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Variability and change in the west Antarctic Peninsula marine system: Research priorities and opportunities

Sian F. Henley

Oscar M. Schofield

Katherine R. Hendry

Irene R. Schloss

Deborah K. Steinberg
Virginia Institute of Marine Science

See next page for additional authors

Authors

Sian F. Henley, Oscar M. Schofield, Katherine R. Hendry, Irene R. Schloss, Deborah K. Steinberg, and et al

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2 opportunities

3 *Sian F. Henley[1]*, Oscar M. Schofield[2], Katharine R. Hendry[3], Irene R. Schloss[4], Deborah K. Steinberg[5],*
4 *Carlos Moffat[6], Lloyd S. Peck[7], Daniel P. Costa[8], Dorothee C. E. Bakker[9], Claire Hughes[10], Patrick D.*
5 *Rozema[11], Hugh W. Ducklow[12], Doris Abele[13], Jacqueline Stefels[11], Maria A. Van Leeuwe[11], Corina P.*
6 *D. Brussaard[14], Anita G. J. Buma[11], Josh Kohut[2], Ricardo Sahade[15], Ari S. Friedlaender[16], Sharon E.*
7 *Stammerjohn[17], Hugh J. Venables[7], Michael P. Meredith[7]*

8 [1]School of GeoSciences, University of Edinburgh, James Hutton Road, Edinburgh, EH9 3FE, UK
9 [2]Department of Marine and Coastal Sciences, Rutgers University, 71 Dudley Road, New Brunswick,
10 NJ 08901, USA
11 [3]School of Earth Sciences, University of Bristol, Queens Road, Bristol, BS8 1RJ, UK
12 [4]Instituto Antártico Argentino, Centro Austral de Investigaciones Científicas, Bernardo Houssay 200
13 (9410), Ushuaia, Tierra del Fuego, Argentina, and Universidad Nacional de Tierra del Fuego,
14 Argentina
15 [5]Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, VA 23062, USA
16 [6]School of Marine Science and Policy, University of Delaware, Newark, DE 19716, USA
17 [7]British Antarctic Survey, High Cross, Madingley Road, Cambridge, CB3 0ET, UK
18 [8]Ecology and Evolutionary Biology Department, University of California Santa Cruz, 100 Shaffer Road,
19 Santa Cruz, CA 95060, USA
20 [9]Centre for Ocean and Atmospheric Sciences, University of East Anglia, Norwich Research Park,
21 Norwich, NR4 7TJ, UK
22 [10]Environment Department, University of York, Heslington, York, YO10 5NG, UK
23 [11]University of Groningen, GELIFES, Nijenborgh 7, 9747 AG Groningen, The Netherlands
24 [12]Lamont-Doherty Earth Observatory, Columbia University, 61 Route 9W, Palisades, NY 10964, USA
25 [13]Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Am Handelshafen 12,
26 27570 Bremerhaven, Germany
27 [14]Royal Netherlands Institute for Sea Research, 1790 AB Den Burg, Texel, The Netherlands
28 [15]Instituto de Diversidad y Ecología Animal, Universidad Nacional de Córdoba, Avenida Vélez
29 Sarsfield 299, 5000 Córdoba, Argentina
30 [16]Marine Mammal Institute and Department of Fisheries and Wildlife, Oregon State University,
31 Newport, OR 97365, USA
32 [17]Institute of Arctic and Alpine Research, University of Colorado, Campus Box 450, Boulder, CO
33 80309, USA
34
35 Corresponding author: s.f.henley@ed.ac.uk

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41   <u>Highlights</u>

42   The WAP shelf ecosystem is regionally important for krill and higher trophic levels

43   Long-term climate change and short-term natural variability control sea ice dynamics

44   Physical changes regulate ecosystem functioning, biogeochemistry and air-sea exchange

45   The WAP is a model system for how sea ice changes can restructure polar ecosystems

46   Future research requires international cooperation and interdisciplinary integration

47

48   Abstract

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

70

71   Introduction

72   The west Antarctic Peninsula (WAP) continental shelf hosts a productive marine ecosystem, which is
73   regionally important for krill stocks over the shelf and downstream in the Southern Ocean circulation
74   system (e.g. Atkinson et al. 2004; Quetin et al. 1996), and for larger marine organisms as a breeding
75   and/or feeding ground for migratory and year-round species (e.g. Costa and Crocker 1996; Ducklow
76   et al. 2007; Friedlaender et al. 2006). From a climatic and biogeochemical perspective, the WAP is
77   important because the southern flank of the Antarctic circumpolar current (ACC) flows particularly
78   close to the shelf edge in this region (Orsi et al. 1995). As such, circumpolar deep water (CDW) from
79   its mid-depths incurs directly on to the shelf in a less modified form than elsewhere around
80   Antarctica, facilitating greater connectivity and exchange of physical and biogeochemical properties
81   between these intermediate water masses and the atmosphere and surface ocean (Hofmann et al.
82   1996; Klinck 1998). Significant variability in the physical environment, modulated by strong coupling
83   to climate processes over interannual and decadal timescales, is having a strong impact on regional
84   biogeochemistry and all levels of the shelf ecosystem, making the WAP an important model region in
85   which to understand the impacts of climate on polar marine systems.

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

94   2014). Significant surface freshening has been observed closer to coastal glacial meltwater sources,
95   whilst upper layer salinification has occurred further offshore (Bers et al. 2013; Meredith and King
96   2005; Schloss et al. 2012).

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

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

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

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

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

152 Figure 2 shows the major sustained research efforts along the WAP, delineation of the northern,
153 central and southern sub-regions referred to in this paper, and the major circulation and
154 bathymetric features of the shelf system. The US Palmer Antarctica Long-Term Ecological Research
155 (LTER) project has been in operation since 1990, and consists of spring/summer time-series sampling
156 adjacent to Palmer Station, Anvers Island, and an annual summer cruise occupying a grid of stations
157 over the WAP shelf between Anvers and Charcot Islands. The US National Oceanic and Atmospheric
158 Administration Antarctic Marine Living Resources (AMLR) program has been active around the South
159 Shetland Islands in the northern WAP since 1986, conducting annual research surveys and land-
160 based field measurements with a focus on ecosystem-based management of fisheries, primarily krill.
161 Since 1997, the Rothera Time Series (RaTS) of the British Antarctic Survey, located in Ryder Bay,
162 northern Marguerite Bay adjacent to Rothera Research Station on Adelaide Island, has made year-
163 round quasi-weekly measurements of physical and biogeochemical oceanographic parameters,
164 benthic ecology and sea ice cover, with a large number of linked and complementary studies
165 conducted by UK and international partners. The establishment of additional laboratories at Rothera
166 by the Netherlands Organisation for Scientific Research (NWO) in 2012 increased the Dutch research
167 effort in the WAP region substantially. The Argentinian Antarctic Program consists of time-series and
168 process studies at a number of research stations along the WAP, as well as ship-based campaigns
169 across the shelf. Year-round time-series monitoring of hydrographic and biological variables in Potter
170 Cove, King George Island/ Isla 25 de Mayo, South Shetland Islands, has been conducted fortnightly-
171 monthly since 1991, based at Carlini Station, which has been in operation since 1982. A joint
172 Argentinian-German research program at Dallmann Laboratory on Carlini Station focusing on Potter
173 Cove started in 1994, and forms an important part of the German research efforts in the WAP
174 region, coordinated by the Alfred Wegener Institute (AWI). The Chilean Antarctic Institute (INACH)
175 conducts scientific research programs at four bases along the WAP, supported by the Armed Forces.
176 Chilean base Yelcho on Doumer Island was reopened in 2015 and there are plans to reopen Base
177 Carvajal on Adelaide Island to complete a latitudinal transect from King George Island to Adelaide
178 Island, as well as developing a long-term monitoring program. The Peruvian National Antarctic
179 Program comprises summertime studies at Machu Picchu Research Station on King George Island,
180 which was established in 1989, and oceanographic cruises. Spanish research programs centre on
181 Juan Carlos I and Gabriel de Castilla Stations in the South Shetland Islands, which were opened in the
182 late 1980s, as well as ship-based research. Brazilian research efforts have been underway in the
183 northern WAP since the 1980s, with dedicated ship-based monitoring programs conducted through
184 a number of initiatives coordinated by the Brazilian Antarctic Program since 2000. Chinese
185 monitoring programs at Great Wall Station on King George Island have been in operation as part of
186 the Chinese National Antarctic Program since the base was established in 1985. The Korea Polar
187 Research Institute (KOPRI) runs a year-round marine ecosystem monitoring program in operation
188 since 1996 at King Sejong Station on King George Island, which was inaugurated in 1988. The Henryk
189 Arctowski Polish Antarctic Station, which opened in 1977 and is managed by the Institute of

190   Biochemistry and Biophysics of the Polish Academy of Sciences, has also served as a base for a
191   number of marine studies around King George Island.

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

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

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

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

216

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

219   1.1. Physical oceanography

220   The hydrography and circulation of the WAP shelf are influenced by intrusions of oceanic water from
221   the ACC, inflow around the tip of the Peninsula from the Weddell Sea, and coupling with the
222   atmosphere, cryosphere and land (Klinck et al. 2004; Martinson et al. 2008). Modulated by shelf
223   dynamics, these processes lead to significant spatial and temporal property gradients in this region.
224   Large seasonal variability occurs in surface waters, driven by strong heat loss and ice growth and
225   advection in autumn and winter that leads to the formation of a deep winter mixed layer, and ice
226   melting and partial restratification during spring and summer (Klinck et al. 2004; Meredith et al.
227   2008). Precipitation, glacial melt and sea ice melt modulate the freshwater content and stratification
228   of the surface layer, with significant variability driven by ENSO and SAM over interannual timescales
229   (Meredith et al. 2010; Meredith et al. 2017). A main feature of the surface circulation is the Antarctic
230   Peninsula Coastal Current (APCC), a seasonal buoyancy- and wind-forced surface current, which
231   flows southwestwards along the coast south of Anvers Island and west of Adelaide and Alexander

232 Islands during summer and autumn with a cyclonic circulation inferred within Marguerite Bay
233 (Beardsley et al. 2004; Moffat et al. 2008; Savidge and Amft 2009).

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

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

264 1.2. Phytoplankton community dynamics

265 1.2.1. Pelagic primary production

266 The WAP shelf is a productive marine ecosystem, where primary production varies significantly in
267 time and space, due to its regulation by upper ocean physics, light availability and the supply of
268 macro- and micronutrients. As well as the role of phytoplankton in taking up nutrients and carbon
269 dioxide, thus mediating air-sea gas exchange and larger-scale biogeochemical cycling, these primary
270 producers constitute a critical food source for the entire WAP shelf ecosystem. High-biomass
271 phytoplankton blooms occur during spring and summer (Hart 1942; Nelson and Smith 1991; Prézelin
272 et al. 2000; Smith et al. 2008), when solar illumination increases and sea ice has retreated, leaving an
273 exposed ocean surface (Moline and Prézelin 1996; Smith and Stammerjohn 2001). There is a strong
274 productivity gradient with high productivity (~1000 mg C m^{-2} d^{-1}) inshore compared with offshore
275 waters (~100 mg C m^{-2} d^{-1}) (Vernet et al. 2008). Seasonal satellite studies and *in situ* measurements
276 show that net community production peaks first offshore and follows the inshore retreat of the sea
277 ice (Arrigo et al. 2017; Li et al. 2016). The magnitude of primary productivity on an annual basis is

278 linked to climate modes such as ENSO and SAM, and their effect on the ASL, which influence the
279 amount of sea ice present in the winter (Stammerjohn et al. 2008a), and this in turn affects primary
280 productivity in the following spring and summer seasons (Saba et al. 2014). The duration of winter
281 sea ice and the extent of winter wind-driven mixing, combined with the timing of ice retreat and
282 mixing during spring, has been shown to control upper ocean stability during spring and summer,
283 thus preconditioning the water column for phytoplankton growth (Venables et al. 2013; Saba et al.
284 2014; Schofield et al. 2017; Rozema et al. 2017a). In high-ice years, less wind-induced mixing over
285 winter and a subsequent strong seasonal melt results in a more stable water column that retains
286 phytoplankton in a shallower surface layer, where light conditions are favourable for growth (Moline
287 1998; Vernet et al. 2008; Carvalho et al. 2016). In low-ice years, enhanced wind-driven mixing and
288 subsequently deeper mixed layers, combined with a smaller input of meltwater to restabilise the
289 upper ocean, result in phytoplankton cells being mixed over a greater depth interval, experiencing
290 lower light levels overall, such that primary productivity is reduced (Figure 4). Superimposed on the
291 seasonal bloom dynamics are shorter-lived phytoplankton blooms (days-week) facilitated by periods
292 of low wind that lead to increased water column stability (Moline 1998; Vernet et al. 2008; Carvalho
293 et al. 2016). High primary productivity supports a productive food web that is tightly coupled to the
294 seasonal phytoplankton dynamics, suggesting strong bottom-up control of the ecosystem (Saba et
295 al. 2014).

