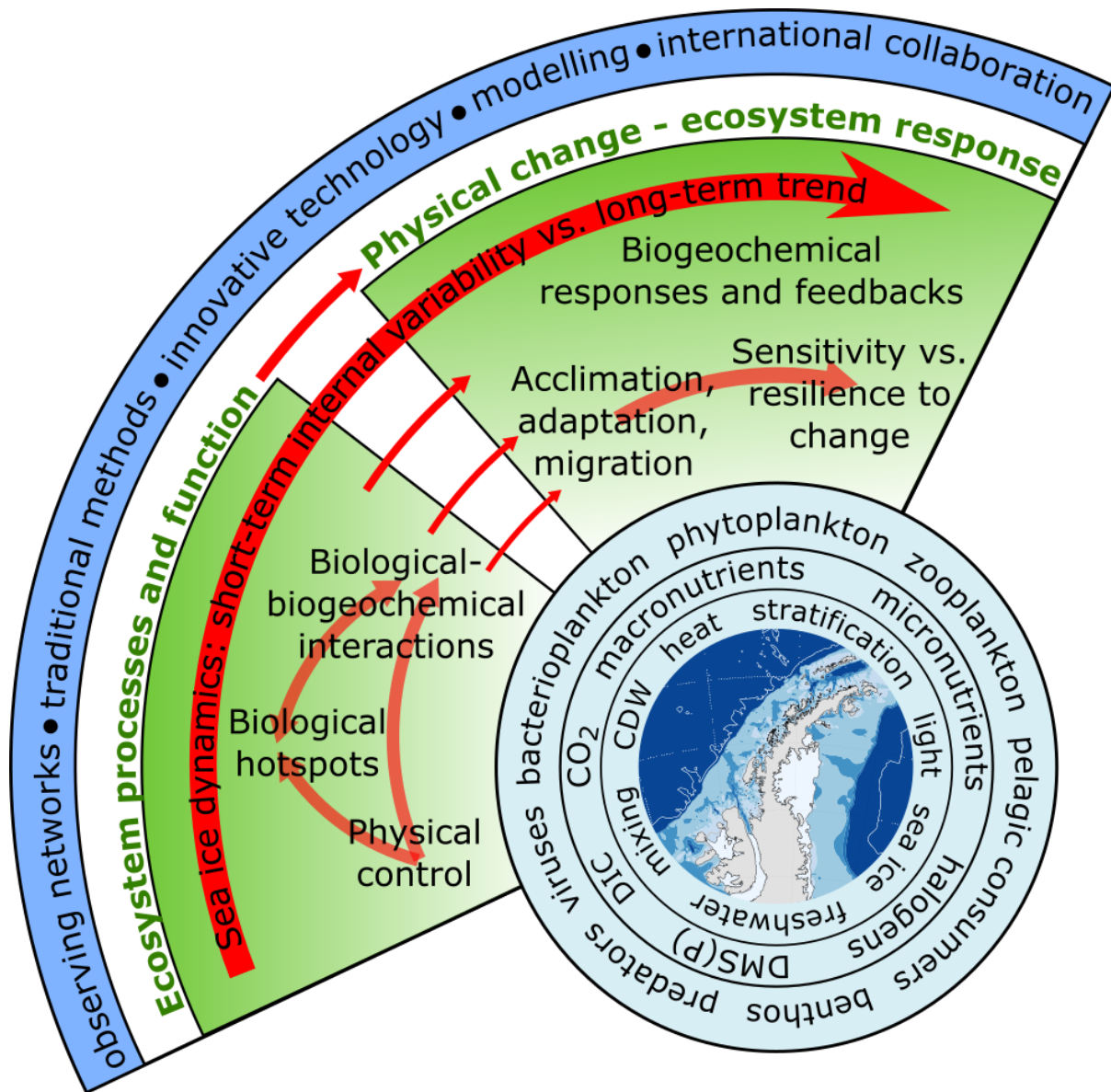
1325 Figure 1. (a) Trend in winter air temperature (June, July, August; JJA) as recorded at Faraday/  
1326 Vernadsky Station (65.4 °S, 64.4 °W) from 1951 to 2017. The long-term linear trend (solid line: 1951-  
1327 2017) is significant at the  $p < 0.001$  level, while the shorter-term trends (dotted: 1979-1997;  
1328 1999-2017) are not significant at the  $p < 0.1$  level. (b) Trend in the annual ice season duration  
1329 determined using the GSFC Bootstrap version 2 sea ice concentration time series from Nimbus-7  
1330 SMMR and DMSP SSM/I-SSMIS and methods described in Stammerjohn and Maksym (2017). The  
1331 trend was determined for the WAP continental shelf, extending from Anvers Island to Charcot  
1332 Island. The long-term trend (solid line: 1979-2017) is significant at the  $p < 0.05$  level, while the  
1333 shorter-term trends (dotted: 1979-1997; dashed: 1999-2017) are not significant at the  $p < 0.1$  level.



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Figure 2. Map of the WAP showing the major sustained research efforts represented, delineation of the northern, central and southern sub-regions referred to in the text (white dashed lines; N = northern sub-region, C = central sub-region, S = southern sub-region), and the major circulation and bathymetric features of the shelf system. Modified from Moffat and Meredith (2018).

