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- 1 Variability and change in the west Antarctic Peninsula marine system: research priorities and
- 2 <u>opportunities</u>
- 3 Sian F. Henley¹*, Oscar M. Schofield², Katharine R. Hendry³, Irene R. Schloss⁴, Deborah K. Steinberg⁵,
- 4 Carlos Moffat⁶, Lloyd S. Peck⁷, Daniel P. Costa⁸, Dorothee C. E. Bakker⁹, Claire Hughes¹⁰, Patrick D.
- 5 Rozema¹¹, Hugh W. Ducklow¹², Doris Abele¹³, Jacqueline Stefels¹¹, Maria A. Van Leeuwe¹¹, Corina P.
- 6 D. Brussaard¹⁴, Anita G. J. Buma¹¹, Josh Kohut², Ricardo Sahade¹⁵, Ari S. Friedlaender¹⁶, Sharon E.
- 7 Stammerjohn¹⁷, Hugh J. Venables⁷, Michael P. Meredith⁷
- 8 ¹School of GeoSciences, University of Edinburgh, James Hutton Road, Edinburgh, EH9 3FE, UK
- ²Department of Marine and Coastal Sciences, Rutgers University, 71 Dudley Road, New Brunswick,
 NJ 08901, USA
- ³School of Earth Sciences, University of Bristol, Queens Road, Bristol, BS8 1RJ, UK
- ⁴Centro Austral de Investigaciones Científicas, Bernardo Houssay 200 (9410), Ushuaia, Tierra del
- 13 Fuego, Argentina
- ¹⁴ ⁵Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, VA 23062, USA
- ⁶School of Marine Science and Policy, University of Delaware, Newark, DE 19716, USA
- ⁷British Antarctic Survey, High Cross, Madingley Road, Cambridge, CB3 0ET, UK
- ⁸Ecology and Evolutionary Biology Department, University of California Santa Cruz, 100 Shaffer Road,
 Santa Cruz, CA 95060, USA
- ⁹Centre for Ocean and Atmospheric Sciences, University of East Anglia, Norwich Research Park,
 Norwich, NR4 7TJ, UK
- ¹⁰Environment Department, University of York, Heslington, York, YO10 5NG, UK
- ¹¹University of Groningen, GELIFES, Nijenborgh 7, 9747 AG Groningen, The Netherlands
- ¹²Lamont-Doherty Earth Observatory, Columbia University, 61 Route 9W, Palisades, NY 10964, USA
- ¹³Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Am Handelshafen 12,
- 25 27570 Bremerhaven, Germany
- ¹⁴Royal Netherlands Institute for Sea Research, 1790 AB Den Burg, Texel, The Netherlands
- 27 ¹⁵Instituto de Diversidad y Ecología Animal, Universidad Nacional de Córdoba, Avenida Vélez
- 28 Sarsfield 299, 5000 Córdoba, Argentina
- ¹⁶Marine Mammal Institute and Department of Fisheries and Wildlife, Oregon State University,
- 30 Newport, OR 97365, USA
- ¹⁷Institute of Arctic and Alpine Research, University of Colorado, Campus Box 450, Boulder, CO
- 32 80309, USA
- 33
- 34 Corresponding author: s.f.henley@ed.ac.uk
- 35
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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 21st 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 winter (King et al. 2003; Vaughan et al. 2003). This has been accompanied by a significant decadal 79 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; Schmidtko 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).

Atmospheric and oceanic warming trends have been accompanied by strong changes in ice dynamics along the WAP, with the regional extent and duration of sea ice cover declining significantly since the late 1970s (Stammerjohn et al. 2012). Climate change appears more advanced in the northern region of the WAP as the warmer maritime climate moves southwards displacing the colder drier continental climate that dominated previously (Ducklow et al. 2007; Montes-Hugo et al. 2009). Substantial and widespread glacial retreat along the WAP has been attributed primarily to increasing 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
- assessing how changes in climate might restructure ecosystems here and in other polar regions
 where sea ice changes are underway or expected in future. This importance is one of the key
- 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
- 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 Argentinian-German research program at Dallmann Laboratory on Carlini Station focusing on Potter 163 164 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. Chilean base Yelcho on Doumer Island was reopened in 2015 and there are plans to reopen Base 167 Carvajal on Adelaide Island to complete a latitudinal transect from King George Island to Adelaide 168 169 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
- 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
- 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:
- 1) What are the key mechanisms and interactions regulating ecosystem functioning and ocean-atmosphere coupling along the WAP shelf?
- 192 2) How is the WAP shelf environment changing and what are the ecosystem responses to and ocean-climate feedbacks on the changes underway?
- 194 We take a whole ecosystem approach and consider the full range of dynamics and interactions from
- 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 modified CDW to the surface layer are small (on average $\sim 1 \text{ W/m}^2$), with stronger fluxes observed in 238 239 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