296 While WAP phytoplankton communities are often dominated by diatoms, other taxa are increasingly
297 recognised as important components of the food web. The importance of nanoplankton (<20 μm)
298 and picoplankton (<2 μm) has been documented, with cryptophytes being the dominant nano-
299 flagellate over much of the region (e.g. Krebs 1983; Buma et al. 1991; Kopczynska 1992; Garibotti et
300 al. 2003; Varela et al. 2002; Rodriguez et al. 2002). Other major phytoplankton taxa include mixed
301 flagellates and haptophytes, with haptophytes (e.g. the prymnesiophyte *Phaeocystis antarctica*)
302 being more prominent than cryptophytes in Marguerite Bay (Garibotti et al. 2003; Kozlowski et al.
303 2011; Rozema et al. 2017a; Stefels et al. 2018). *P. antarctica* dominated the phytoplankton
304 community during spring 2014 in the central WAP prior to the peak of the diatom bloom (Arrigo et
305 al. 2017). During high-chlorophyll years, the late-spring/summer phytoplankton community is
306 dominated by larger cells, primarily diatoms, with only a minor contribution from smaller size
307 classes, primarily haptophytes and cryptophytes (Moline et al. 2004; Rozema et al. 2017a; Schofield
308 et al. 2017; Schloss et al. 2014). In low-ice low-chlorophyll years, the haptophyte and cryptophyte
309 contributions increase, whilst the diatom contribution is reduced. Cryptophyte abundance increases
310 when a shallow meltwater lens, probably of glacial origin, overlies a well-mixed upper water column
311 (Mura et al. 1995; Moline et al. 2004). Cryptophytes take up less CO_2 per unit chlorophyll than
312 diatoms, such that a greater cryptophyte contribution may lead to reduced carbon uptake compared
313 to diatom-dominated assemblages (Schofield et al. 2017).

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

323 1.2.2. Coupling between sea ice and pelagic ecosystems

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 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 release being more likely to be consumed by pelagic zooplankton or benthic communities (e.g. Riebesell et al. 1991).

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

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 ~0.2 g m^{-2} 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).

1.3. Nutrient biogeochemistry

The supply and cycling of inorganic and organic macro- and micronutrients along the WAP is regulated by physical and biological processes, and influences the spatial and temporal variation in 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, such that phytoplankton biomass is higher and more diatom-dominated over the canyons compared with adjacent shelf areas (Kavanaugh et al. 2015). The supply of inorganic nitrogen and silicic acid 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. 2010). A glacial source of silicic acid in basal meltwater has been demonstrated around Greenland (Hawkings et al. 2017), and warrants investigation along the WAP.

Vertical nutrient fluxes from the modified CDW source into the surface ocean vary substantially in space and time. Vertical nitrate fluxes during summer in Marguerite Bay and along Marguerite Trough were estimated as 0.18 ± 0.17 mmol NO$_3$ m^{-2} d^{-1} with a maximum of 0.56 mmol NO$_3$ m^{-2} d^{-1}

370 (Henley et al. 2018). The mean summertime vertical nitrate flux for the Palmer LTER grid for 1998-
371 2007 was estimated as 1.36 ± 1.79 mmol NO_3 m^{-2} d^{-1} (Pedulli et al. 2014), although the latter study
372 used a uniform value for the vertical eddy diffusivity (K_z) that is likely to overestimate fluxes.
373 Seasonal variability is poorly constrained, although vertical nutrient fluxes are expected to be
374 greatest following the initial retreat of sea ice, in agreement with heat fluxes (Brearley et al. 2017).
375 Whilst macronutrients are normally replete in WAP surface waters, intense biological drawdown by
376 phytoplankton can lead to transient nutrient limitation in coastal areas during some summers
377 (Henley et al. 2017). Interannual variability in CDW-derived nutrient supply is attributed to the
378 degree of wintertime mixing at Palmer Station (Kim et al. 2016), but this cannot fully account for the
379 observed variability at Rothera (Henley et al. 2017).

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

396 Nitrate, phosphate and inorganic carbon are progressively enriched in subsurface waters as CDW
397 moves across the shelf, and the stable nitrogen ($\delta^{15}N$) and oxygen ($\delta^{18}O$) isotope composition of
398 nitrate (Figure 6) and nutrient stoichiometry show that this is driven by local remineralisation of
399 organic matter and nutrient recycling in the upper water column (≤200 m) (Henley et al. 2017, 2018).
400 Nitrification (regeneration of nitrate via ammonium oxidation) occurs in the deeper darker part of
401 the euphotic layer, making the regenerated nitrate contribution to surface ocean primary production
402 sensitive to whether the base of the euphotic layer resides within the mixed layer. Nitrate and
403 phosphate regenerated in subsurface shelf waters, as opposed to that supplied from the CDW
404 source, can account for up to one third of the surface ocean nutrient pools during summer, with
405 implications for new production, net CO_2 uptake and organic matter export. Silicic acid is also
406 enriched across the shelf, with maximum enrichment at depth (Henley et al. 2018). This indicates
407 biogenic silica dissolution occurring deeper in the water column than organic matter
408 remineralisation, and potentially in sediment porewaters, driving a return flux of silicic acid to the
409 water column. New porewater silicon isotope data provide evidence for down-core changes in silicic
410 acid being driven by dissolution of diatom frustules and potentially reverse weathering reactions
411 (Cassarino et al. *in prep*).

412 Our understanding of organic nutrient budgets and cycling is more limited. Dissolved organic carbon
413 (DOC) and nitrogen (DON) concentrations are low in the Southern Ocean compared to other ocean
414 regions, with a labile to semi-labile pool in the upper ocean and a large refractory pool in CDW
415 (Hansell et al. 2009; Kirchman et al. 2009; Ogawa et al. 1999). Low DOC concentrations and low
416 bacterial production rates and biomass along the WAP suggest that bacterial production may be

417   limited by the availability of dissolved organic matter (DOM) (Ducklow et al. 2012a; Kim et al. 2016),
418   but this is yet to be fully understood.

419   The essential micronutrient iron is supplied to the WAP surface ocean primarily from glacial
420   meltwater and shallow sedimentary sources (Annett et al. 2015; Annett et al. 2017; Bown et al.
421   2018; Monien et al. 2017; Sherrell et al. 2018). Iron concentrations are replete in inshore regions,
422   but can be drawn down by phytoplankton blooms to limiting levels further offshore. Micronutrients
423   other than iron show temporal and spatial variability, although their roles in regulating primary
424   productivity along the WAP are yet to be determined (Bown et al. 2017; Hendry et al. 2008).

425   1.4. Climate-active gases

426   1.4.1. Marine carbonate chemistry and air-sea CO_2 fluxes

427   Carbonate chemistry and air-sea CO_2 fluxes along the WAP are influenced strongly by ocean physics
428   and biological processes. Year-round measurements of dissolved inorganic carbon (DIC) and total
429   alkalinity (TA) taken at the Rothera Time Series since 2010 show that all carbonate chemistry
430   parameters have a strong, asymmetric seasonal cycle in surface waters with some year-to-year
431   variation (Figure 7; Legge et al. 2015, 2017; Jones et al. 2017). Concurrent with the late spring/early
432   summer phytoplankton bloom, DIC, TA and the fugacity of carbon dioxide (fCO$_2$) decrease sharply,
433   while pH and the saturation state (Ω) of the calcium carbonate minerals calcite and aragonite
434   increase sharply. Values for all parameters then gradually return to winter values. Aragonite
435   saturation state shows notably low wintertime values, just above 1, a critical boundary below which
436   aragonitic organisms can become susceptible to growth impairment and dissolution (Jones et al.
437   2017). Photosynthesis and respiration dominate these seasonal changes in surface water carbonate
438   chemistry, with biological uptake driving the substantial reductions in DIC during spring and summer
439   (Carrillo et al. 2004; Legge et al. 2017; Tortell et al. 2014). Upwelling and vertical mixing of carbon-
440   rich deep water increase upper ocean DIC, especially during winter, whilst sea ice reduces CO_2
441   outgassing. Ryder Bay is a net sink for atmospheric CO_2 of 0.90-1.39 mol C m^{-2} yr^{-1} (Legge et al. 2015).
442   It remains unclear whether the WAP shelf as a whole is a net annual sink or source for atmospheric
443   CO_2.

444   Across the WAP shelf, carbonate system parameters show strong onshore-offshore gradients in the
445   upper ocean during summer, with low DIC and fCO$_2$ and high pH and aragonite saturation state in
446   near-shore waters, due to strong biological carbon uptake, especially in the southern WAP sub-
447   region (Figure 8) (Carrillo et al. 2004; Hauri et al. 2015; Ruiz-Halpern et al. 2014). The degree of
448   summertime DIC and fCO$_2$ drawdown is closely related to phytoplankton biomass and primary
449   production (Moreau et al. 2012), which are regulated by winter sea ice coverage and wind patterns
450   during spring (Montes-Hugo et al. 2010). In the central WAP, dilution by meltwater inputs reduces
451   TA and DIC in near-shore waters (Hauri et al. 2015). Most of the WAP shelf exhibited fCO$_2$
452   undersaturation and net CO_2 uptake during summers between 2005 and 2009, although there was a
453   region of fCO$_2$ supersaturation and net CO_2 release in the outer shelf region to the north of Anvers
454   Island (Ruiz-Halpern et al. 2014). Air-sea CO_2 fluxes in Bransfield Strait are highly variable, with
455   surface waters switching between sink and source behaviour in consecutive summer seasons (Ito et
456   al. 2018).

457   1.4.2. Halogens

458   Halogen gases can be released from phytoplankton and ice algal communities along the WAP, with
459   consequences for atmospheric chemistry and regional climate. The halogens play an important role
460   in the Antarctic atmospheric boundary layer, being involved in the cycling of O_3, HO$_x$, NO$_x$, Hg, CH$_4$

461 and the formation of precursor molecules to cloud condensation nuclei (CCN) (reviewed by Saiz-
462 Lopez and von Glasow 2012). Destruction by bromine radicals is thought to be the primary driver for
463 ozone depletion events, during which Antarctic boundary layer O_3 can decrease from around 30 ppb
464 to below instrumental detection (1-2 ppb) for up to a few days (e.g. Jones et al. 2013). Additionally,
465 modelling studies suggest that some halogen oxides are involved in controlling CCN formation
466 through oxidation of the semi-volatile organic sulphur compound dimethyl sulphide by bromine
467 monoxide (Breider et al. 2015) and possibly new particle formation involving iodine oxides (e.g. Saiz-
468 Lopez et al. 2008; Roscoe et al. 2015).

469 Biotic and abiotic sources of halogens to the Antarctic atmospheric boundary layer have been
470 identified. The 'explosive' emission of bromine needed to initiate ozone depletion events is driven by
471 catalytic liberation from condensed-phase sea-salt bromide present on airborne particulates, and
472 snow and sea ice surfaces (reviewed by von Glasow and Hughes 2015). Sea salt aerosol (Legrand et
473 al. 2016) and blowing saline snow (Yang et al. 2008, 2010; Lieb-Lappen and Obbard 2015) are also
474 thought to be important sources of gaseous inorganic bromine in Antarctica. Whilst these abiotic
475 sources are thought to dominate, Hughes et al. (2009, 2012) show that high rates of biogenic
476 bromoform ($CHBr_3$) flux from diatom blooms in the seasonal ice zone of the WAP could also
477 contribute significantly to gaseous inorganic bromine during certain times of year. Similar to the
478 uptake of macronutrients being reduced during relatively low-productivity spring/summer seasons
479 following winter periods with reduced fast-ice duration (Henley et al. 2017), biogenic bromoform
480 ($CHBr_3$) emissions are also reduced in low-ice low-productivity years (Hughes et al. 2012).

481 Whilst iodine emissions to the Antarctic atmosphere have also been linked to abiotic reactions on
482 the snowpack (Saiz-Lopez et al. 2008; Freiss et al. 2010), additional biological sources have been
483 proposed for coastal regions at the WAP and elsewhere. These include iodocarbon (e.g. CH_2I_2, CH_3I)
484 emissions from surface waters and sea ice (Chance et al. 2010; Granfors et al. 2013), and microalgal-
485 mediated inorganic iodine flux from sea ice brine channels (Saiz-Lopez et al. 2015).

486 1.4.3. Organic sulphur compounds

487 Dimethyl sulphide (DMS) is the most important natural sulphur source to the atmosphere, where it
488 is oxidised to form sulphate aerosols, which act as CCNs and exert a cooling effect through albedo
489 feedbacks. DMS can also be released from phytoplankton and ice algal communities along the WAP,
490 resulting in a direct feedback between the ecosystem and regional climate. Climatologies of DMS
491 concentrations and fluxes show that the Southern Ocean as a whole is a global hotspot of DMS
492 production, and its modelled contribution to atmospheric sulphate is especially high (Gondwe et al.
493 2003; Lana et al. 2011). The Southern Ocean also exhibits the highest temporal variability in DMS
494 concentrations, and the highest concentrations in the marginal ice zone. The latest Southern Ocean
495 climatology indicates that the WAP is not a particular hotspot of DMS production (Jarníková and
496 Tortell 2016), although this may reflect a shortage of published datasets, particularly from the
497 marginal ice zone. Two time series from the Palmer LTER show highest DMS concentrations in
498 January between 5 and 15 nM (Asher et al. 2017; Herrmann et al. 2012), which compare well with
499 the climatological mean for January of 10.8 ± 6.9 (SD) nM for the whole Austral Polar province (Lana
500 et al. 2011). A recent continuous 5-year time series at Rothera shows large seasonal fluctuations in
501 northern Marguerite Bay, with considerably higher concentrations in January, reaching an average of
502 24 ± 35 (SD) nM and a maximum of 160 nM in January 2015 (Webb et al. *in review*). This new time
503 series documents a 3-fold higher flux of DMS to the atmosphere than previously calculated. High
504 concentrations were also observed throughout Marguerite Bay and out to the shelf edge in January
505 2015, and are likely associated with the location of the marginal ice zone (Figure 9; Stefels et al.
506 2018).