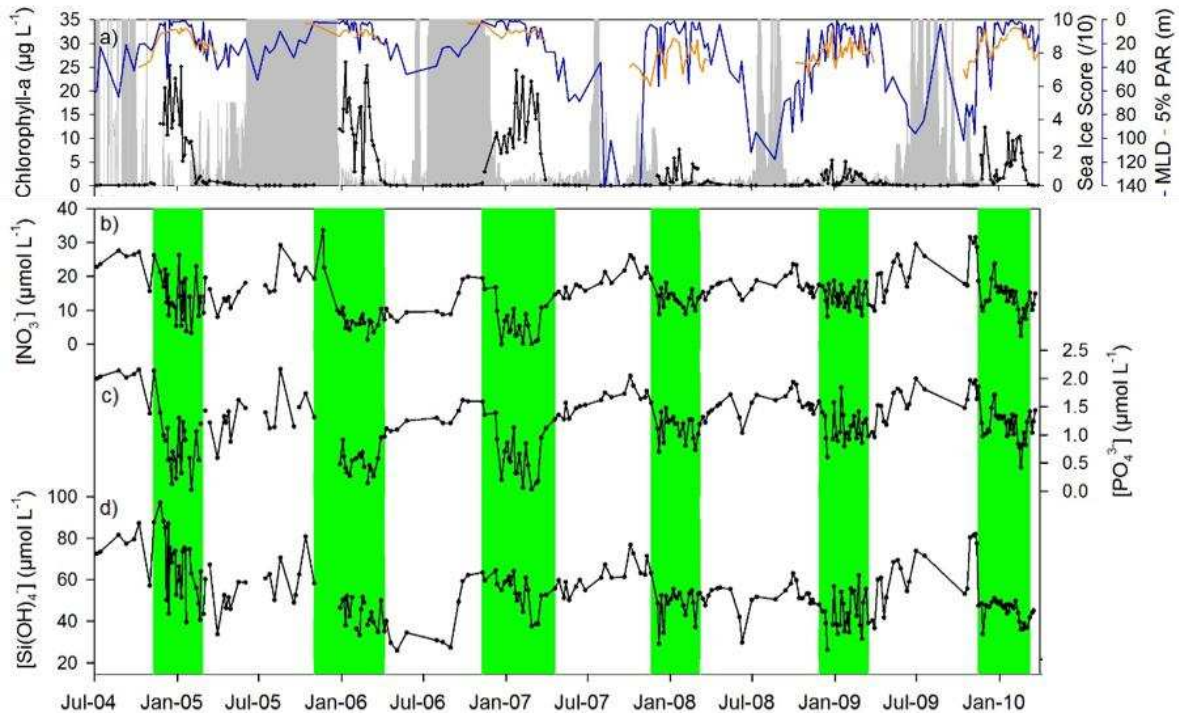




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1342 Figure 3: Infographic summarising the key components of the WAP marine system, the most  
 1343 important mechanisms and interactions in the context of the two overarching questions addressed  
 1344 in this paper, and the major priorities and approaches for future marine research at the WAP.

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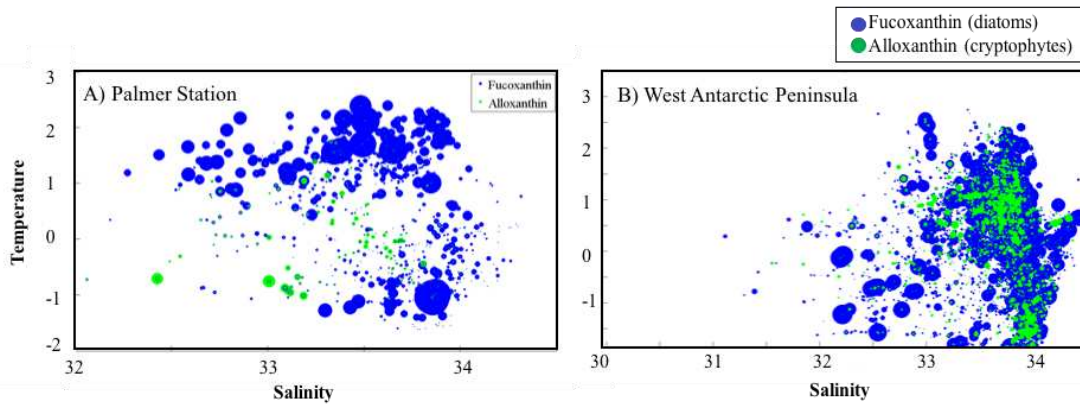