The WAP shelf is a productive marine ecosystem, where primary production varies significantly in 254 255 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 exposed ocean surface (Moline and Prézelin 1996; Smith and Stammerjohn 2001). There is a strong 261 productivity gradient with high productivity (~1000 mg C m⁻² d⁻¹) inshore compared with offshore 262 waters (~100 mg C m⁻² d⁻¹) (Vernet et al. 2008). Seasonal satellite studies and in situ measurements 263 show that net community production peaks first offshore and follows the inshore retreat of the sea 264 265 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 μ m) 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_2 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
- can also play an important role in seeding the pelagic community. Primary production rates in
- Antarctic sea ice are highly variable, ranging from 0.5 to 1250 mg C m⁻² d⁻¹ (Arrigo 2017), and
- reaching maxima in spring and summer, when ice algae can contribute up to 50-60 % of total

- primary production in a given area (e.g. McMinn et al. 2010). The direct coupling between sea ice
- 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
- under-ice algal blooms (Lizotte 2001), although differences in species composition between sea ice
- and water column communities have been documented (e.g. Riaux-Gobin et al. 2011). The timing
 and pulse size of release act as strong controls on the fate of sympagic (ice-associated) algae (Selz et
- 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).

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
- chlorophyll increased from ~5 μ g L⁻¹ to ~500 μ g L⁻¹ from September to December 2014 in land-fast
- 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
- benthic ecosystems occurs at rates determined by its composition (Riebesell et al. 1991) and the
- dynamics of ice retreat (e.g. Norkko et al. 2007; Wing et al. 2012). Whilst organic carbon fluxes
- during ice-covered seasons are small compared to summertime fluxes along the WAP, sea ice algae
- are most relevant for local and episodic inputs preceding pelagic blooms, and in providing source
- material that is remineralised in winter to support detritus feeders (Mincks et al. 2005). Biogenic
- 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
- 25 de Mayo (Khim et al. 2007), and would be expected to increase dramatically during ice melt in
 spring. In the Ross Sea, tracer analysis shows that sea ice organic carbon fluxes can contribute >50 %
- 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
- ecosystems primarily by CDW intruding onto the shelf from the ACC (Klinck et al. 2004; Prezelin et al.
- 2000). Cross-shelf transport of CDW in deep glacially-scoured canyons increases the supply of
- 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 50 from sea is a small compared to CDW, and dominated by regenerated putrients (Frinist et al. 2015).
- from sea ice is small compared to CDW, and dominated by regenerated nutrients (Fripiat et al. 2015;
 Henley et al. 2017). Phosphate accumulates in sea ice (Fripiat et al. 2017), but its effect on water
- column phosphate and micronutrient inventories remains unclear (Hendry et al. 2017). A glacial
- source of silicic acid in basal meltwater has been demonstrated around Greenland (Hawkings et al.
- 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
- Trough were estimated as 0.18 ± 0.17 mmol NO₃ m⁻² d⁻¹ with a maximum of 0.56 mmol NO₃ m⁻² d⁻¹ (Harley et al. 2018). The mean symptotic particle situates for the Selected TSP with a maximum of 0.56 mmol NO₃ m⁻² 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 ± 1.79 mmol NO₃ m⁻² d⁻¹ (Pedulli et al. 2014), although the latter study
- 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 s 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