507 The role of sea ice in the sulphur cycle is complex and the processes involved are poorly quantified.
508 Large phytoplankton blooms and spikes of DMS have been linked to melting sea ice (Trevena and
509 Jones 2006), potentially caused by the release of large amounts of ice algae that produce the DMS
510 precursor, dimethylsulphoniopropionate (DMSP) (Stefels et al. 2018). This is supported by extremely
511 high DMSP concentrations common in sea ice, 2-3 orders of magnitude higher than in underlying
512 surface waters. However, release from sea ice does not necessarily result in high DMS
513 concentrations (Tison et al. 2010). The efficiency of DMSP conversion to DMS depends strongly on
514 phytoplankton community structure, as *Phaeocystis* and dinoflagellates readily convert DMSP into
515 DMS whilst diatoms do not, on bacterial processes, which often demethylate DMSP rather than
516 producing DMS, and on abiotic factors (Stefels et al. 2007). With particular relevance to Antarctic ice
517 and surface waters, high levels of UV radiation can photo-oxidise DMS to dimethylsulphoxide
518 (DMSO), as well as inhibiting algal and bacterial activity (Toole and Siegel 2004; Zemmelink et al.
519 2008a). Whilst high DMS fluxes have been found above sea ice, it remains unclear how much is
520 derived from surface ice communities, which are often dominated by the well-known DMS producer
521 *Phaeocystis*, and/or from leads between ice floes, where surface-microlayer concentrations of DMS
522 can be an order of magnitude higher than in the underlying water column (Zemmelink et al. 2008a,
523 b). Ice-derived DMS fluxes are likely to be largest during early spring, when surface ice communities
524 are developing and surface ice and snow layers become permeable due to rising temperatures. Sea
525 ice dynamics also impact on pelagic DMSP production, both directly via DMSP release from ice algae
526 input to surface waters, and indirectly by shaping the conditions for pelagic blooms that produce
527 DMSP (Stefels et al. 2018; Webb et al. *in review*).

528 1.5. Microbial processes

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

2011). Bacterioplankton itself could be an underestimated source of DOM through grazing by zooplankton and mixotrophic algae, or by viral lysis; an important loss factor for Antarctic bacterioplankton (Brum et al. 2015; Evans et al. 2017; Evans and Brussaard 2012; Vaqué et al. 2017). 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).

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

Stark contrasts exist between surface and deep (>100 m) community composition along the WAP, with diversity being more stable over time and space at depth than in surface waters (Luria et al. 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). 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 Ocean, the dominant phyla are Alpha- and Gamma- Proteobacteria, Actinobacteria and Bacteroidetes (the Cytophaga-Flavobacterium-Bacteroides group) (Abell and Bowman 2005; Delmont et al. 2014; Gentile et al. 2006; Landa et al. 2016).

The pelagic archaeal community along the WAP is dominated by ammonia-oxidising *Thaumarchaeota* (previously Marine Group I *Crenarchaeota*) (Abele et al. 2017; Grzymski et al. 2012; Hernández et al. 2015; Luria et al. 2014; Signori et al. 2014)*. Thaumarchaeota* were also found to dominate sea ice and benthic archaeal communities (Cowie et al. 2011; Learman et al. 2016). The widespread distribution of *Thaumarchaeota* suggests an important ecological function involved in 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; 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).

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 understanding of the microbial processes at work. Bacterioplankton are involved in chemoheterotrophy, photoheterotrophy or aerobic anoxygenic photosynthesis during summer, whilst chemolithoautotrophic pathways dominate during winter (Grzymski et al. 2012; Williams et al. 2012). Abundant Flavobacteria have been shown to bind and exploit polymeric substrates, including carbohydrates, polypeptides, and lipids, thereby providing a crucial function in microbial 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 et al. 2017; Hernández et al. 2015).

1.6. Zooplankton dynamics

Zooplankton abundance, distribution and species assemblages along the WAP are influenced strongly by the availability and composition of their phytoplankton food source, as well as the 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 macrozooplankton) assemblage composition along the WAP are well known, with the Antarctic krill, *Euphausia superba*, being well-established as a keystone species in the regional food web (e.g. Quetin and Ross 2003). The WAP is an important spawning and nursery area for *E. superba*, where 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). 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, South Shetland Islands, inshore macrozooplankton assemblages are numerically dominated by the small copepod *Oithona similis*, whereas large copepods such as *Rhincalanus gigas* and *Calanus propinquus* 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).

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

A year-round time-series sediment trap located over the WAP shelf indicates that zooplankton fecal pellets (mostly from krill) dominate export, comprising on average 67 % of the total POC flux over 170 m (Gleiber et al. 2012). By comparing copepod fecal pellet flux from the same sediment trap and copepod egestion rates from experiments, Gleiber et al. (2015) estimate on average 58 % retention of copepod fecal pellets in the upper 170 m, such that copepod pellets are likely recycled in surface waters to a greater extent than those from krill. *Salpa thompsoni* along the WAP produce large fecal pellets that sink on average 700 m per day, and have defecation rates that can exceed those of krill (Phillips et al. 2009). Changes in zooplankton species composition can therefore have a significant effect on POC fluxes, biogeochemical cycling, benthic food supply and the biological carbon pump

649   (Gleiber et al. 2012; Steinberg and Landry 2017). *E. superba* is known to forage on the benthos,
650   which has further implications for benthic-pelagic coupling, including the vertical transfer of
651   particulate iron ingested at depth into surface waters where it is subsequently metabolised and
652   made bioavailable to phytoplankton (Schmidt et al. 2011; Schmidt et al. 2016).

653   1.7. Higher trophic levels

654   The WAP ecosystem comprises diverse assemblages and high biomass of top predators that
655   represent both Antarctic and sub-Antarctic habitats, supported by the large and persistent biomass
656   of krill predominantly in the central and southern WAP and the pack ice zone (Costa and Crocker
657   1996; Ducklow et al. 2007; Friedlaender et al. 2011; Kock and Shimadzu 1994; Nowacek et al. 2011).
658   Along the northern slope and in oceanic waters where copepods dominate, mesopelagic fish and
659   squid act as intermediate consumers. Predator hotspots develop in areas where bathymetric troughs
660   facilitate intrusions of nutrient-rich CDW onto the continental shelf (Dinniman et al. 2011;
661   Friedlaender et al. 2011; Friedlaender et al. 2006; Kavanaugh et al. 2015). More ephemeral predator
662   hotspots are found along fronts and filaments that aggregate and concentrate prey (Bost et al. 2009;
663   Cotté et al. 2015; Dragon et al. 2010; Scheffer et al. 2010; Warren et al. 2009). The biophysical
664   coupling by which predators use and rely on mesoscale features that can aggregate their prey, and
665   the dive behaviours that determine the decisions predators make in response to prey availability
666   (Friedlaender et al. 2016), are critical to how top predators partition their habitat.

667   While top predators exist in similar regions and often share the same prey, they have different life
668   history patterns and habitat preferences that likely alleviate some of the potential for competition.
669   During the summer, penguins, flying seabirds and fur seals forage along the shelf break and the
670   southern boundary of the ACC, periodically returning to their breeding colonies (Ribic et al. 2011). In
671   winter, seabirds are found near the ice edge, along the shelf break and around the Polar Front to the
672   north (Chapman et al. 2004). While gentoo penguins (*Pygoscelis papua)* remain near their breeding
673   colonies throughout the year (Cimino et al. 2016; Miller et al. 2009), Adélie (*P. adeliae)* and chinstrap
674   (*P. antarcticus)* penguins move far away from their colonies in winter, with Adélie penguins
675   preferring winter sea ice, and chinstrap penguins preferring open water (Hinke et al. 2015;
676   Trivelpiece et al. 2007). Adélie penguins forage in shallow (<200 m) waters near land and in deeper
677   waters (200–500 m) near the edge of deep troughs cross-cutting the shelf (Erdmann et al. 2011).
678   Crabeater (*Lobodon carcinophagus*), Weddell (*Leptonychotes weddellii*) and leopard (*Hydrurga
679   leptonyx*) seals remain in the WAP year-round, maintaining access to ice or land to haul out and
680   reproduce (Figure 11) (Costa et al. 2010). While Weddell seals remain in the fjords, crabeater seals
681   move extensively along the shelf, staying closer to the coast in regions with greatest change in
682   bathymetry, and deep within the pack ice throughout the winter (Burns et al. 2004). The short
683   breeding season of southern elephant seals (*Mirounga leonina*) enables them to spend months at
684   sea moving into the pack ice, along the outer shelf and offshore into pelagic waters (Costa et al.
685   2010). Seals partition their habitat by foraging depth and duration, with the longest and deepest
686   dives by elephant seals (Hindell et al. 2016). Fur seals (*Arctocephalus gazella*) show significant
687   seasonal variability in their distribution, remaining within a few hundred kilometres of their breeding
688   colonies during summer and dispersing widely during winter (Figure 11). Humpback whales
689   (*Megaptera novaeangliae*) forage broadly across the WAP shelf during summer, moving inshore in
690   autumn, with their density and distribution controlled by those of their krill prey and their
691   preference for ice-free conditions and dense aggregations of larger, older krill (Friedlaender et al.
692   2006; Johnston et al. 2012; Murphy et al. 2007; Weinstein and Friedlaender 2017; Weinstein et al.
693   2017). Humpback whales forage in a manner consistent with optimal foraging theory to maximize
694   their energetic gains (Friedlaender et al. 2013; Friedlaender et al. 2016; Tyson et al. 2016) and
695   remain in significant numbers in ice-free areas until the beginning of winter. Minke whales
696   (*Balaenoptera bonaernsis*) avoid competition with humpback whales by foraging on deeper krill

aggregations (Friedlaender et al. 2009) and, being smaller and more manoeuvrable, they can forage under the ice, their preferred habitat (Friedlaender et al. 2014). Recent work found long-term preferences of minke whales for ice edge regions during summer (Williams et al. 2014) and throughout the foraging season (Lee et al. 2017). While they are known to be the only endemic cetacean species, present year-round, evidence suggests that some portion of the population migrates to sub-tropical latitudes in winter (Lee et al. 2017). Blue (*Balaenoptera musculus)* and right (*Eubalena glacialis*) whales are also seasonally present and similarly feed on krill. Different ecotypes of killer whales (*Orcinus orca*) are seasonally present in the WAP following the distribution of their prey (e.g. seals, whales or fish) (Pitman and Ensor 2003).

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

1.8. Benthic ecosystems

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

In general, benthic organisms in the WAP region are characterised by very slow growth and development rates, which are slowed beyond the expected effects of low 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 growth and development are likely caused by restricted protein manufacture at low temperatures (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-latitude species (Arntz et al. 1994; Peck 2018).

Benthic organisms assimilate carbon fixed by primary producers in the overlying water column and/or sea ice, and can store carbon more efficiently and over longer periods than pelagic organisms

743 (Barnes 2017; Peck et al. 2010). The degree and timescale of carbon sequestration is dependent on
744 sea ice dynamics and the duration of the ice algal and phytoplankton blooms, local oceanographic
745 conditions such as current speeds and nutrient supply, organisms' lifespans and behaviours, and the
746 frequency of ice scour, which has a major role in structuring shallow benthic ecosystems (Barnes et
747 al. 2018). The contribution of benthic processes to pelagic productivity via nutrient supply at the
748 WAP is a current area of debate. Nutrient release from sediments and porewaters by diffusion,
749 physical disturbance and bioturbation by burrowing organisms, such as polychaetes, echinoderms
750 and bivalve molluscs (Poigner et al. 2013), has the potential to act as a significant source of nutrients
751 to water column biota. Physical disturbance by iceberg scour can expose buried sediments from
752 water depths exceeding 300 m, and can produce sediment scours over 10 m deep (Lien et al. 1989),
753 releasing large quantities of sediment-derived nutrients. Currents entrained by moving icebergs can
754 redistribute sediment several metres up into the water column for short periods and across many
755 metres of the seabed (Bigg 2016; Peck et al. 2005). Icebergs can also distribute sediments over
756 considerable distances and through the water column as ice melts, and act as a dispersal mechanism
757 for some benthic species (Peck 2018). Mixing of the upper water column by icebergs, winds and
758 currents will regulate the extent to which sediment-derived nutrients reach the surface ocean and
759 influence pelagic primary productivity.

760

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

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

768 2.1. Physical oceanography and ice dynamics

769 The long-term change in atmospheric and oceanic properties along the WAP has been a strong focus
770 of scientific efforts given its large magnitude, and its observed and potential impact on the regional
771 ecosystem (Constable et al. 2014a, b; Ducklow et al. 2013; Martinson et al. 2008; Meredith et al.
772 2017; Schofield et al. 2017; Venables et al. 2013). The evolution of sea ice cover on timescales from
773 seasonal to inter-decadal is a key modulator of physical and biogeochemical processes on the shelf.
774 For example, sea ice extent and its growth and retreat modulate vertical mixing, air-sea fluxes, light
775 penetration, and the salt and heat content of the surface ocean. On average, sea ice extent in the
776 WAP region varies between 1 and 6 x 10^5 km^2 over the annual cycle (Meredith et al. 2017). Alongside
777 substantial warming of the atmosphere and ocean, the period of seasonal sea ice cover has
778 shortened by more than three months since the late 1970s, with autumn advance being delayed by
779 two months and spring retreat occurring more than one month earlier (Stammerjohn et al. 2012;
780 Stammerjohn et al. 2008a). Strong correspondence between retreat and subsequent advance
781 suggests a strong feedback in ocean thermal properties in autumn in response to changes in the
782 timing of retreat in spring. The trend is less clear in the northern WAP (Schloss et al. 2012) where
783 substantial sea ice declines have already occurred, although Bers et al. (2013) showed the strong
784 effect of climatic forcing even in inshore waters of King George Island.

785 The warming trends and salinity changes documented in the surface and deep water layers across
786 much of the WAP shelf have not been observed in Bransfield Strait, likely because of the modulation
787 by Weddell Sea inflow around the northern tip of the Peninsula (Bers et al. 2013; Meredith and King

788   2005; Schloss et al. 2012; Schmidtko et al. 2014). This highlights strong gradients along the shelf in
789   the processes controlling long-term property trends, as well as the mean properties themselves. The
790   alongshore structure of mid-depth (>100 m) ocean temperature plays a pivotal role in glacier retreat
791   rates along the WAP, with warmer subsurface waters in the southern and central WAP (south of
792   Bransfield Strait) acting as the primary driver of substantial glacial retreat along the adjacent coast
793   (Cook et al. 2016; Padman et al. 2012). In contrast, glaciers along Bransfield Strait terminate in
794   colder Weddell-modulated waters and are retreating at slower rates, with some even advancing. In
795   cases where glaciers in the northern WAP are experiencing high melt rates and retreat, for example
796   at King George Island, atmospheric forcing is thought to be the primary driver (Falk and Sala 2015).