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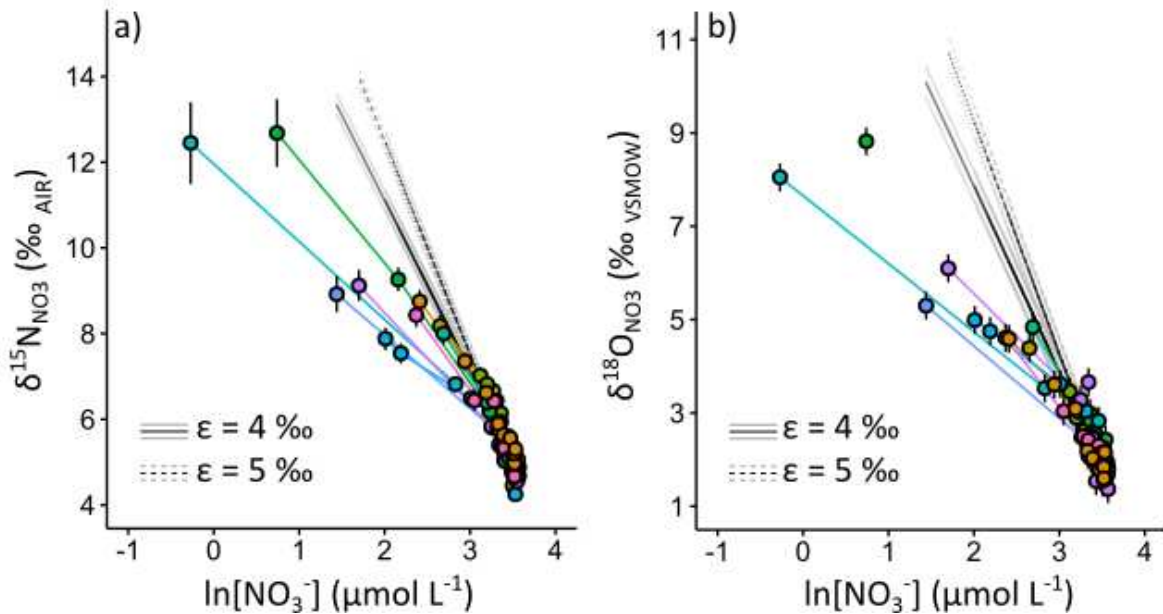
1348 Figure 4. Time-series data from RaTS, July 2004 to April 2010, showing that high sea ice winters lead  
 1349 to shallow mixed layers, high chlorophyll and strong nutrient drawdown, whilst low sea ice years  
 1350 lead to deeper mixing, lower chlorophyll and less nutrient drawdown. (a) sea ice score (grey shading;  
 1351 coverage normalised to ice type, out of ten where ten is full fast-ice cover), mixed layer depth (MLD;  
 1352 blue line; depth where  $\sigma = \sigma_{\text{surface}} + 0.05 \text{ kg m}^{-3}$ ), 5 % PAR depth (orange line; depth where  
 1353 photosynthetically active radiation is 5 % of its surface value), chlorophyll *a* concentration at 15 m  
 1354 (black line). Nutrient concentrations (b) nitrate, (c) phosphate, (d) silicic acid. Green shading depicts  
 1355 the period when chlorophyll *a* >1  $\mu\text{g L}^{-1}$ . Modified from Henley et al. (2017); sea ice, MLD, PAR and  
 1356 chlorophyll data from Venables et al. (2013).

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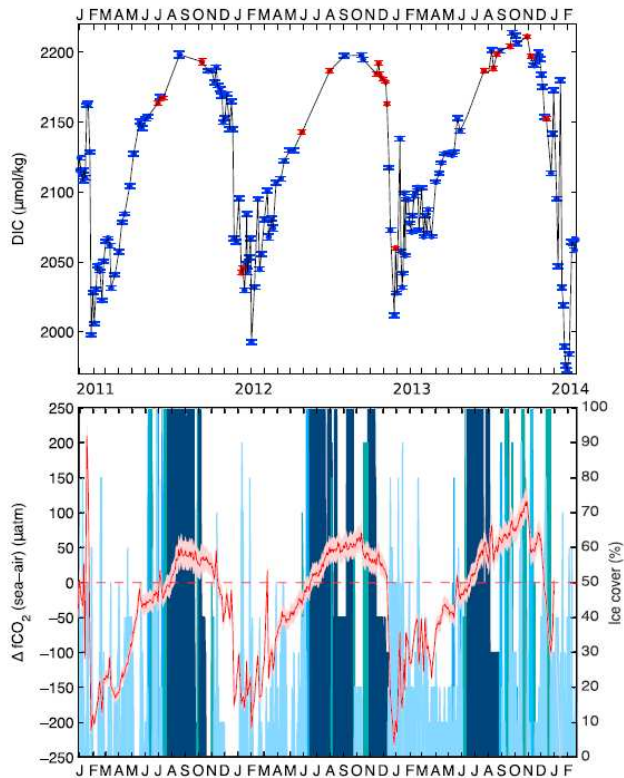
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Figure 5. The relative presence of diatoms (from fucoxanthin, blue) and cryptophytes (from alloxanthin, green) plotted in temperature-salinity phase space for (a) Palmer stations B and E, and (b) the Palmer LTER grid. The size of the circles indicates the relative concentration of chlorophyll *a* for discrete samples. Modified from Schofield et al. (2017).