greatest following the initial retreat of sea ice, in agreement with heat fluxes (Brearley et al. 2017).
Whilst macronutrients are normally replete in WAP surface waters, intense biological drawdown by
phytoplankton can lead to transient nutrient limitation in coastal areas during some summers
(Henley et al. 2017). Interannual variability in CDW-derived nutrient supply is attributed to the
degree of wintertime mixing at Palmer Station (Kim et al. 2016), but this cannot fully account for the
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 ~13, indicative of diatom-dominated phytoplankton communities under bloom 375 conditions, and ~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 ≥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 composition (δ^{30} Si) of silicic acid from northern Marguerite Bay show strong silicic acid drawdown by 381 diatoms, interspersed with wind-driven mixing events that replenish the silicic acid reservoir from 382 383 underlying waters (Cassarino et al. 2017).

Nitrate, phosphate and inorganic carbon are progressively enriched in subsurface waters as CDW 384 moves across the shelf, and the stable nitrogen ($\delta^{15}N$) and oxygen ($\delta^{18}O$) isotope composition of 385 nitrate (Figure 6) and nutrient stoichiometry show that this is driven by local remineralisation of 386 387 organic matter and nutrient recycling in the upper water column (≤ 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 CO₂ 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).

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

The essential micronutrient iron is supplied to the WAP surface ocean primarily from glacial
 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 CO₂ fluxes

Carbonate chemistry and air-sea CO₂ fluxes along the WAP are influenced strongly by ocean physics 415 416 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 parameters have a strong, asymmetric seasonal cycle in surface waters with some year-to-year 418 419 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 (fCO_2) decrease sharply, 421 while pH and the saturation state (Ω) 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 CO₂ outgassing. Ryder Bay is a net sink for atmospheric CO₂ of 0.90-1.39 mol C m⁻² yr⁻¹ (Legge et al. 2015). 429 430 It remains unclear whether the WAP shelf as a whole is a net annual sink or source for atmospheric 431 CO₂.

432 Across the WAP shelf, carbonate system parameters show strong onshore-offshore gradients in the 433 upper ocean during summer, with low DIC and fCO₂ 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 fCO₂ 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 fCO_2 440 undersaturation and net CO₂ uptake during summers between 2005 and 2009, although there was a 441 region of fCO₂ supersaturation and net CO₂ release in the outer shelf region to the north of Anvers 442 Island (Ruiz-Halpern et al. 2014). Air-sea CO₂ fluxes in Bransfield Strait are highly variable, with surface waters switching between sink and source behaviour in consecutive summer seasons (Ito et 443 444 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_3 , HO_x , NO_x , Hg, CH_4 449 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 O₃ 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

through oxidation of the semi-volatile organic sulphur compound dimethyl sulphide by bromine
 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 (CHBr₃) 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 (CHBr₃) emissions are also reduced in low-ice low-productivity years (Hughes et al. 2012). 468

- 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. CH₂I₂, CH₃I)

- 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 ± 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 ± 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).

The role of sea ice in the sulphur cycle is complex and the processes involved are poorly quantified. Large phytoplankton blooms and spikes of DMS have been linked to melting sea ice (Trevena and Jones 2006), potentially caused by the release of large amounts of ice algae that produce the DMS precursor, dimethylsulphoniopropionate (DMSP) (Stefels et al. 2018). This is supported by extremely 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; Zemmelink 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 (Zemmelink 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 temporal variability is evident as abundance increases from winter minima of $2.0 \pm 0.8 \times 10^8$ cells L⁻¹ 529 to a maximum of ~2-3 x 10^9 cells L⁻¹ during summers with high phytoplankton biomass (Ducklow et 530 531 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 (~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

survey revealed that ~35 % of dissolved amino acids, and thus potentially a large proportion of the
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
- 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
- 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
- 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
- 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,
- 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
- 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
- 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