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

805   2.2. Phytoplankton and microbial community dynamics

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

824   Coastal time-series data from Potter Cove at King George Island/ Isla 25 de Mayo (Schloss et al.
825   2012) and Palmer Station at Anvers Island (Schofield et al. 2017) suggest that the observed declines
826   in phytoplankton biomass reversed around 2010. In Potter Cove, chlorophyll concentrations were
827   typically low between 1991 and 2009, with maximum values (~4 mg m^{-3}) during short-lived episodic
828   events, when phytoplankton assemblages were dominated by large diatoms from several genera
829   (*Corethron criophilum, Odontella weissflogii, Eucampia antarctica, Thalassiosira sp., Porosira sp.*)
830   (Schloss et al. 1997). Nutrients were not limiting, and low phytoplankton biomass was attributed to
831   adverse physical conditions, with intense turbulent mixing and sediment-rich meltwater inputs
832   limiting light conditions for phytoplankton growth and preventing bloom formation (Schloss et al.
833   2002; Kim et al. 2018). A first high-chlorophyll bloom (~14 mg m^{-3}) lasted approximately two weeks
834   in January 2010 and was followed by several subsequent high-chlorophyll seasons, with the same

835 genera present as earlier in the time series (Schloss et al. 2014; Kim et al. 2018). Whilst a
836 combination of low air temperatures, which delayed the melting of the surrounding Fourcade
837 glacier, and low wind intensities can explain the bloom duration in January 2010, different
838 mechanisms are behind increased productivity in more recent years. Experimental work has shown
839 that smaller diatoms (e.g. *Navicula*, *Nitzschia*, etc.) have greater tolerance to low salinities than large
840 diatoms (Hernando et al. 2015), such that the phytoplankton response to glacial meltwater inputs
841 may differ depending on community composition and the timing of inputs relative to bloom
842 progression.

843 Chlorophyll concentrations have also increased since the late 2000s at Palmer Station, ~400
844 kilometres to the south, concurrent with an increase in the number of days of sea ice cover each
845 year and shallower spring/summer mixed layers, which have led to larger phytoplankton blooms
846 dominated primarily by diatoms (Schofield et al. 2017). This is in contrast to much of the duration of
847 the Palmer time series, where a statistically significant decline in sea ice duration was observed. At
848 the Rothera Time Series (RaTS) in northern Marguerite Bay, ~400 kilometres south of Palmer Station,
849 short-lived winter sea ice cover led to a substantial reduction in summertime chlorophyll levels
850 between 2007 and 2010 (Venables et al. 2013). Since 2010, sea ice duration and chlorophyll have
851 increased again, with sea ice persisting into December and large phytoplankton blooms (chlorophyll
852 >15 mg m^{-3}) in the most recent years. A recent synthesis of chlorophyll and physical oceanographic
853 time-series data from Potter Cove, Palmer and Rothera demonstrates that whilst large-scale climate
854 forcing influences all three sites, local processes such as ice melt and mixing superpose distinct
855 interannual patterns and trends (Kim et al. 2018). Longer-term changes in primary production and
856 community structure over the WAP shelf will depend on the interaction of long-term climatic
857 warming trends and large natural internal variability in regulating seasonal sea ice dynamics over
858 interannual-to-decadal timescales.

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

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

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

882   2.3. Biogeochemical changes and air-sea exchange

883   Physical and biological changes along the WAP are closely related to changes in ocean chemistry and
884   biogeochemistry, in particular the budgets and cycling of macro- and micronutrients, and the
885   production and air-sea exchange of climate-active gases, with the potential for larger-scale
886   consequences and feedbacks. For example, continued glacial retreat can be expected to increase the
887   supply of iron and other micronutrients (Zn, Cd, Co etc.) from glacial and shallow sediment sources,
888   and potentially their availability to phytoplankton (Annett et al. 2015; Annett et al. 2017; Bown et al.
889   2017, 2018; Hendry et al. 2008; Monien et al. 2017). Seasonal biological uptake of nutrients and
890   carbon will be determined by the documented variability and ongoing changes in seasonal
891   phytoplankton dynamics driven by changes in sea ice and upper ocean conditions (Henley et al.
892   2017; Legge et al. 2015; Kim et al. 2016).

893   Changes in the properties, transport and circulation of CDW across the shelf, particularly in the
894   southern and central WAP regions to the south of Bransfield Strait (Martinson et al. 2008; Schmidtko
895   et al. 2014), are likely to increase the supply of macronutrients and CO_2 to subsurface shelf waters.
896   The extent to which this affects surface ocean nutrient and carbon budgets will depend on the
897   evolution of mixing processes in response to sea ice and atmospheric forcing. Carbonate system
898   parameters (DIC, TA, pCO_2) on the Palmer LTER grid do not show statistically significant trends
899   during summer seasons between 1993 and 2012 (Hauri et al. 2015). However, a continuation of the
900   long-term reduction in seasonal sea ice cover and continued strengthening and southward shifting of
901   westerly winds (Le Quéré et al. 2007; Stammerjohn et al. 2008b; Landschützer et al. 2015) may
902   increase upwelling of DIC-rich water and CO_2 outgassing in winter, as well as altering the
903   phytoplankton community and potentially reducing biological CO_2 uptake in summer (Legge et al.
904   2015; Saba et al. 2014). The resultant reduction in net annual CO_2 uptake along the WAP is unlikely,
905   in itself, to make a significant difference to the functioning of the Southern Ocean CO_2 sink, due to
906   the small size of the WAP shelf region. However, if the changes anticipated at the WAP are manifest
907   across larger areas of the Southern Ocean in the coming decades, the detailed knowledge of the
908   physical and biological mechanisms regulating CO_2 fluxes obtained in the WAP system will be useful
909   in projecting change at the wider scale, which could be significant terms in the global carbon budget.

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

916   2.4. The WAP pelagic food web

917   Interannual variability in phytoplankton biomass has strong implications for the productivity of the
918   entire food web, with low chlorophyll years leading to less successful recruitment of the keystone
919   species Antarctic krill *(Euphausia superba)* (Atkinson et al. 2004; Saba et al. 2014). As such, low sea
920   ice conditions are likely to hold negative consequences for higher trophic levels such as penguins,
921   flying sea birds, seals and whales (Constable et al. 2014a, b; Costa et al. 2010; Trivelpiece et al.
922   2011). Conversely, the recent increases in chlorophyll are likely to be beneficial for zooplankton and
923   their pelagic and benthic consumers (Saba et al. 2014).

924   Seasonal changes in WAP macrozooplankton abundance are driven by a combination of long-term
925   trends linked to warming and sea ice declines, sub-decadal shifts attributed to oscillations in
926   atmospheric forcing, such as SAM and ENSO, which affect sea ice dynamics and sea surface

temperature, and local and regional changes in primary production, all of which have strong
interdependences (Figure 13; Steinberg et al. 2015). For example, a decrease in krill density between
the 1970s and early 2000s in the WAP and southwest Atlantic sector of the Southern Ocean was
attributed to long-term warming and sea ice declines, which reduce the availability of the winter and
spring ice algal food source required to promote larval survival and recruitment, as well as driving
the overall decline in the summer phytoplankton food source (Atkinson et al. 2004; Montes-Hugo et
al. 2009). It has been contested that this decline in krill resulted from a period in the decadal-scale
population 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 shown a southward contraction of krill distribution throughout the sector over the last 90 years,
with a concomitant reduction in juvenile recruitment linked to reduced food availability, and a
concentration of the population over the WAP shelf (Atkinson et al. 2019). Since the early 1990s, krill
abundance on the Palmer LTER grid (central and southern WAP) has shown a stable 5-year cycle that
reflects variability in reproductive and recruitment success linked to ENSO cycles and their influence
on sea ice dynamics (Loeb et al. 2009; Quetin and Ross 2003; Ross et al. 2014; Steinberg et al. 2015),
in broad agreement with findings from the northern WAP around the South Shetland Islands (Loeb
and Santora 2015; Richerson et al. 2017). Accordingly, both *E. superba* and *Thysanoessa macrura* are
positively correlated to regional primary production two years prior (Figure 13; Steinberg et al.
2015). Local effects can also be pronounced, for instance high krill mortality in Potter Cove in recent
years is attributed to unfavourable conditions caused by high meltwater-sourced particle loads from
a retreating glacier (Fuentes et al. 2016). In contrast to krill, abundance of the major copepod taxa
showed a regional long-term increase over the shelf between 1993 and 2013 (Gleiber 2015).
Variability in *Salpa thompsoni* over the shelf is influenced by both ENSO (Loeb and Santora 2012) and
SAM (Figure 13; Steinberg et al. 2015), whilst long-term increases throughout the southwest Atlantic
sector have accompanied the declines in krill (Atkinson et al. 2004). Variability in abundance of the
pteropod *Limacina helicina* along the WAP is also linked to ENSO cycles (Figure 13; Loeb et al. 2009;
Loeb and Santora 2013; Ross et al. 2014; Steinberg et al. 2015). Shifts in phytoplankton community
structure can also affect the abundance of krill relative to other major zooplankton taxa, because the
grazing efficiency of *E. superba* is reduced significantly on particles <20 µm, such that diatom-
dominated communities are likely to favour krill, whilst communities dominated by cryptophytes
and/or haptophytes are likely to favour salps and other taxa (Haberman et al. 2003; Meyer and El-
Sayed 1983; Moline et al. 2004). Shifts in the dominance of krill compared to other taxa have major
consequences for higher trophic levels that rely on krill as their primary food source, as well as for
carbon export and nutrient recycling, and may lead to substantial reorganisations of the pelagic food
web (e.g. Atkinson et al. 2004, 2019; Quetin and Ross 2003).

The distribution and abundance of a number of krill-dependent pelagic consumers are changing in
concert with changes in the physical environment and the availability of krill (Constable et al. 2014a,
b). Winter sea ice conditions along the WAP are particularly important for krill predators, because
they regulate krill availability and therefore foraging conditions, which are a key determinant of
recruitment and overwinter survival of adult and juvenile animals (Hinke et al. 2017b). Sea ice-driven
changes in phenology can also lead to trophic mismatches between predator foraging needs and
prey availability, with major demographic consequences (Youngflesh et al. 2017). Populations of ice-
dependent Adélie and chinstrap penguins have declined significantly (e.g. Figure 14; Ducklow et al.
2013; Hinke et al. 2017a; Juares et al. 2015; Trivelpiece et al. 2011) and the only Emperor penguin
colony at the WAP has been lost due to changes in seasonal sea ice duration (Trathan et al. 2011).
Southward shifts of the maritime climate, displacing the Antarctic climate, have also increased
precipitation and snow accumulation, which reduces the survival of Adélie penguin chicks (Carlini et
al. 2009; Chapman et al. 2011). In the northern WAP in particular, the shift to a more maritime
climate is likely to shift southward the distributions of ice- and krill-dependent species, such as
Weddell and crabeater seals, minke whales and Adélie penguins, leading to local declines as their

977 habitat contracts with diminishing sea ice (Ducklow et al. 2013; Huckstadt et al. 2012a; Siniff et al.
978 2008). In contrast, ice-tolerant species such as fur seals, humpback whales and gentoo penguins and
979 those less dependent on krill, such as elephant seals, have increased in number (Costa et al. 2010;
980 Ducklow et al. 2013) and in the length of time they remain feeding locally (e.g. Friedlaender et al.
981 2016; Weinstein and Friedlaender 2017). The decline in Adélie penguin numbers slowed down in the
982 mid-2000s and the total number of penguins stabilised, although this was a consequence of
983 increasing gentoo penguin numbers (Figure 14). Some krill predators exhibit trophic plasticity and
984 can increase their consumption of fish in years of lower krill availability (e.g. crabeater seals;
985 Huckstadt et al. 2012a), although the extent to which this plasticity can relieve the dependence on
986 krill remains unknown. Sub-Antarctic King penguins (*Aptenodytes patagonicus*) have extended their
987 distribution southwards, recently being recorded for the first time at King George Island (Juares et al.
988 2017). Increasing westerly wind intensity has benefitted wandering albatrosses (*Diomedea exulans*),
989 by increasing their foraging speeds and reducing trip length, thus enhancing their foraging efficiency
990 and breeding success (Weimerskirch et al. 2012).

991 2.5. The WAP benthic food web

992 Benthic communities along the WAP are sensitive to variability in physical and biogeochemical
993 forcing, because many organisms are sessile and therefore unable to migrate. Benthic responses to
994 ocean warming depend on organisms' abilities to adapt or acclimate to altered conditions. Antarctic
995 benthos have a reduced capacity to adapt compared to lower-latitude populations, due to their low
996 production rates of novel genetic material that enhance survival, which arise from longer generation
997 times and production of fewer larger eggs, without an increase in mutation rate or population size
998 (Arntz et al. 1994; Higgs et al. 2009; Johnson et al. 2001; Peck 2018). Geneflow between Antarctic
999 populations is also slower than for temperate or tropical populations due to relatively high levels of
1000 protected development and proportionally fewer species using pelagic larval dispersal (Arntz et al.
1001 1994; Peck 2018; Hoffman et al. 2011, 2012). For species that do use pelagic dispersal, rising ocean
1002 temperatures increase larval development rates, thus shortening the larval phase substantially (Peck
1003 2016, 2018). This reduces dispersal distances and increases isolation between populations, as well as
1004 altering the timings of reproductive cycles in relation to key environmental events (Bowden et al.
1005 2009), such that larval success may decline significantly due to phenological mismatches as warming
1006 proceeds.