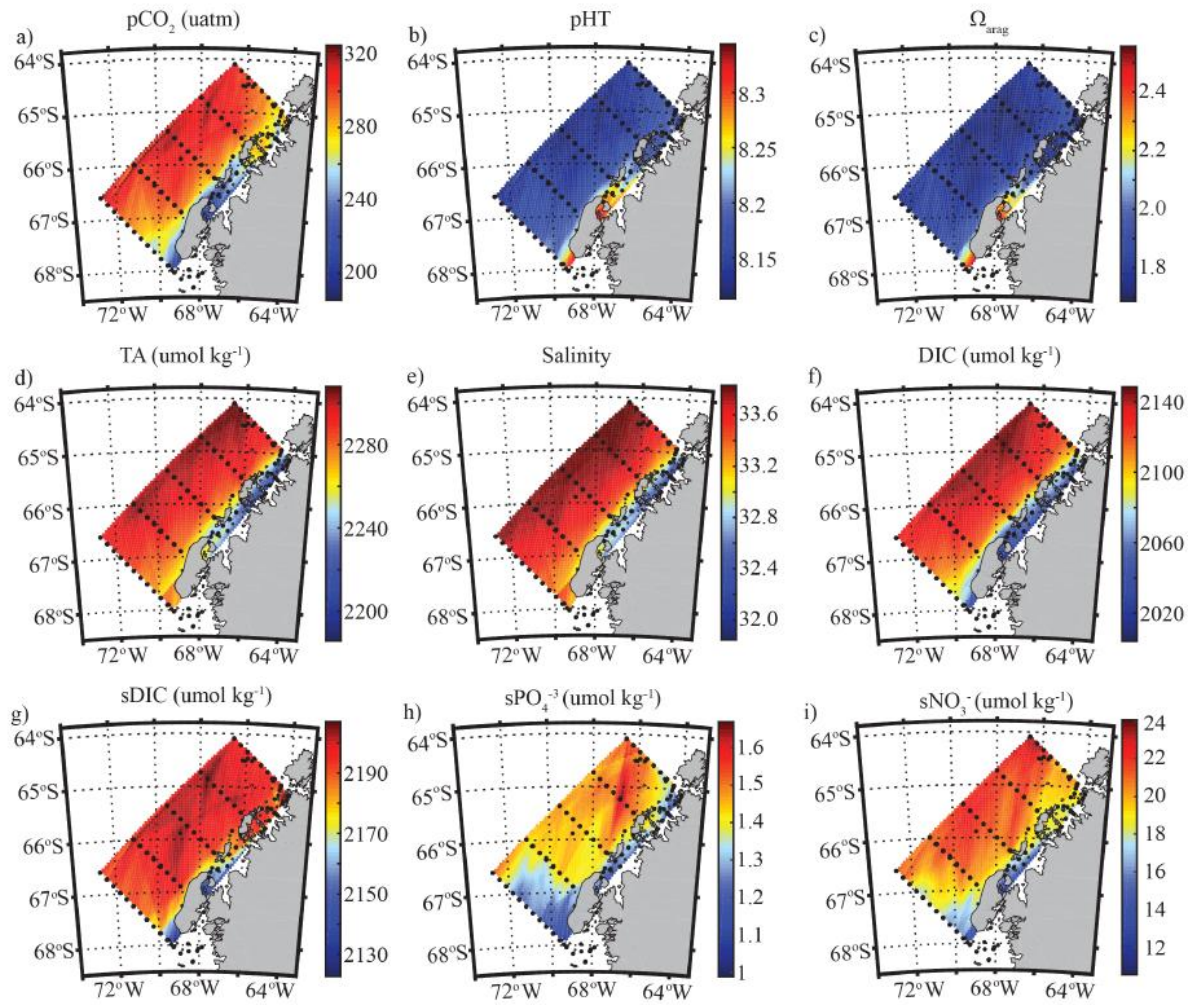
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Figure 6. Relationships between nitrate concentration and its (a) nitrogen and (b) oxygen isotope composition, compared to modelled relationships based on nitrate uptake alone with fractionation factors ( $\epsilon$ ) of 4 and 5 ‰ (solid and dashed black lines, respectively). Both  $\delta^{15}\text{N}$  and  $\delta^{18}\text{O}$  plotting below the modelled lines indicates remineralisation of organic nitrogen where nitrate uptake is high, and subsequent nitrification in the subsurface water column. Data point colours represent different stations. Modified from Henley et al. (2018).



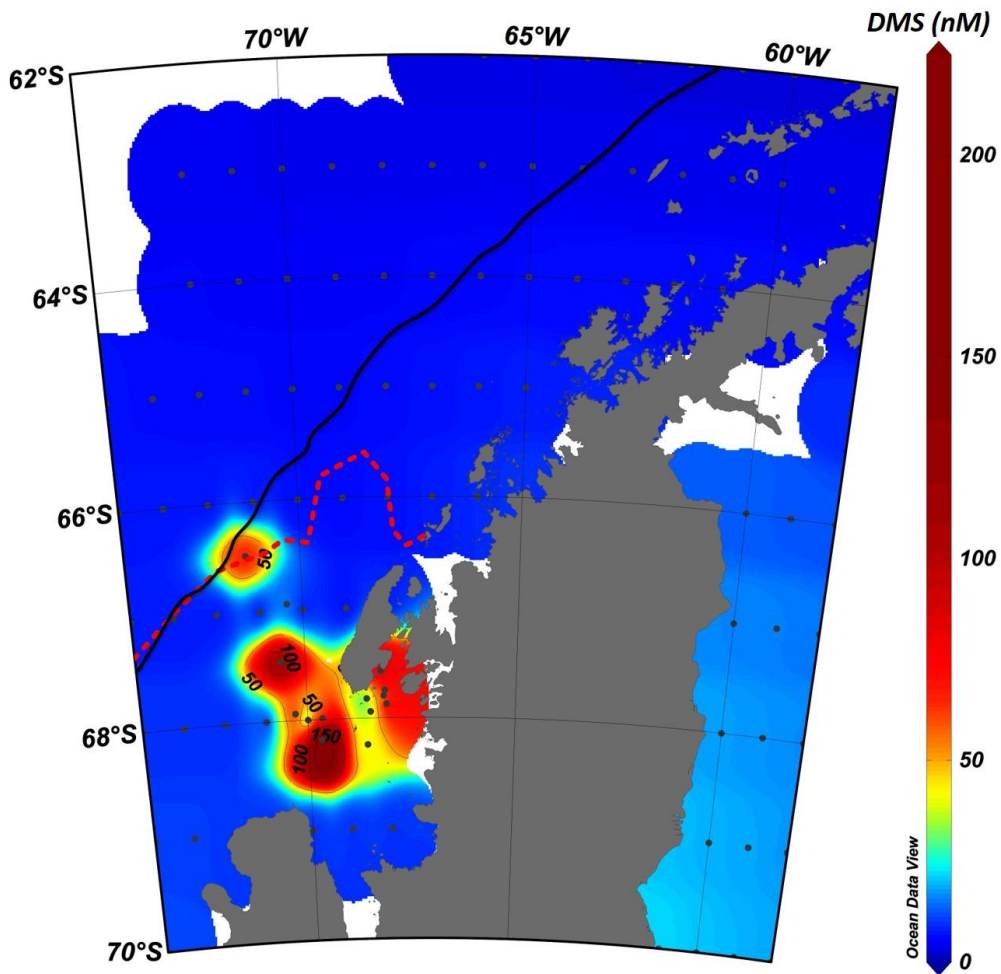
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1375 Figure 7. (a) Seasonal cycle of DIC from December 2010 to February 2014 at 15 m depth at RaTS sites  
1376 1 (blue) and 2 (red), both in Ryder Bay. Error bars are uncertainty (2SD) based on measurement  
1377 precision. (b) Red solid line shows the seasonal cycle of the difference in  $f\text{CO}_2$  between the sea and  
1378 air ( $\Delta f\text{CO}_2$ ), with the pink shaded region representing approximate 95 % confidence from uncertainty  
1379 analysis. Red dashed line shows  $\Delta f\text{CO}_2 = 0$ , where ocean  $\text{CO}_2$  concentration is in equilibrium with the  
1380 atmosphere.  $\Delta f\text{CO}_2 > 0$  during winter indicates supersaturated conditions and an efflux of  $\text{CO}_2$  to the  
1381 atmosphere;  $\Delta f\text{CO}_2 < 0$  during summer indicates undersaturated conditions and oceanic uptake of  
1382 atmospheric  $\text{CO}_2$ . Blue bars show percentage ice cover, with dark blue representing fast ice,  
1383 turquoise representing pack ice and light blue representing brash ice. Reproduced with permission  
1384 from Legge et al. (2015).