- dependent on winter sea ice coverage through provision of the ice algal food source and by setting
- 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
- across the southwest Atlantic (Atkinson et al. 2004). The important roles of other taxa, such as the
- salp *Salpa thompsoni* and the pteropod *Limacina helicina*, in WAP food web dynamics and
 biogeochemical cycling are increasingly being recognised (e.g. Bernard et al. 2012). In Potter Cove,
- 500 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 *propinguus* tend to dominate in terms of biomass (Garcia et al. 2016).
- WAP microzooplankton (<200 μm) assemblages are dominated by aloricate ciliates and athecate
 dinoflagellates (Calbet et al. 2005; Garzio and Steinberg 2013), with tintinnids associated with sea ice
 (Alder and Boltovskoy 1991). In summer, aloricate ciliate and tintinnid biomass increases with
 increasing latitude, with high microzooplankton biomass hot spots in productive inner-shelf areas to
 the south, such as Marguerite Bay (Garzio and Steinberg 2013). Microzooplankton biomass is
 positively correlated with chlorophyll *a* and particulate organic carbon (POC) concentrations (Garzio
 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; Sailley 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 (P. antarcticus) penguins move far away from their colonies in winter, with Adélie penguins 662 663 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 bonaernsis) 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 (Dewelte et al. 2016) Determine et al. 2016)
- 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 water column. WAP benthic ecosystems are characterised by a rich diversity of macro- and 699 700 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
- temperate and tropical species (Figure 12) (Peck 2016, 2018). Rates of activity and other processes
 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
- deferred maturity (longer generation times), which has been demonstrated in amphipods (Johnson
- et al. 2001), the bivalve *Adacnara nitens* (Higgs et al. 2009), and a range of other molluscs,
- brachiopods and echinoderms (Peck 2018). High-latitude Southern Ocean benthic organisms, such as
- fish (Leis et al. 2013), hyppolytid shrimps (Clarke 1985) and several starfish (Bosch and Pearse 1990),
- 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

- 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
- depths exceeding 300 m, and can produce sediment scours over 10 m deep (Lien et al. 1989),
- releasing large quantities of sediment-derived nutrients. Currents entrained by moving icebergs can
 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
- for some benthic species (Peck 2018). Mixing of the upper water column by icebergs, winds and
- currents will regulate the extent to which sediment-derived nutrients reach the surface ocean and
- 746 influence pelagic primary productivity.
- 747

2) How is the WAP shelf environment changing and what are the ecosystem responses to and ocean-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 penetration, and the salt and heat content of the surface ocean. On average, sea ice extent in the 762 WAP region varies between 1 and 6 x 10^5 km² over the annual cycle (Meredith et al. 2017). Alongside 763 764 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 substantial sea ice declines have already occurred, although Bers et al. (2013) showed the strong 770 771 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; Schmidtko 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

colder Weddell-modulated waters and are retreating at slower rates, with some even advancing. In
 cases where glaciers in the northern WAP are experiencing high melt rates and retreat, for example

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 trends of oceanic warming over the southern and central WAP shelf, or glacial retreat along much of 790 791 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 in phytoplankton biomass reversed around 2010. In Potter Cove, chlorophyll concentrations were 813 typically low between 1991 and 2009, with maximum values (~4 mg m⁻³) during short-lived episodic 814 815 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 (~14 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 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,

increased surface stratification would potentially favour cryptophytes and smaller diatoms over 849

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,

e.g. phytoplankton (Bertrand et al. 2015), zooplankton, benthic organisms, seeding from 865

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 consequences and feedbacks. For example, continued glacial retreat can be expected to increase the
supply of iron and other micronutrients (Zn, Cd, Co etc.) from glacial and shallow sediment sources,
and potentially their availability to phytoplankton (Annett et al. 2015; Annett et al. 2017; Bown et al.
2017, 2018; Hendry et al. 2008; Monien et al. 2017). Seasonal biological uptake of nutrients and
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_2 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, pCO₂) 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 CO₂ outgassing in winter, as well as altering the 890 phytoplankton community and potentially reducing biological CO₂ uptake in summer (Legge et al. 891 2015; Saba et al. 2014). The resultant reduction in net annual CO₂ uptake along the WAP is unlikely, 892 in itself, to make a significant difference to the functioning of the Southern Ocean CO₂ 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 CO₂ 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.