1007 Given limited rates of adaptation, Antarctic benthos need sufficient phenotypic plasticity to
1008 acclimate to altered conditions and survive the projected climate change in coming decades (Peck
1009 2011). Antarctic fish (Bilyk and DeVries 2011) and invertebrates (Morley et al. 2016; Peck 2018; Peck
1010 et al. 2009, 2014) have very limited tolerance to warming in laboratory-based experiments,
1011 indicating that acclimation to elevated temperature is poor in Antarctic species (Peck et al. 2014).
1012 Thermal tolerances are influenced by a number of different species-specific factors (Clark et al.
1013 2017), including heat shock responses to warming (Clark and Peck 2009; Clark et al. 2008), and upper
1014 temperature limits being set by accumulation of toxic metabolic end-products (Heise et al. 2007),
1015 limitation of energy reserves (Peck 2018; Peck et al. 2014), and temperature sensitivity of critical
1016 enzymes (Clark et al. 2016). In general, the rate of oxygen supply to tissues (Pörtner and Farrell
1017 2008; Pörtner et al. 2012) does not appear to exert a major limitation on thermal tolerance (e.g.
1018 Devor et al. 2016). The first *in situ* warming experiment in the Southern Ocean, conducted at
1019 Rothera Station, showed that growth of biofouling species was significantly faster at 1°C above
1020 ambient than at ambient (Figure 15). This was attributed to factors including more efficient protein
1021 synthesis and faster processing of food allowing greater nutrient intake in a summer season (Ashton
1022 et al. 2017). Mixed results from +2°C treatments likely indicate that growth of some species was
1023 restricted by their temperature limits.

1024 Benthic community structure is strongly influenced by ice dynamics along the WAP. Whereas sea ice
1025 organic fluxes are an important food source for the benthos, solid ice can have a devastating effect
1026 by removing a significant proportion of macro- and meiofauna from the seabed (Peck et al. 1999;
1027 Lee et al. 2001). Iceberg impacts can be very frequent in shallow waters along the WAP (Brown et al.
1028 2004), and ongoing increases in iceberg scour driven by glacial retreat, receding ice shelves and an
1029 overall decline in fast ice have caused a marked drop in biomass of shallow benthic fauna in Ryder
1030 Bay, Adelaide Island (Barnes and Souster 2011). This is expected to continue, and potentially
1031 intensify in the coming decades (Barnes 2015; Smale et al. 2008). In Potter Cove, South Shetland
1032 Islands, increased sedimentation from a retreating glacier was the most important factor driving
1033 sudden shifts in nearby benthic assemblage composition with unexpectedly rapid loss of diversity
1034 and biomass (Sahade et al. 2015; Torre et al. 2017). Contrary to the adverse effects of ice scour and
1035 ice-derived sedimentation, the retreat of coastal glaciers and disintegration of ice shelves along the
1036 WAP has opened up new ocean areas for pelagic productivity and benthic ecosystem development
1037 (Peck et al. 2010). The loss of benthic carbon storage caused by increased iceberg scour during
1038 glacial retreat and ice shelf disintegration is significantly outweighed by the increase in carbon
1039 storage resulting from increased primary production and benthic biomass, such that these ice losses
1040 lead to a substantial net increase in carbon drawdown to the seabed (Barnes 2015, 2017; Barnes et
1041 al. 2018). Glacial retreat has also opened up newly ice-free areas in Potter Cove, including a new
1042 island, which have been colonised by communities exhibiting high diversity, biomass and a complex
1043 structure at rates far exceeding previously observed or predicted rates in Antarctic benthos (Lagger
1044 et al. 2017a, b). Macroalgal forests can colonise recently ice-free hard substrates (Campana et al.
1045 2018; Quartino et al. 2013), and may expand further in the northern WAP in future as more frequent
1046 ice-free winters and early spring fast-ice disintegration are expected to increase the annual light
1047 budget (Deregibus et al. 2016). Bacterial groups that dominate in sediments enriched with
1048 macroalgal detritus (e.g. Proteobacteria, Bacteroidetes, Planctomycetes and Verrucomicrobia) would
1049 also become increasingly important with continued macroalgal expansion (Abele et al. 2017; Pasotti
1050 et al. 2015). The net effect of ongoing ice changes for benthic communities along the WAP will
1051 depend on water depth and proximity to glaciers and/or ice shelves, and their effect on iceberg
1052 scour, sedimentation and light availability. Results from Potter Cove show that benthic ecosystem
1053 responses may be non-linear and particularly rapid, intense and heterogeneous in fjordic systems.
1054 Throughout the coastal WAP, longer-term losses of glaciers and ice shelves may reduce ice scour and
1055 sedimentation significantly, increasing benthic carbon drawdown substantially, but the timing of
1056 these changes is unknown.

1057 Invasive species occur on the WAP shelf as a result of larval dispersal and anthropogenic vectors
1058 such as ship ballast water and hull biofouling (Clayton et al. 1997; Hughes and Ashton 2017; Lee and
1059 Chown 2009). The long-term warming and sea ice trends are altering the natural barriers to species
1060 invasions along the WAP, by dampening the effect of sea ice cover in reducing dispersal and killing
1061 potential invasives, by increasing the coverage of year-round ice-free shallow benthic habitats, and
1062 by weakening the temperature limitation of biological processes in warmer-water species (McCarthy
1063 et al. 2019). These trends combined with increasing ship traffic are likely to promote the import and
1064 success of invasives along the WAP, with potential for major ecosystem disruption, although the
1065 timing, magnitude and impact of these invasions is not known.

1066 2.6. Ecosystem responses to ocean acidification

1067 Ocean acidification is expected to be particularly pronounced and to occur earlier in the Southern
1068 Ocean, which absorbs more than 40 % of global anthropogenic CO_2 (Fletcher et al. 2006; Orr et al.
1069 2001), than in other ocean regions (Feely et al. 2009; McNeil and Matear 2008; Orr et al. 2005).
1070 Whilst statistically significant trends in inorganic carbon and pH have not yet been detected at the
1071 WAP (Hauri et al. 2015), aragonite Ω close to 1 has recently been documented in the coastal WAP

1072 during winter (Jones et al. 2017), making aragonitic organisms susceptible to small changes in pH.
1073 Decadal enrichment in inorganic carbon and acidification have been documented in the Drake
1074 Passage to the north (Hauri et al. 2015; Takahashi et al. 2014), suggesting that this mechanism may
1075 have significant ecosystem consequences along the WAP in future.

1076 Ocean acidification has the potential to impact on WAP phytoplankton communities, as experiments
1077 from the Ross Sea have shown a shift from the small haptophyte *Phaeocystis antarctica* or pennate
1078 diatoms at low CO_2 to large centric chain-forming *Chaetoceros* diatoms at elevated CO_2 levels (Tortell
1079 et al. 2008; Feng et al. 2010). These findings were supported by laboratory studies that suggest
1080 diatoms may have a competitive advantage over other taxa at elevated CO_2 (Chen and Gao 2004;
1081 Sobrino et al. 2008; Wu et al. 2010). An acidification-driven shift towards larger diatoms would act
1082 against the proposed shift towards smaller diatoms, haptophytes and cryptophytes driven by
1083 changing ice distributions and freshwater inputs (e.g. Hernando et al. 2015; Rozema et al. 2017a;
1084 Schofield et al. 2017). As such, the phytoplankton response to competing physical and biological
1085 forcings along the WAP could vary significantly over time and space, compounding variability in the
1086 forcings themselves. Shifts in phytoplankton species composition could have significant
1087 consequences throughout the food web due to different feeding preferences of the major
1088 zooplankton taxa and their consumers.

1089 The effects of ongoing atmospheric CO_2 uptake and ocean acidification on polar zooplankton are not
1090 well understood. To the north of the WAP in the Scotia Sea, live pteropods (*L. helicina*) showed signs
1091 of shell dissolution in a region undersaturated with aragonite (Bednaršek et al. 2012). Conversely,
1092 recent evidence for *L. helicina* from the Arctic repairing their shells after mechanical and dissolution
1093 damage suggests that these pteropods may be more resilient to ocean acidification than previously
1094 thought (Peck et al. 2018). *E. superba* in the WAP region have been shown to increase their feeding
1095 and excretion rates under high CO_2 conditions, especially in the case of pregnant krill (Saba et al.
1096 2012).

1097 Antarctic benthos are thought to be vulnerable to current and future ocean acidification, because
1098 many have calcified skeletons that use up a greater proportion of the organism's energy budget than
1099 lower-latitude species (Watson et al. 2017), as well as low physiological rates and a limited ability to
1100 resist environmental change in general. Research on the capacity of Antarctic benthos to acclimate
1101 to lowered pH is conflicting, with some studies showing poor capacities in certain organisms (e.g.
1102 Schram et al. 2016), whilst most studies demonstrate little effect of lowered pH, even on early
1103 stages (e.g. Catarino et al. 2012), and several studies demonstrate greater effects of temperature
1104 than pH (Byrne et al. 2013; Cross et al. 2015; Kapsenberg and Hofmann 2014). Recent studies show
1105 that although long acclimation periods are required, Antarctic benthos can acclimate to altered pH,
1106 at least to end-century conditions, and acclimated organisms exhibit physiological and reproductive
1107 performance similar to those in controls (Cross et al. 2015; Suckling et al. 2015; Morley et al. 2016).

1108 3. Overarching priorities and approaches for future work

1109 Whilst significant progress has been made in recent decades in understanding the functioning of the
1110 WAP shelf ecosystem, its physical and biogeochemical drivers, the coupling between the ocean and
1111 atmosphere, and how these interactions are changing over time, critical knowledge gaps remain.
1112 Further elucidation is required regarding the relative importance of the different controlling
1113 mechanisms and the interactions between these mechanisms, in order to develop a whole-system
1114 understanding of the WAP shelf ecosystem and its response to ongoing changes in climate and the
1115 physical environment over seasonal-to-decadal timescales. As sea ice dynamics exert such an
1116 important control on ocean physics, chemistry and ecosystem functioning, a fundamental challenge
1117 for the observational and modelling communities is to unravel the importance of long-term climate-

1118   driven trends compared with large natural internal variability, and consequently the extent to which
1119   the recent slow-down in warming and sea ice losses will persist against the background long-term
1120   trend. This challenge is a highly active area of research for the international community (Reid and
1121   Massom 2015; Reid et al. 2018), but will ultimately require longer time series of satellite and *in situ*
1122   ocean and sea ice measurements, and an improvement in the performance of IPCC-class models for
1123   the forthcoming Coupled Model Intercomparison Project Phase 6 (CMIP6). Regional models can be
1124   used to elucidate the important local-scale ice-ocean-atmosphere feedbacks modulated by relatively
1125   small-scale processes (e.g. ocean eddies with scales of a few kilometres). However, given the known
1126   dependence of WAP climate on remote processes (e.g. ENSO, and its interaction with the SAM),
1127   these models would need to take reliable boundary conditions from global climate/Earth System
1128   models that reproduce both the low-latitude modes and their propagation to high latitudes. Such a
1129   framework would allow us to increase the reliability of the relevant signals in the IPCC-class models
1130   and improve our ability to project future changes in ice coverage and duration.

1131   Table 1 outlines the important discipline-specific research objectives in WAP marine science over the
1132   next 2-10 years, and Table 2 outlines the key approaches and innovations required to address these
1133   objectives. One of the major findings over the last three decades has been the importance of
1134   physical oceanographic processes in modulating biological and biogeochemical processes, from
1135   nutrient supply and phytoplankton dynamics to zooplankton distributions and foraging behaviour of
1136   pelagic consumers. This degree and multilateral nature of physical control makes defining the
1137   processes of oceanic water mass transport onshore, and its modification and vertical ventilation on
1138   the shelf, a key priority. The importance of ice-ocean interactions necessitates full characterisation
1139   of sea ice dynamics, glacial meltwater and other freshwater inputs, and their modulation of these
1140   physical processes. Quantifying these physical dynamics will pave the way for projecting their
1141   impacts on biogeochemical and biological processes throughout the entire food web. Pronounced
1142   spatial heterogeneity and temporal variability on timescales of several days to decades necessitates
1143   longer time series capturing the complete annual cycle and increased temporal and spatial
1144   resolution of observations across the shelf, including under the sea ice. This increased resolution and
1145   capability can be achieved by developing an observing system for the WAP shelf combining
1146   traditional ship- and station-based approaches with novel technologies based on gliders,
1147   autonomous underwater vehicles (AUVs), and mooring and high-frequency (HF) radar networks.

1148   HF radar measures ocean surface (upper 1 m) current velocities over hundreds of square miles
1149   simultaneously. A shore-based three-site HF radar network deployed recently at the WAP provides
1150   hourly surface current data over the entire Palmer Station region (Figure 16), and has been used
1151   with penguin foraging data to identify the selection of foraging locations relative to mapped
1152   convergent features over the Palmer Deep canyon (Kohut et al. 2014). These systems have proven to
1153   be robust and cost-effective with many applications, and a significant opportunity exists to develop a
1154   shelf-wide integrated system to define the regional surface ocean circulation, which is currently one
1155   of the least understood aspects of the shelf circulation.

1156   Moorings have been deployed routinely along the WAP, providing high-frequency time-series
1157   measurements year-round for over a decade. These moorings have been critical in documenting the
1158   frequency and mechanisms of subsurface intrusions of modified CDW onto the continental shelf
1159   (Martinson and McKee 2012; Moffat et al. 2009). A key limitation of moorings is that they are
1160   typically unable to collect data near the surface, due to the presence of seasonal ice and icebergs
1161   (Savidge and Amft 2009), and their spatial coverage is limited.