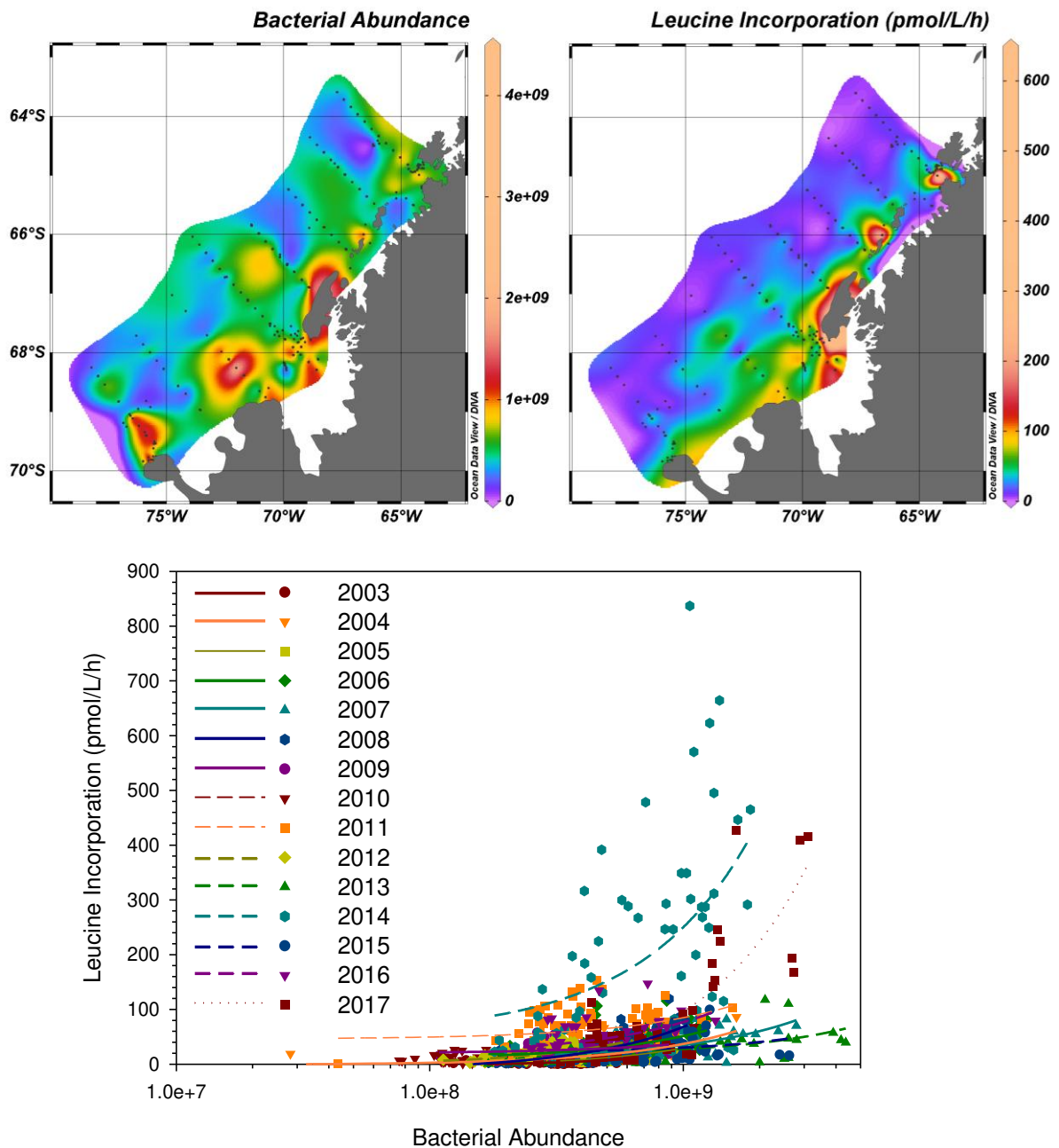
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1387 Figure 8. Summertime distribution of inorganic carbon system and other biogeochemical parameters  
1388 in surface water for the Palmer LTER grid for the period 1993 to 2012, showing onshore-offshore and  
1389 north-south gradients in carbonate chemistry, salinity and inorganic nutrients. Reproduced with  
1390 permission from Hauri et al. (2015).