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

903 2.4. The WAP pelagic food web

Interannual variability in phytoplankton biomass has strong implications for the productivity of the
entire food web, with low chlorophyll years leading to less successful recruitment of the keystone
species Antarctic krill (*Euphausia superba*) (Atkinson et al. 2004; Saba et al. 2014). As such, low sea
ice conditions are likely to hold negative consequences for higher trophic levels such as penguins,
flying sea birds, seals and whales (Constable et al. 2014a, b; Costa et al. 2010; Trivelpiece et al.
2011). Conversely, the recent increases in chlorophyll are likely to be beneficial for zooplankton and
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 change over subsequent decades (Loeb and Santora 2015). However, more recent evidence has 922 923 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; Juares 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 habitat contracts with diminishing sea ice (Ducklow et al. 2013; Huckstadt et al. 2012a; Siniff et al. 964 965 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

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

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 (Juares 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.

Benthic community structure is strongly influenced by ice dynamics along the WAP. Whereas sea ice organic fluxes are an important food source for the benthos, solid ice can have a devastating effect by removing a significant proportion of macro- and meiofauna from the seabed (Peck et al. 1999; Lee et al. 2001). Iceberg impacts can be very frequent in shallow waters along the WAP (Brown et al. 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 trends combined with increasing ship traffic are likely to promote the import and success of 1050 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 CO₂ (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 Ω 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 CO₂ to large centric chain-forming *Chaetoceros* diatoms at elevated CO₂ 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 CO₂ (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 forcings along the WAP could vary significantly over time and space, compounding variability in the 1072 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 CO₂ 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 CO₂ 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 that although long acclimation periods are required, Antarctic benthos can acclimate to altered pH, 1092 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
- small-scale processes (e.g. ocean eddies with scales of a few kilometers). However, given the known
- 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
- 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
- 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,
- autonomous underwater vehicles (AUVs), and mooring and high-frequency (HF) radar networks.
- HF radar measures ocean surface (upper 1 m) current velocities over hundreds of square miles
 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.
- Autonomous gliders (Sherman et al. 2001; Eriksen et al. 2001; Webb et al. 2001) are complementing mooring measurements by providing high-resolution spatial measurements over the full shelf depth (Carvalho et al. 2016; Carvalho et al. 2017; Couto et al. 2017; Brearley et al. 2017). These gliders are capable of sampling over thousands of kilometres and spending months at sea, making them ideal for maintaining a sustained presence and filling critical observational gaps between ship-board surveys, research stations and mooring arrays, and at smaller spatial scales than are captured by shipboard sampling (Venables et al. 2017). These systems are cost-effective, capable of carrying a

- range of sensors, and have been proven to be effective tools to leverage data collection across abroad range of applications and ocean regions (Schofield et al. 2015).
- Powered AUVs have been used in the Southern Ocean for bathymetric, physical oceanographic and biological surveys under and in the vicinity of sea ice (e.g. Brierley et al. 2002). Expanding the use of such AUVs in the WAP region has the potential to provide a wealth of water column data from under-ice environments. Most under-ice powered AUV missions to date have been conducted by large complex platforms capable of under-ice navigation and advanced autonomous decisionmaking, 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

timescales will also be critical to making progress. Adopting such an interdisciplinary whole-system
approach offers perhaps the most promising opportunity for driving a step-change in our
understanding of the functioning of the WAP marine ecosystem and its response to, and role in,
ongoing climatic and environmental changes, making this a clear overarching priority for the
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 pCO₂, 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 behaviour data (Treasure et al. 2017), with significantly greater coverage than otherwise available. 1220 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 spatial scales than ship-based efforts. Systematic deployment of multi-frequency acoustics on ships, 1223 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, pCO₂ and Ω) 1233 and ecological (grazing pressure, viral infection) conditions, and therefore their ability to acclimate. Rates of geneflow within and between populations are needed to quantify the capacity of benthic 1234 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.