1162   Autonomous gliders (Sherman et al. 2001; Eriksen et al. 2001; Webb et al. 2001) are complementing
1163   mooring measurements by providing high-resolution spatial measurements over the full shelf depth
1164   (Carvalho et al. 2016; Carvalho et al. 2017; Couto et al. 2017; Brearley et al. 2017). These gliders are

1165 capable of sampling over thousands of kilometres and spending months at sea, making them ideal
1166 for maintaining a sustained presence and filling critical observational gaps between ship-board
1167 surveys, research stations and mooring arrays, and at smaller spatial scales than are captured by
1168 shipboard sampling (Venables et al. 2017). These systems are cost-effective, capable of carrying a
1169 range of physical and biogeochemical sensors, and have been proven to be effective tools to
1170 leverage data collection across a broad range of applications and ocean regions (Schofield et al.
1171 2015).

1172 Powered AUVs have been used in the Southern Ocean for bathymetric, physical oceanographic and
1173 biological surveys under and in the vicinity of sea ice (e.g. Brierley et al. 2002). Expanding the use of
1174 such AUVs in the WAP region has the potential to provide a wealth of water column data from
1175 under-ice environments. Most under-ice powered AUV missions to date have been conducted by
1176 large complex platforms capable of under-ice navigation and advanced autonomous decision-
1177 making, requiring ship support and making deployments expensive. Transitioning to smaller, less
1178 complex and less expensive systems capable of sustained missions would increase the number and
1179 scope of deployments at the WAP and elsewhere.

1180 Using autonomous technologies will be of particular value in improving observational coverage
1181 during ice formation in autumn, the ice-covered winter period and the springtime transition from
1182 winter into the ice-free phytoplankton growing season. These times of year are critically important
1183 in regulating phytoplankton bloom dynamics, and other key ecosystem processes, yet remain
1184 severely undersampled across all disciplines of WAP marine science. In future, real-time sampling
1185 and data transfer using these technologies has the potential to inform predictions of key ecosystem
1186 processes at the seasonal scale, e.g. phytoplankton bloom timing, magnitude and distribution based
1187 on satellite, mooring and profiling float data, with gliders providing
1188 measurements/parameterisations of mixed layer depth and stability. Upscaling the use of gliders
1189 and powered AUVs in the seasonally ice-covered WAP shelf environment would require a robust and
1190 well-integrated system for under-ice navigation, using compact accurate inertial navigation systems
1191 and/or acoustic telemetry networks that allow AUVs to triangulate their position. Such systems
1192 would facilitate major innovations in future observational studies, for example in elucidating the role
1193 of small- and meso-scale processes under the ice, the transports they produce, and their effect on
1194 the larger-scale circulation, under-ice ecosystems and biogeochemical cycles. Alongside
1195 technological developments in observational approaches, improvements in the resolution of
1196 regional ocean circulation models and incorporation of realistic bottom topography are required to
1197 fully resolve the most important physical drivers of the shelf ecosystem.

1198 Utilising the WAP shelf region as a natural laboratory or model system to understand the impacts of
1199 climate and sea ice changes and the resultant physical oceanographic changes here and in other
1200 marginal ice zone settings on phytoplankton dynamics, carbon and nutrient cycling, air-sea fluxes of
1201 climate-active gases, and pelagic, benthic and microbial food webs requires an integrated approach.
1202 Novel process-based experimental, technological and modelling approaches should be combined
1203 with the long-running time-series and spatial measurements that form the backbone of our
1204 knowledge of variability and change in the WAP marine system. Given pronounced heterogeneity
1205 across the shelf, quantifying the importance of biological hotspots for the regional ecosystem and
1206 biogeochemical cycling is a high priority. Detailed process studies and repeat sampling of these
1207 hotspots, including along the sea ice edge and in the high-productivity fjords, will improve our
1208 understanding of the conditions required to create these hotspots and their change over time.

1209 In such a highly coupled system, it is imperative to cross-cut disciplinary boundaries and characterise
1210 the interactions between different system components, e.g. phytoplankton, zooplankton and
1211 microbial dynamics in regulating biogeochemical cycling and the biological carbon pump, bottom-up

1212   versus top-down predation control of zooplankton distributions, and benthic faunal composition and
1213   behaviours and benthic-pelagic nutrient fluxes. Further application of genomics, transcriptomics and
1214   proteomics approaches has the potential to revolutionise our understanding of microbial processes
1215   and interactions, and marine ecosystem functioning in general, by revealing vital functions of
1216   phytoplankton and bacterioplankton, and identifying the many viruses infecting a range of hosts.
1217   Combining a range of methodologies relevant to different processes, interactions and timescales will
1218   also be critical to making progress. Adopting such an interdisciplinary whole-system approach offers
1219   perhaps the most promising opportunity for driving a step-change in our understanding of the
1220   functioning of the WAP marine ecosystem and its response to, and role in, ongoing climatic and
1221   environmental changes, making this a clear overarching priority for the international community.

1222   Temporal and spatial coverage of data illuminating these physical-biological-biogeochemical
1223   interactions can be augmented by maintaining and strategically enhancing the existing programs of
1224   sustained observations, by adopting the essential ocean variables (EOVs; Constable et al. 2016; A
1225   Framework for Ocean Observing, 2012) as a framework for an observing system for the WAP, and by
1226   employing technological innovations to fill data gaps and increase resolution in time and space. In
1227   addition to the discipline-specific approaches and innovations outlined in Table 2 and the physics-
1228   based technologies detailed above, a number of sensor-based innovations can be employed across
1229   disciplines and provide a more integrated perspective. For example, the utility of AUVs, gliders and
1230   moorings can be expanded substantially by increasing the number and reliability of sensors capable
1231   of measuring a range of physical, biological and chemical parameters (e.g. turbulence, fluorescence,
1232 pCO_2, nitrate). Equipping seals with small CTD tags has provided the extensive hydrographic MEOP
1233   (Marine Mammals Exploring the Oceans from Pole to pole) dataset alongside complementary animal
1234   behaviour data (Treasure et al. 2017), with significantly greater coverage than otherwise available.
1235   Developing and deploying a greater range of sensors (e.g. fluorescence, dissolved oxygen etc.) would
1236   facilitate more detailed sampling in ice-covered regions, near-shore embayments and over larger
1237   spatial scales than ship-based efforts. Systematic deployment of multi-frequency acoustics on ships,
1238   moorings and AUVs would allow us to estimate krill biomass and distribution, and the movement
1239   and foraging behaviour of their pelagic predators, with unprecedented accuracy and coverage across
1240   the shelf, including in the data-sparse southern region and under ice.

1241   In the context of physical controls on ecosystem structure and functioning, a major question to be
1242   addressed is the extent to which organisms at all trophic levels can acclimate, adapt, migrate, and/or
1243   change their behaviours, and the rates at which these processes can occur. Process studies and
1244   manipulation experiments are required, focusing on the physiological profiles of the major species of
1245   phytoplankton, bacterioplankton, viruses, zooplankton and benthic organisms across current and
1246   future physical (temperature, salinity, mixing), chemical (macro- and micronutrients, pCO_2 and Ω)
1247   and ecological (grazing pressure, viral infection) conditions, and therefore their ability to acclimate.
1248   Rates of geneflow within and between populations are needed to quantify the capacity of benthic
1249   and pelagic communities to adapt to altered environments. Top predators can be used as sentinels
1250   of ecosystem change as their abundance and distributions reflect those of their prey. Reproductive
1251   studies targeting major zooplankton taxa and higher trophic level organisms and in-depth studies of
1252   the growth, diet and behaviours of juveniles would inform our assessments of recruitment success
1253   and population dynamics of key species, and their responses to different conditions. Understanding
1254   organisms' abilities to acclimate, adapt, migrate and/or change behaviours, and over what
1255   timescales, will shed light on the resilience and sensitivity of different ecosystem components in the
1256   face of pronounced environmental variability and change, and their response to multiple natural and
1257   anthropogenic stressors.

1258   Direct human pressure on regional krill stocks is increasing as a result of expanding commercial
1259   fishing activity, particularly in the northern WAP and adjacent open ocean, potentially reducing food

1260 availability for krill predators (Trivelpiece et al. 2011). Management of this fishery by the Convention
1261 on Conservation of Antarctic Marine Living Resources (CCAMLR) must be informed by our knowledge
1262 of the foraging behaviour of krill predators, for instance using satellite tags and motion-sensing tags
1263 to determine the critical locations and times of year for their feeding (Weinstein et al. 2017), so that
1264 any overlap and potential competition with fishing activity can be minimised (Hinke et al. 2017b).

1265 Enhancements of our observational capacity and coverage across the WAP shelf must be
1266 accompanied by continued development of modelling frameworks and capabilities to reveal the
1267 most important mechanisms behind variability and change at all levels of the ecosystem. Improving
1268 the resolution and scope of regional physical, biogeochemical and habitat or ecosystem models is a
1269 particular priority, given large heterogeneity spatially and over daily to decadal timescales. Better-
1270 constraining the rates of key processes, such as onshelf CDW transport, meltwater inputs, algal
1271 growth and organic matter remineralisation, and the major fluxes of heat, nutrients, gases and
1272 particles based on coherent high-quality observational data is needed for optimisation of model
1273 input parameters and boundary conditions. Ongoing development of regional system models will
1274 allow us to test the relative importance of different processes, elucidate the combined and/or
1275 competing effects of multiple stressors, and explore the feedbacks between the drivers and
1276 consequences of change amongst the different system components over a range of timescales.
1277 Further, only once we can represent accurately the key processes and interactions at work in
1278 modelling frameworks can we be confident in our projections of future changes in upper ocean
1279 mixing, nutrient supply, primary production, ecosystem functioning and resilience, and air-sea
1280 exchange of climate-active gases as the changes in sea ice extent, duration and atmospheric forcing
1281 continue to evolve. Ultimately, better quantification of the processes and feedbacks at the WAP, and
1282 their interactions with systems up- and down-stream in regional atmospheric and oceanic circulation
1283 systems, will enable us to better-represent this Southern Ocean region in global climate models and
1284 understand its role in contemporary global change.

1285 4. Closing remarks

1286 We have demonstrated the importance of the WAP marine system due to pronounced variability
1287 and change in the physical environment and ocean-climate interactions, strong biological and
1288 biogeochemical consequences locally and regionally, and its utility as a natural laboratory for
1289 examining how climate and sea ice changes might restructure ecosystems here and elsewhere. We
1290 have summarised the state of knowledge regarding the key mechanisms and interactions regulating
1291 ecosystem functioning and ocean-atmosphere coupling, as well as the changes underway and the
1292 ecosystem responses and ocean-climate feedbacks. We also highlight the overarching priorities and
1293 discipline-specific objectives for future research and present a vision for an observing system
1294 capable of addressing these priorities and objectives. Working towards this vision will require further
1295 improvements in integration, collaboration and co-ordination across national programs, projects and
1296 initiatives, including sharing of expertise, standardisation of field, experimental and analytical
1297 techniques, and optimisation of ship-time, station infrastructure and other resources. To this end,
1298 SOOS has recently launched the Due South online database of ship- and station-based fieldwork
1299 programs in the Southern Ocean (https://data.aad.gov.au/duesouth/), as well as establishing
1300 regional working groups for the WAP and other regions. More effective engagement with other
1301 research communities, such as the climate science, meteorology, glaciology, terrestrial
1302 biogeochemistry and paleoclimate communities will be critical in defining the most important
1303 external controls on the WAP marine environment, the key fluxes into and out of the system, and
1304 the longer-term context of the changes underway.

1305 Improvements in data accessibility across disciplines and national programs is also called for,
1306 following the examples of the Palmer LTER project (http://pal.lternet.edu/data), the KRILLBASE

database for zooplankton survey data (Atkinson et al. 2017) and the Surface Ocean CO_2 Atlas (Bakker et al. 2016). Widespread adoption of similar data policies and practices across the international 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. Co-ordinating and opening up all data sources is recommended as a significant scientific opportunity for the international community working across multiple disciplines in the WAP region and beyond.