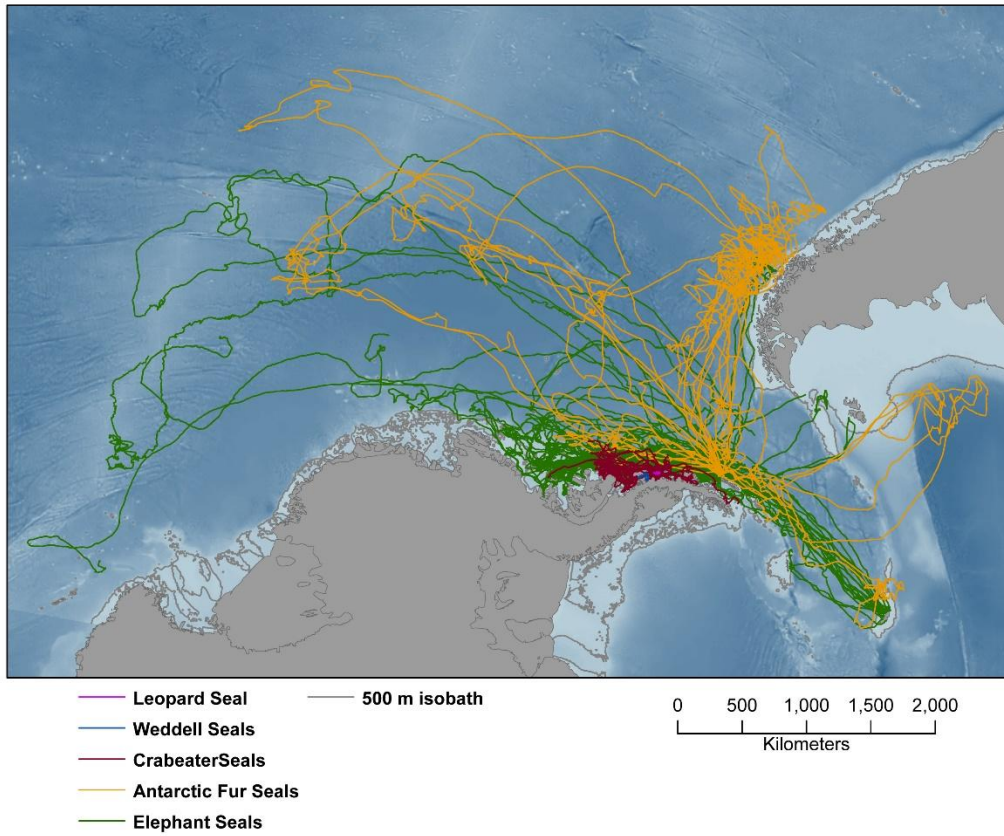
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1393 Figure 9. Surface DMS concentrations during cruise JR307 in January 2015 plotted on top of the 1x1  
1394 gridded January DMS climatology (Lana et al. 2011). JR307 data were calculated from filtered  
1395 DMS(P) values (Stefels et al. 2018). The black line depicts the shelf edge; the red dotted line  
1396 indicates the approximate position of the northern edge of the marginal ice zone during the second  
1397 half of December 2014, immediately preceding the cruise.



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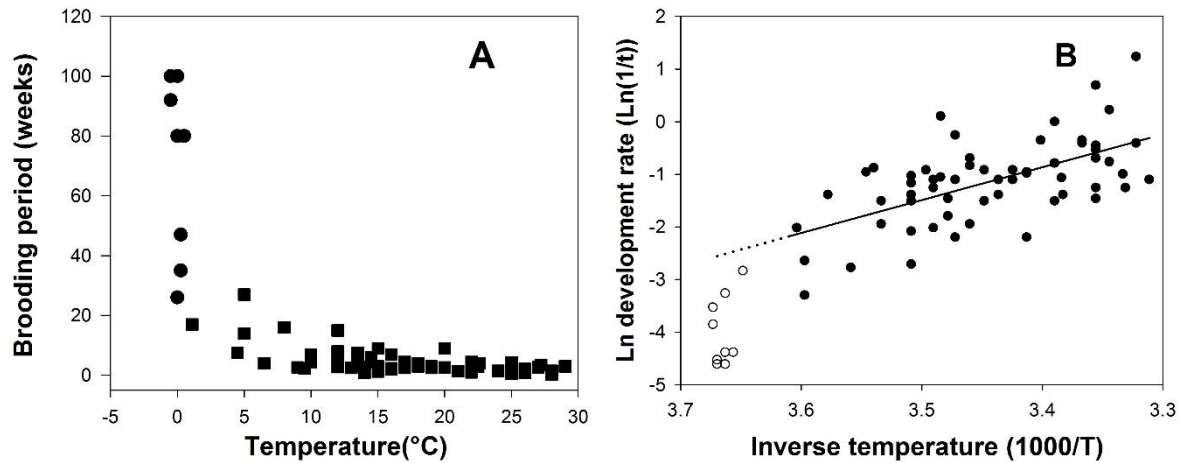
1400 Figure 10. Long-term averages (2003-2017) for January of both bacterial abundance (top left) and  
 1401 production (top right) in the surface ocean (maximum depth 10 m), showing intense spatial  
 1402 heterogeneity with higher abundance and production in inshore regions, and higher abundance  
 1403 further south. Lower panel shows strong variability in bacterial production with abundance for  
 1404 individual January cruises, as per legend. All linear regressions are statistically significant ( $p < 0.05$ ),  
 1405 except for 2012. These data were collected as part of the Palmer LTER project and are updated from  
 1406 Ducklow et al. (2012a).