Direct human pressure on regional krill stocks is increasing as a result of expanding commercial fishing activity, particularly in the northern WAP and adjacent open ocean, potentially reducing food availability for krill predators (Trivelpiece et al. 2011). Management of this fishery by the Convention on Conservation of Antarctic Marine Living Resources (CCAMLR) must be informed by our knowledge of the foraging behaviour of krill predators, for instance using satellite tags and motion-sensing tags to determine the critical locations and times of year for their feeding (Weinstein et al. 2017), so that 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 exchange of climate-active gases as the changes in sea ice extent, duration and atmospheric forcing 1266 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 CO₂ 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 SOOSmap online data portal (http://www.soos.aq/data/soosmap), would be of significant benefit. 1296 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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- 1314 manuscript. IRS, DKS, CM, LSP, DPC, DEB, CH, PDR, HWD, DA, JS, MAvL, CPDB, AGJB, JK, RS, ASF, SES
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- 1319

1320 Figures

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



1324

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



- 1335 Figure 2. Map of the WAP showing the major sustained research efforts represented, delineation of
- 1336 the northern, central and southern sub-regions referred to in the text (white dashed lines; N =
- 1337 northern sub-region, C = central sub-region, S = southern sub-region), and the major circulation and
- 1338 bathymetric features of the shelf system. Modified from Moffat and Meredith (2018).



Figure 3: Infographic summarising the key components of the WAP marine system, the most

- important mechanisms and interactions in the context of the two overarching questions addressed
- in this paper, and the major priorities and approaches for future marine research at the WAP.



1347

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



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).



1365

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 (ϵ) of 4 and 5 ‰ (solid and dashed black lines, respectively). Both δ^{15} N and δ^{18} 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).



1374

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 fCO_2 between the sea and 1378 air ($\Delta f CO_2$), with the pink shaded region representing approximate 95 % confidence from uncertainty 1379 analysis. Red dashed line shows $\Delta f CO_2 = 0$, where ocean CO₂ concentration is in equilibrium with the 1380 atmosphere. $\Delta fCO_2 > 0$ during winter indicates supersaturated conditions and an efflux of CO₂ to the 1381 atmosphere; $\Delta fCO_2 < 0$ during summer indicates undersaturated conditions and oceanic uptake of 1382 atmospheric CO₂. 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).



1385 1386

1387Figure 8. Summertime distribution of inorganic carbon system and other biogeochemical parameters1388in surface water for the Palmer LTER grid for the period 1993 to 2012, showing onshore-offshore and1389north-south gradients in carbonate chemistry, salinity and inorganic nutrients. Reproduced with

1390 permission from Hauri et al. (2015).



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

indicates the approximate position of the northern edge of the marginal ice zone during the secondhalf of December 2014, immediately preceding the cruise.



1399

Figure 10. Long-term averages (2003-2017) for January of both bacterial abundance (top left) and 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

1402 further south. Lower panel shows strong variability in bacterial production with abundance for

1403 individual January cruises, as per legend. All linear regressions are statistically significant (*p* < 0.05),

except for 2012. These data were collected as part of the Palmer LTER project and are updated from

1406 Ducklow et al. (2012a).



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 temperate and tropical species (filled circles; brooding rate (1/weeks) = $20.37 - 6.25 \times 1000/T$; r² = 1419 1420 0.36, F = 32.4, 58 df, p < 0.001); Antarctic species fall significantly below. Reproduced from Peck 1421 (2018).



1423 1424 Figure 13. Relationships between annual abundance anomalies of specific zooplankton taxa on the 1425 Palmer LTER grid, 1993-2013, and sub-decadal climate oscillations and annual abundance anomalies 1426 of primary production. (a) Salpa thompsonii and SAM winter index from the year prior, (b) pteropod 1427 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 1428 1429 production from two years prior. Full refers to the full LTER grid, North refers to the northernmost 1430 three sampling lines, which are referred to as the central WAP sub-region in this paper, and South+ 1431 refers to the southernmost five sampling lines, referred to as the southern WAP sub-region in this 1432 paper (Figure 2). Modified with permission from Steinberg et al. (2015).



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).

1437





1439Figure 15. Effects of in situ warming on the growth of common epifaunal marine invertebrates on1440Rothera Point, Adelaide Island. Panels show area covered by the spatially dominant bryozoan1441(*Fenestrulina rugula*) and spirorbid (*Romanchella perrieri*) under warming (+1°C and +2°C) and1442control treatments, showing different growth rate responses between species. Data show the mean1443and interquartile range of panel surface area covered by a single colony (top) or individual (bottom).1444Different letters indicate significantly different areas per age (F(1,9) with *p* <0.01). Modified from</td>1445Ashton et al. (2017).1446



- 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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