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Declaration of interests: none

1334 Table 1. Discipline-specific research objectives for the international community working along the WAP for the next 2-10 years

Ice dynamics and physical oceanography	Phytoplankton communities	Nutrient biogeochemistry	Climate-active gases	Microbial processes	Zooplankton dynamics	Higher trophic levels	Benthic ecosystems
Construct an accurate WAP shelf heat and salt budget over the complete annual cycle: *Eddy formation and onshelf CDW transport Cross-shelf water mass modification Mixing mechanisms and rates, especially during winter-spring/ summer ice retreat* Constrain oceanic processes modulating glacial retreat and impact of freshwater discharge on shelf properties and processes Determine relative influence of internal variability and climate change on property budgets, circulation and sea ice cover	Quantify the drivers of phytoplankton dynamics and diversity on seasonal timescales Identify potential species shifts driven by physical and chemical changes Conduct functional assessments of phytoplankton communities Elucidate the link between sea ice algal and pelagic communities and carbon fluxes Establish the influence of phenological changes on consumers and trophic structure	Construct accurate annual budgets of macro- and micronutrients for the WAP shelf: *Quantify nutrient fluxes onto, across and off the shelf Constrain the factors regulating autumn/winter nutrient resupply Quantify benthic-pelagic coupling through benthic nutrient recycling and exchange Assess sea ice and glacier chemistry, and meltwater influence on ocean chemistry* Identify the role(s) of micronutrients other than iron in primary production Discern the relative importance of new and regenerated production under changing conditions Describe seasonal patterns in organic nutrient dynamics in relation to phytoplankton and microbial processes	Quantify year-round air-sea exchange fluxes of CO_2, halogens and DMS along the WAP: *Assess the role of sea ice in modulating fluxes* Constrain the roles of sea ice, glacial melt and upwelling on gas concentrations and fluxes Estimate the timing of aragonite undersaturation and the sensitivity of carbonate chemistry, CO_2 fluxes and WAP ecosystems to ocean acidification Understand the response of halogen and DMS emissions to environmental change and expected shifts in community composition and phenology	Conduct functional assessments of microbial communities Define microbial provinces by species composition and function Estimate the resilience of the microbial food web to changing conditions Constrain the ecological role of viruses as mortality agents/loss factors and consequences for trophic transfer efficiency Elucidate the interactions between microbial communities and other ecosystem components Describe bacterial decomposition of macroalgal-derived organic matter	Assess mechanisms affecting zooplankton physiological tolerances, reproductive success and food web interactions Constrain micro-zooplankton assemblage composition and dynamics Understand zooplankton-mediated export via diel and seasonal vertical migrations Determine the importance of zooplankton-mediated export for benthic community production Quantify the role of benthic organisms as food sources for krill	Identify controls on juvenile recruitment and juvenile and adult survival Constrain the importance of foraging behaviour, prey availability and habitat requirements in influencing distributions, and their climate-driven biophysical controls Assess species' abilities to change distribution, diet and behaviour under altered conditions	Constrain rates of key processes e.g. adaptation and acclimation, geneflow within and between populations Evaluate benthic organisms' capacities to adapt to altered environments, especially sedimentation rates, pH and temperature Quantify the importance of benthic-pelagic coupling to phytoplankton productivity

31

1335 Table 2. Discipline-specific approaches and innovations to address the key research objectives over the next 2-10 years

| Ice dynamics and physical oceanography	Phytoplankton and microbial communities	Nutrient biogeochemistry	Climate-active gases	Zooplankton dynamics	Higher trophic levels	Benthic ecosystems
Moored time series of ocean currents and hydrographic properties along the shelf break HF radar measurements of surface currents Glider surveys shelf-wide, full-depth, year-round and targeting specific features Improving sensor and geolocation accuracy of seal-borne CTDs Observational and numerical modelling studies focused on ice-ocean interactions Better representation of precipitation, run-off and glacial melt in ocean models Further development of general circulation and coupled atmosphere-ice-ocean models	Incorporate genomics, proteomics and transcriptomics studies into existing monitoring programs to provide finer-resolution taxonomic data and understand unique functions Advances in single-cell sequencing and cell-sorting capabilities Expand culture collections of key species to reveal functional pathways and responses to change Determine viral lysis rates in phytoplankton and microorganisms Combine microbial and physical data to improve niche characterisation Dedicated flux studies using sediment traps, radiogenic isotopes, stable isotope tracers, diatom biomarkers (e.g. $IPSO_{25}$)	Interpret physics data to estimate advective fluxes Experiments to constrain uptake and cycling process rates Conservative and non-conservative geochemical tracers (e.g. Ba, Al), stable and radiogenic isotopes, rare Earth elements Glacier and meltwater chemistry measurements Benthic flux estimates from porewater profiles and chamber experiments Improved models of nutrient supply, uptake, recycling and loss	Development of pCO_2 mapping techniques specific to Antarctic coastal sites Direct CO_2 flux measurements for sea ice and surface waters Continuous DMS measurements by mass spectrometry Rate measurements of gas production and conversion processes using isotope addition experiments	Species-level data collection at higher-resolution spatial scales, including vertical Metagenomic, molecular and isotopic studies, especially to examine micro-zooplankton species composition and trophic role Sampling over a greater range of size fractions, including micro-zooplankton Dietary analysis of key species	Satellite and electronic tracking tags, motion-sensing tags, acoustic receivers Additional sensors on tracking tags e.g. CTD, video Stable isotope analysis of tissues, feathers, whiskers and stomach content Remote-sensing tools e.g. drones, satellite imagery Integration with physical data and models to constrain bio-physical controls on distributions and change over time	In-situ environmental manipulation experiments, repeated regularly Long-term experiments over years and multiple generations Stable isotope and biomarker analysis of benthic organisms to constrain food sources Studies focused on benthic fluxes of dissolved and particulate constituents, connectivity and influence on water column biology and biogeochemistry
		Use of air-sea-ice chambers to develop process understanding				
	Sea ice sampling campaigns with a focus on early spring, including algal, nutrient, carbonate chemistry, halocarbon and DMS(O/P) measurements					

|	Development and deployment of fluorometers and dissolved oxygen, nutrient, pCO_2 and other sensors on autonomous platforms e.g. gliders, AUVs, moorings	Expanded use of video plankton recorders and multi-frequency acoustics from ships and AUVs	

1336

Figures

Note: Figures 2-11 and 13-16 should be published in colour; Figures 1 and 12 should be black and
white.
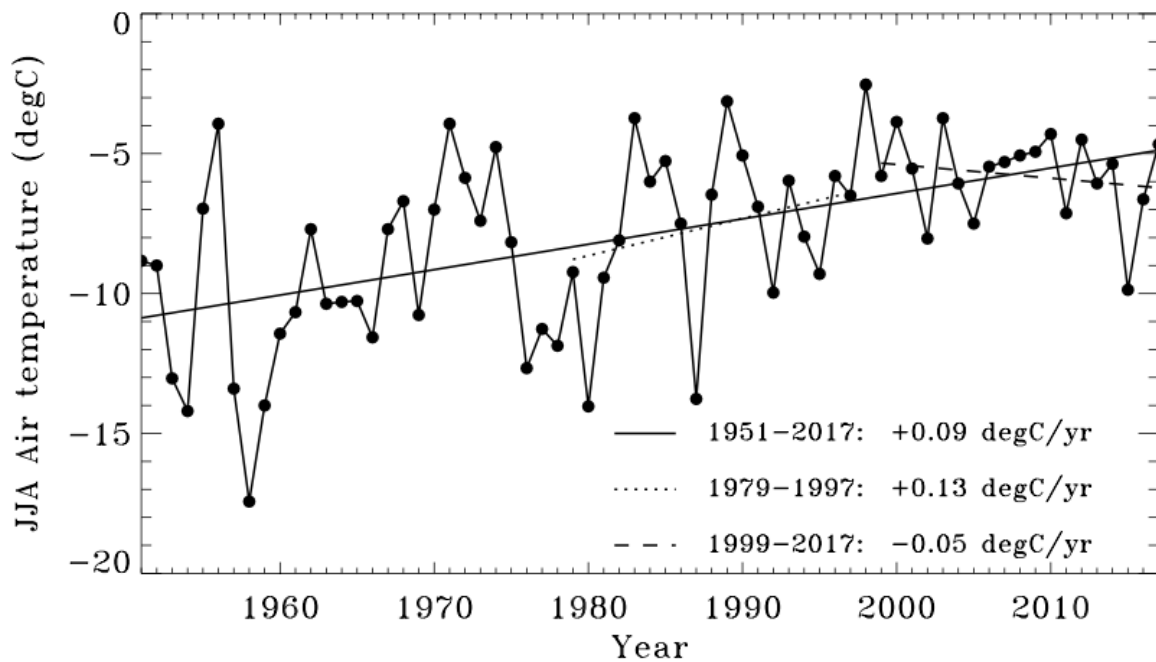
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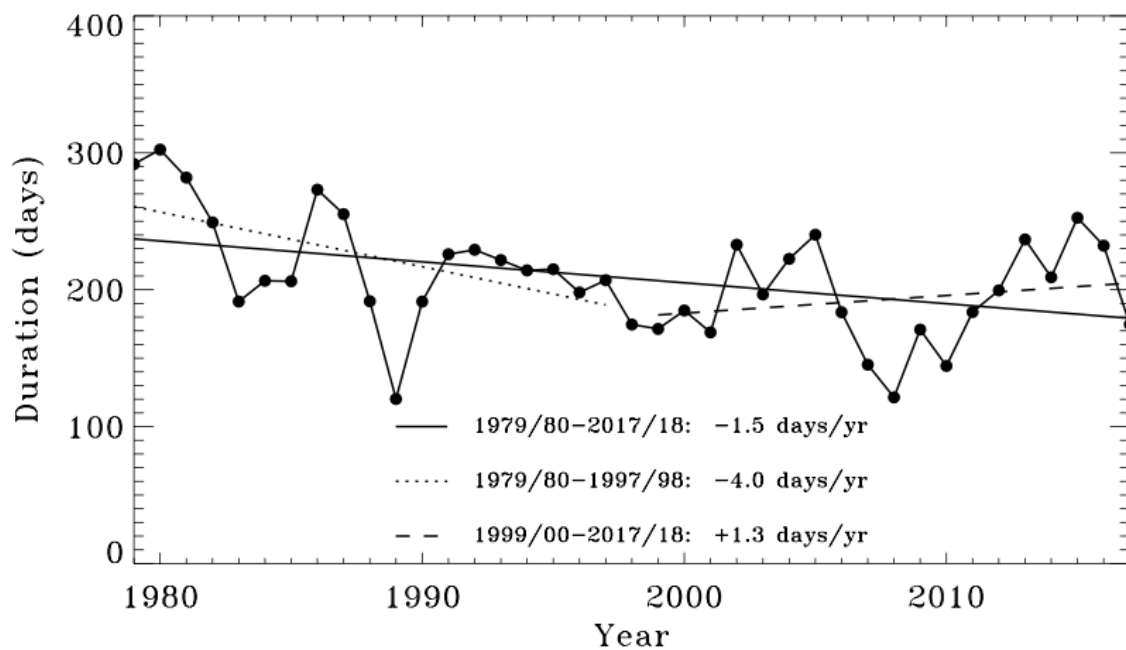
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Figure 1. (a) Trend in winter air temperature (June, July, August; JJA) as recorded at Faraday/
Vernadsky Station (65.4 °S, 64.4 °W) from 1951 to 2017. The long-term linear trend (solid line: 1951-
2017) is significant at the $p <0.001$ level, while 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
determined using the GSFC Bootstrap version 2 sea ice concentration time series from Nimbus-7
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
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.
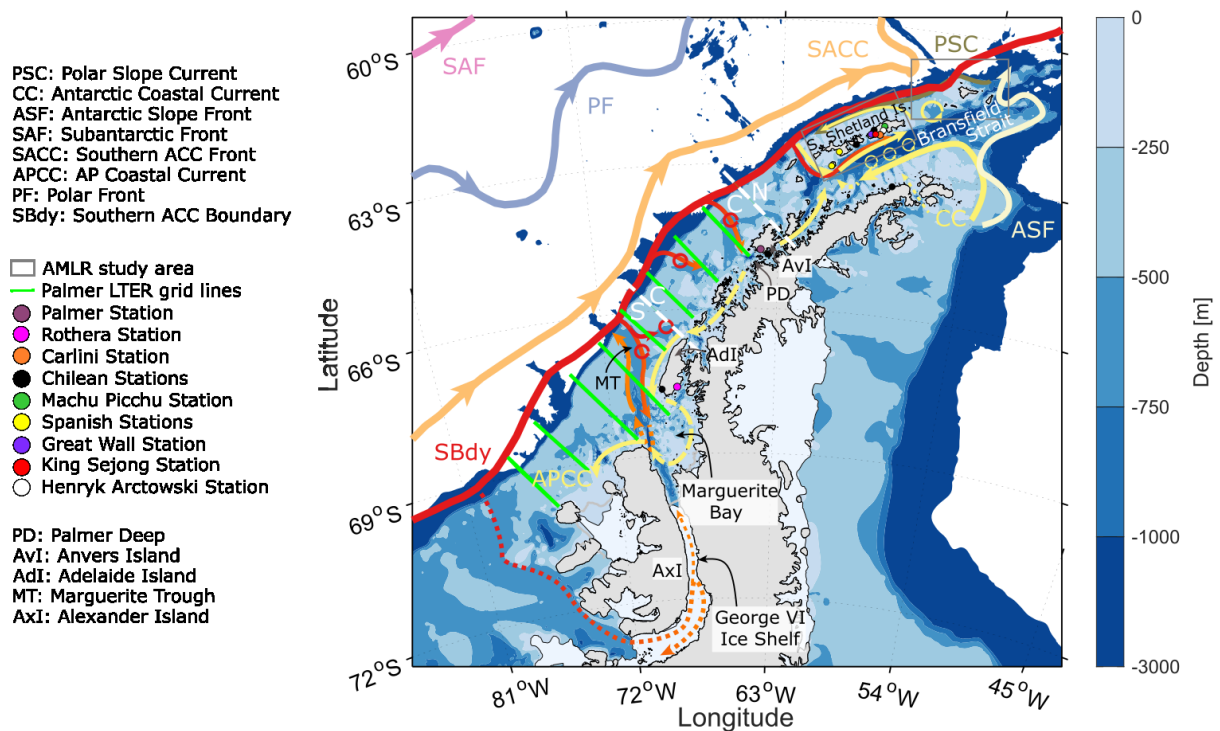
Figure 2. Map of the WAP showing the major sustained research efforts represented, delineation of the northern, central and southern sub-regions referred to in the text (white dashed lines; N = northern sub-region, C = central sub-region, S = southern sub-region), and the major circulation and bathymetric features of the shelf system. Modified from Moffat and Meredith (2018).