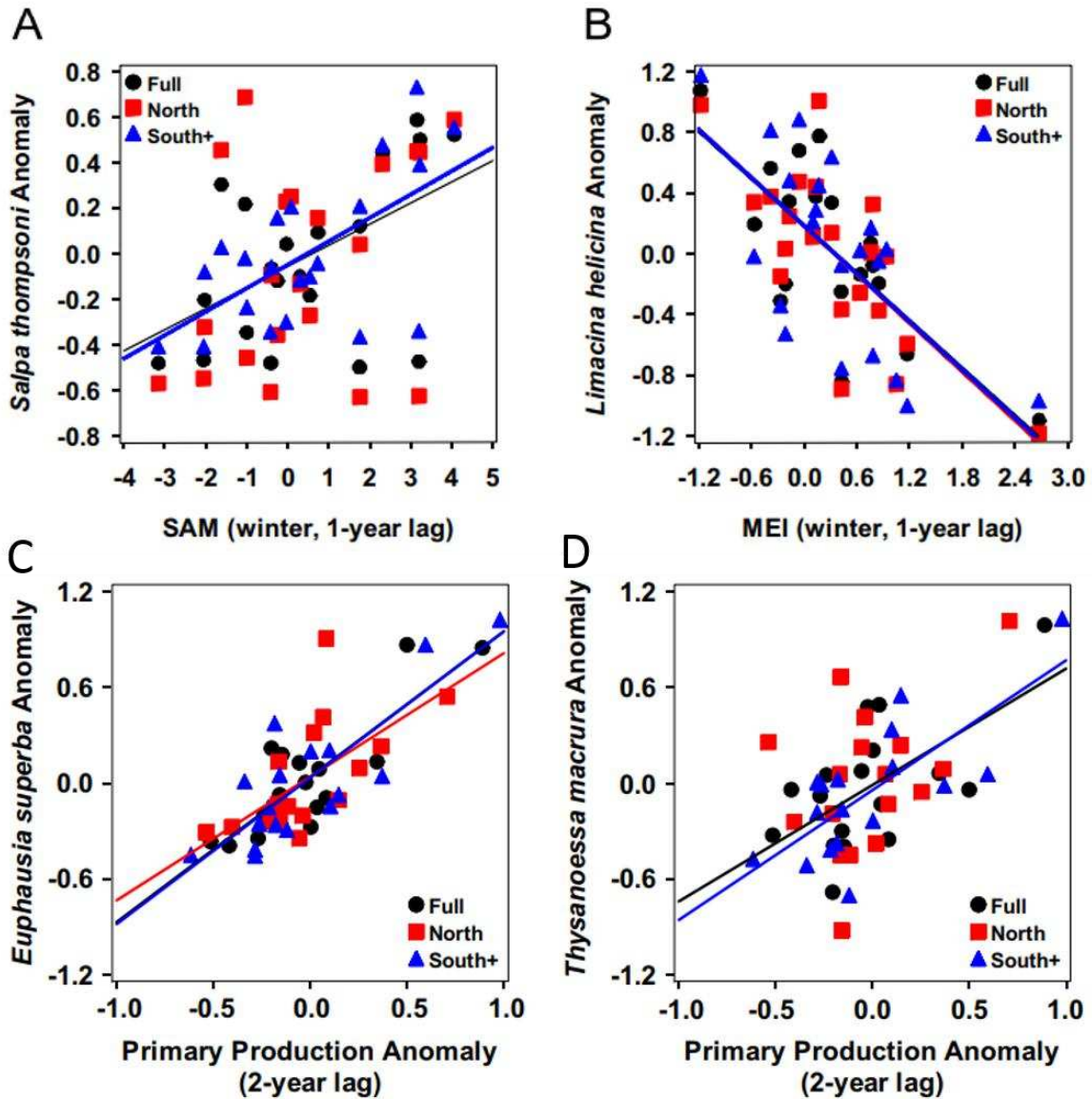
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1408 Figure 11. Comparison of the tracks of crabeater seals (dark red) (Burns et al. 2004), elephant seals  
 1409 (green) (Huckstadt et al. 2012b), Weddell seals (blue), leopard seals (purple) (Costa et al. 2010), and  
 1410 fur seals (yellow) (Arthur et al. 2017) over an annual cycle.



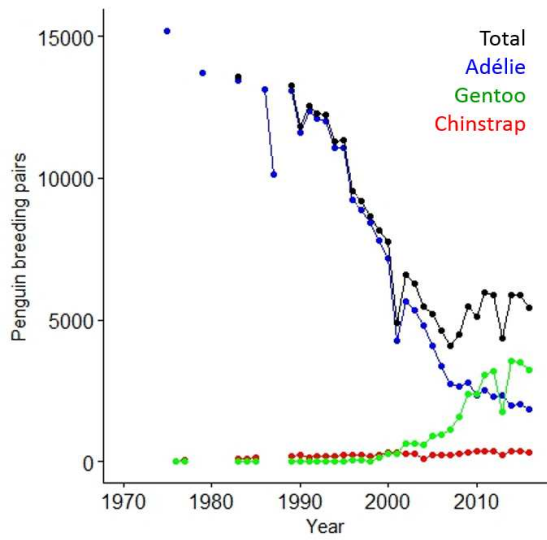


1411  
 1412 Figure 12. Brooding period and development rates of brooding marine gastropod snails at ambient  
 1413 temperatures for tropical to polar species. (a) Time from brood initiation to release (1/development  
 1414 rate) versus ambient temperature. In most cases release is of crawling juveniles, but for two  
 1415 Antarctic species, release is of veliger larvae and development time to juvenile is approximately  
 1416 double that of brooding per se (Peck et al. 2006b). Data shown for 68 gastropod species, nine of  
 1417 which live at temperatures around 0°C, is the full development period to juvenile. (b) Arrhenius plot  
 1418 of Ln developmental rate to juvenile stage for brooding gastropod molluscs. Fitted line is for  
 1419 temperate and tropical species (filled circles; brooding rate (1/weeks) =  $20.37 - 6.25 \cdot 1000/T$ ;  $r^2 =$   
 1420  $0.36$ ,  $F = 32.4$ ,  $58 \text{ df}$ ,  $p < 0.001$ ); Antarctic species fall significantly below. Reproduced from Peck  
 1421 (2018).  
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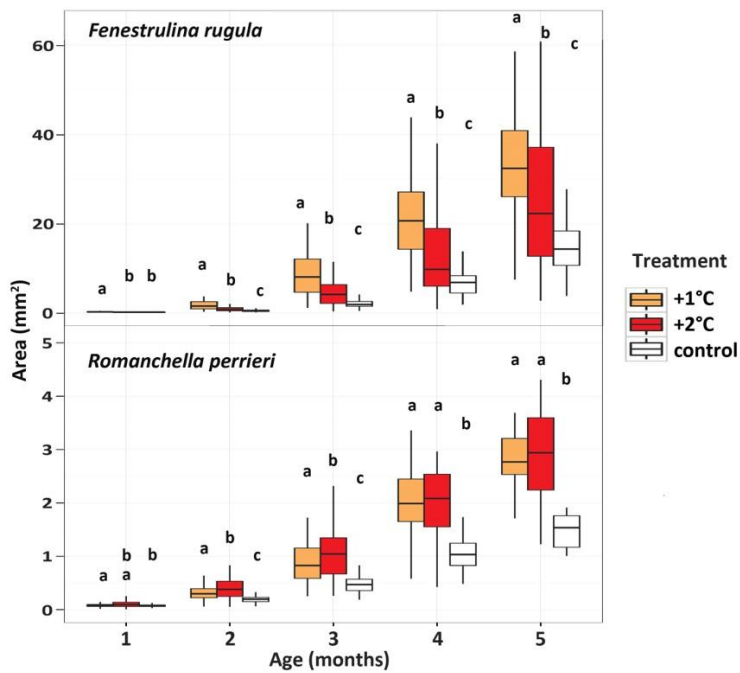
Figure 13. Relationships between annual abundance anomalies of specific zooplankton taxa on the Palmer LTER grid, 1993-2013, and sub-decadal climate oscillations and annual abundance anomalies of primary production. (a) *Salpa thompsonii* and SAM winter index from the year prior, (b) pteropod *Limacina helicina* and multivariate ENSO index (MEI) from winter the year prior, (c) krill *Euphausia superba* and primary production from two years prior, (d) krill *Thysanoessa macrura* and primary production from two years prior. Full refers to the full LTER grid, North refers to the northernmost three sampling lines, which are referred to as the central WAP sub-region in this paper, and South+ refers to the southernmost five sampling lines, referred to as the southern WAP sub-region in this paper (Figure 2). Modified with permission from Steinberg et al. (2015).



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1435 Figure 14. Population census data for Adélie, chinstrap and gentoo penguins in the Palmer Station  
 1436 region, 1975-2016. Updated from Ducklow et al. (2013).

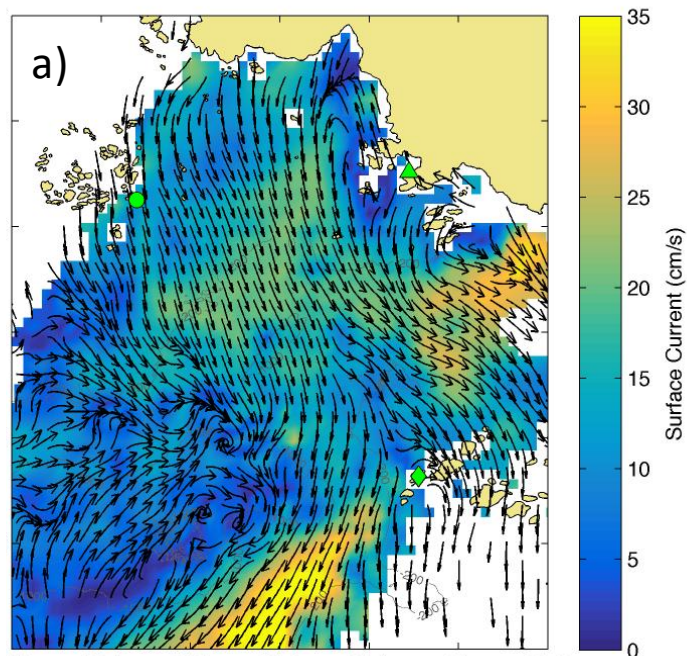
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1439 Figure 15. Effects of in situ warming on the growth of common epifaunal marine invertebrates on  
 1440 Rothera Point, Adelaide Island. Panels show area covered by the spatially dominant bryozoan  
 1441 (*Fenestulina rugula*) and spirorbid (*Romanchella perrieri*) under warming (+1°C and +2°C) and  
 1442 control treatments, showing different growth rate responses between species. Data show the mean  
 1443 and interquartile range of panel surface area covered by a single colony (top) or individual (bottom).  
 1444 Different letters indicate significantly different areas per age ( $F_{(1,9)}$  with  $p < 0.01$ ). Modified from  
 1445 Ashton et al. (2017).

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1448 Figure 16. Hourly surface current map for the Palmer Station region for January 27, 08:00 GMT,  
 1449 2015. The HF radar sites located at Palmer Station (green triangle) and the Wauwermans (green  
 1450 diamond) and Joubin (green circle) island groups are also shown.

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