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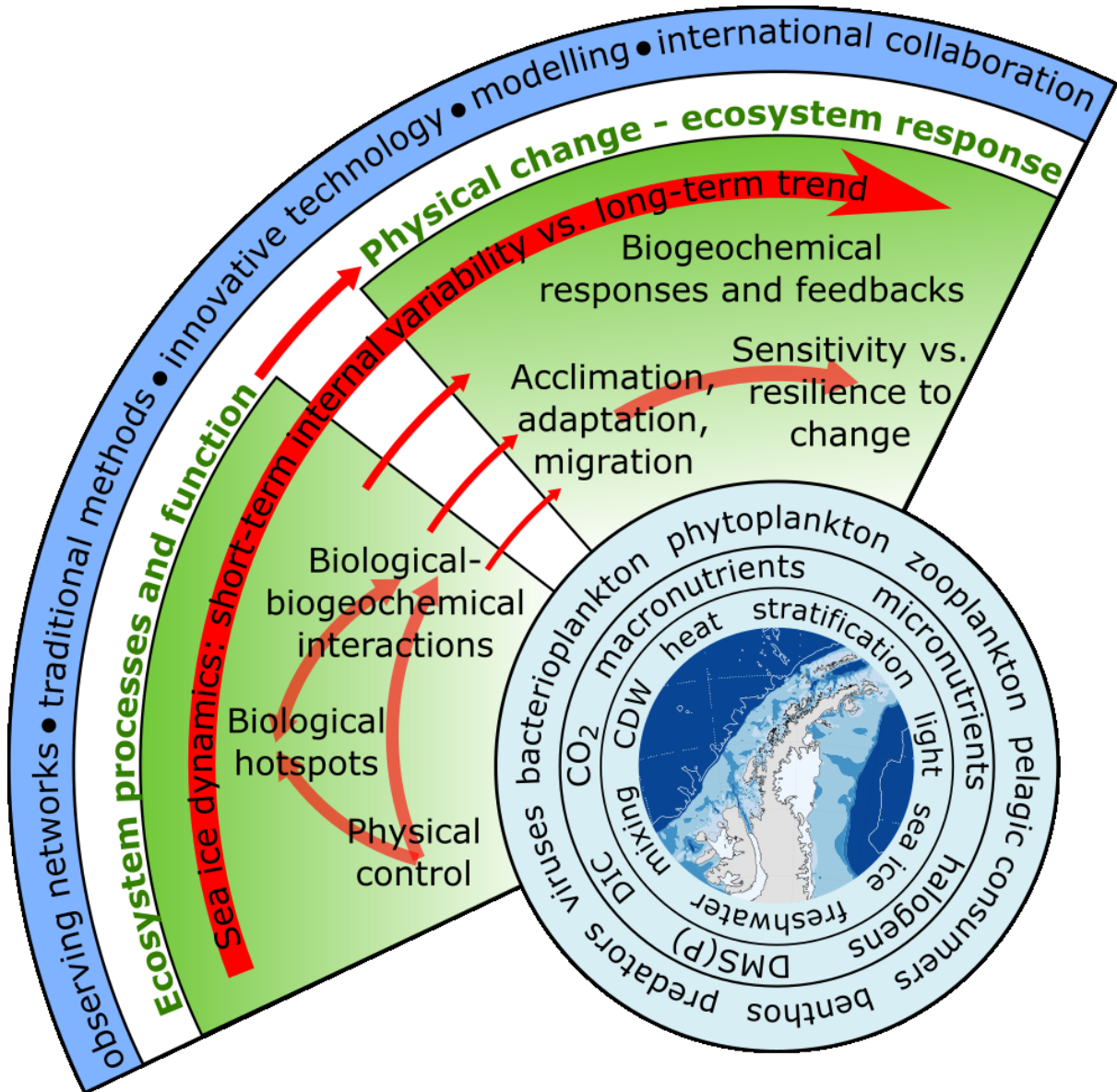
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1359 Figure 3: Infographic summarising the key components of the WAP marine system, the most
1360 important mechanisms and interactions in the context of the two overarching questions addressed
1361 in this paper, and the major priorities and approaches for future marine research at the WAP.

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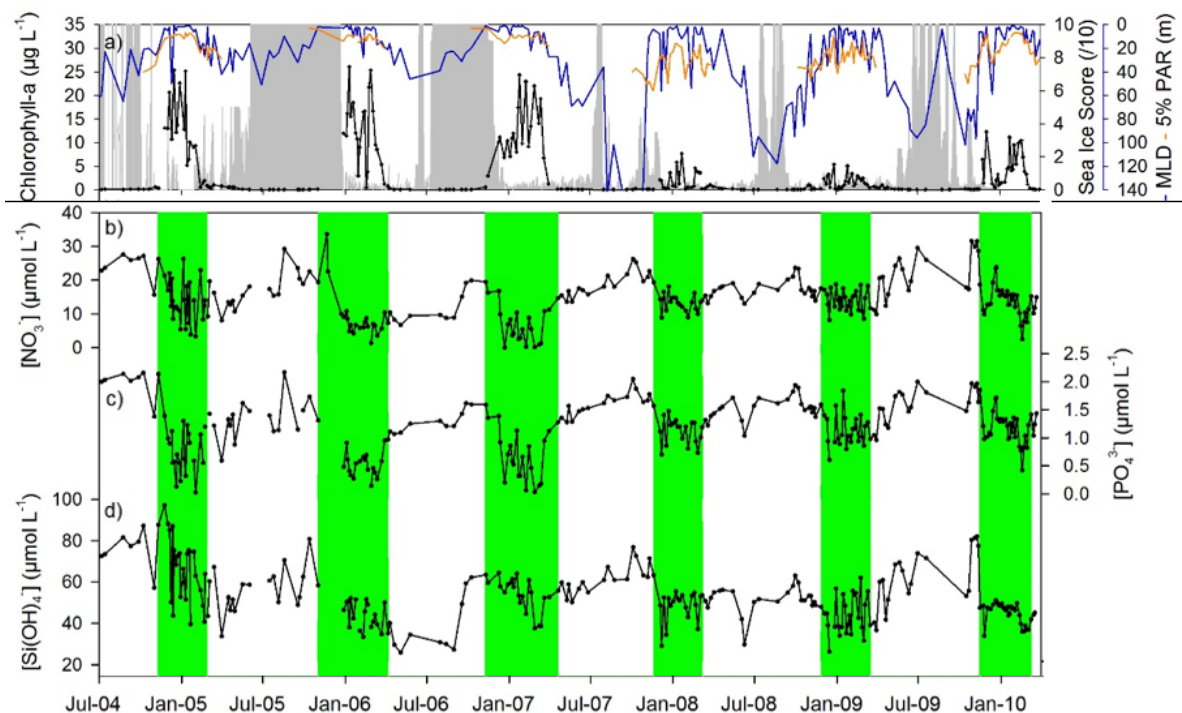
Figure 4. Time-series data from RaTS, July 2004 to April 2010, showing that high sea ice winters lead to shallow mixed layers, high chlorophyll and strong nutrient drawdown, whilst low sea ice years lead to deeper mixing, lower chlorophyll and less nutrient drawdown. (a) sea ice score (grey shading; coverage normalised to ice type, out of ten where ten is full fast-ice cover), mixed layer depth (MLD; blue line; depth where $\sigma = \sigma_{surface} + 0.05$ kg m^{-3}), 5 % PAR depth (orange line; depth where photosynthetically active radiation is 5 % of its surface value), chlorophyll a concentration at 15 m (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 chlorophyll data from Venables et al. (2013).
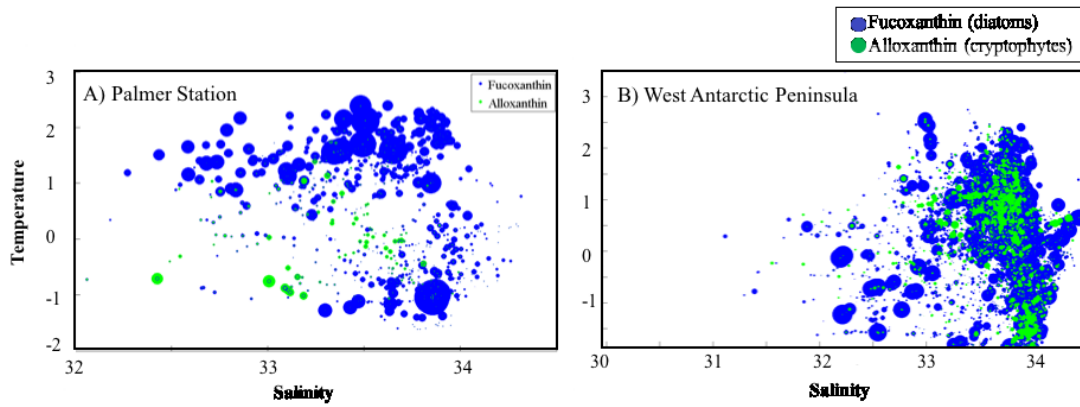
Figure 5. The relative presence of diatoms (from fucoxanthin, blue) and cryptophytes (from alloxanthin, green) plotted in temperature-salinity phase space for (a) Palmer stations B and E, and (b) the Palmer LTER grid. The size of the circles indicates the relative concentration of chlorophyll *a* for discrete samples. Modified from Schofield et al. (2017).
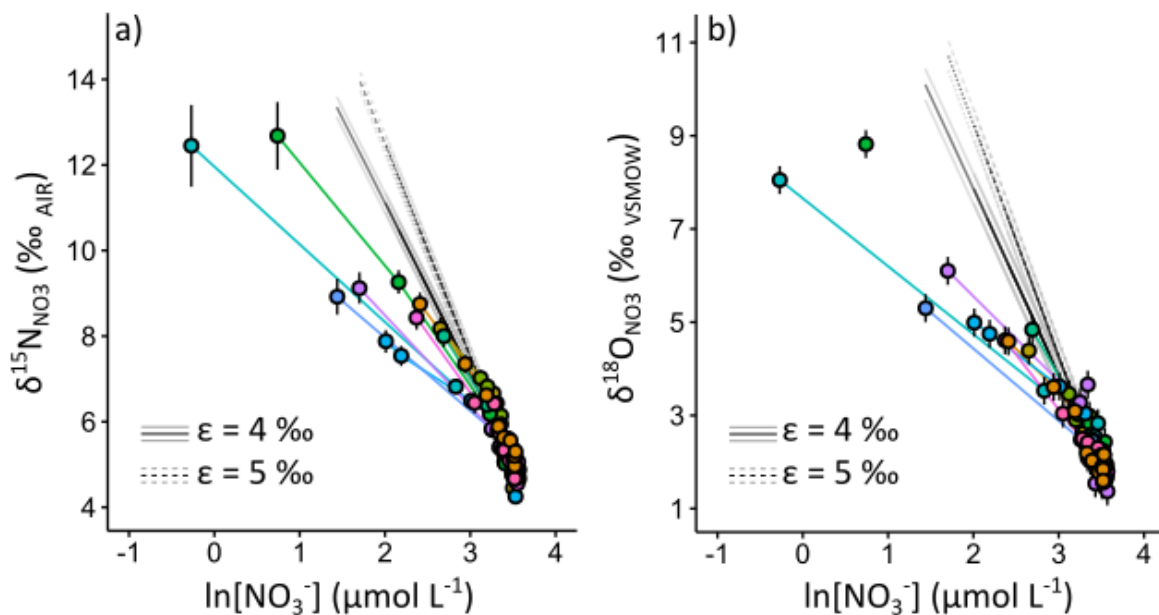
Figure 6. Relationships between nitrate concentration and its (a) nitrogen and (b) oxygen isotope composition, compared to modelled relationships based on nitrate uptake alone with fractionation factors (ε) of 4 and 5 ‰ (solid and dashed black lines, respectively). Both $\delta^{15}N$ and $\delta^{18}O$ 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).
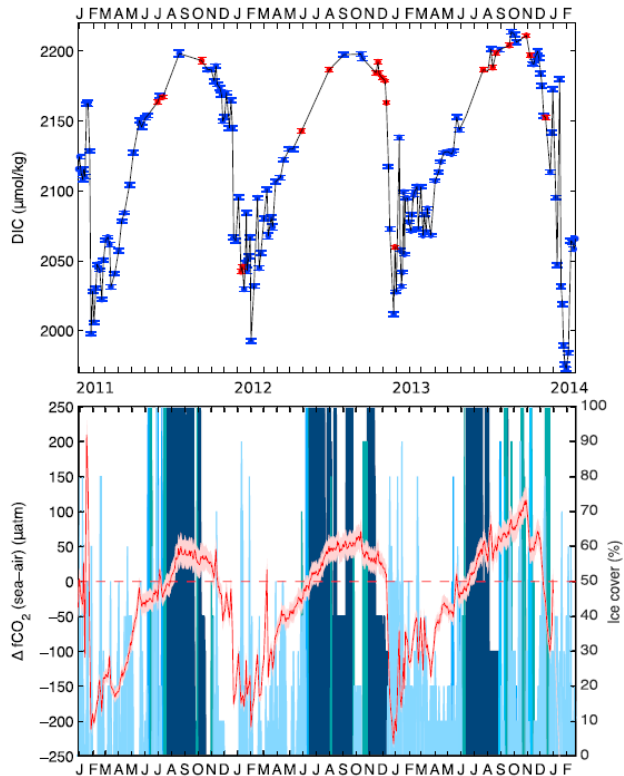
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1392 Figure 7. (a) Seasonal cycle of DIC from December 2010 to February 2014 at 15 m depth at RaTS sites
1393 1 (blue) and 2 (red), both in Ryder Bay. Error bars are uncertainty (2SD) based on measurement
1394 precision. (b) Red solid line shows the seasonal cycle of the difference in fCO_2 between the sea and
1395 air (ΔfCO_2), with the pink shaded region representing approximate 95 % confidence from uncertainty
1396 analysis. Red dashed line shows ΔfCO_2 = 0, where ocean CO_2 concentration is in equilibrium with the
1397 atmosphere. ΔfCO_2 > 0 during winter indicates supersaturated conditions and an efflux of CO_2 to the
1398 atmosphere; ΔfCO_2 < 0 during summer indicates undersaturated conditions and oceanic uptake of
1399 atmospheric CO_2. Blue bars show percentage ice cover, with dark blue representing fast ice,
1400 turquoise representing pack ice and light blue representing brash ice. Reproduced with permission
1401 from Legge et al. (2015).
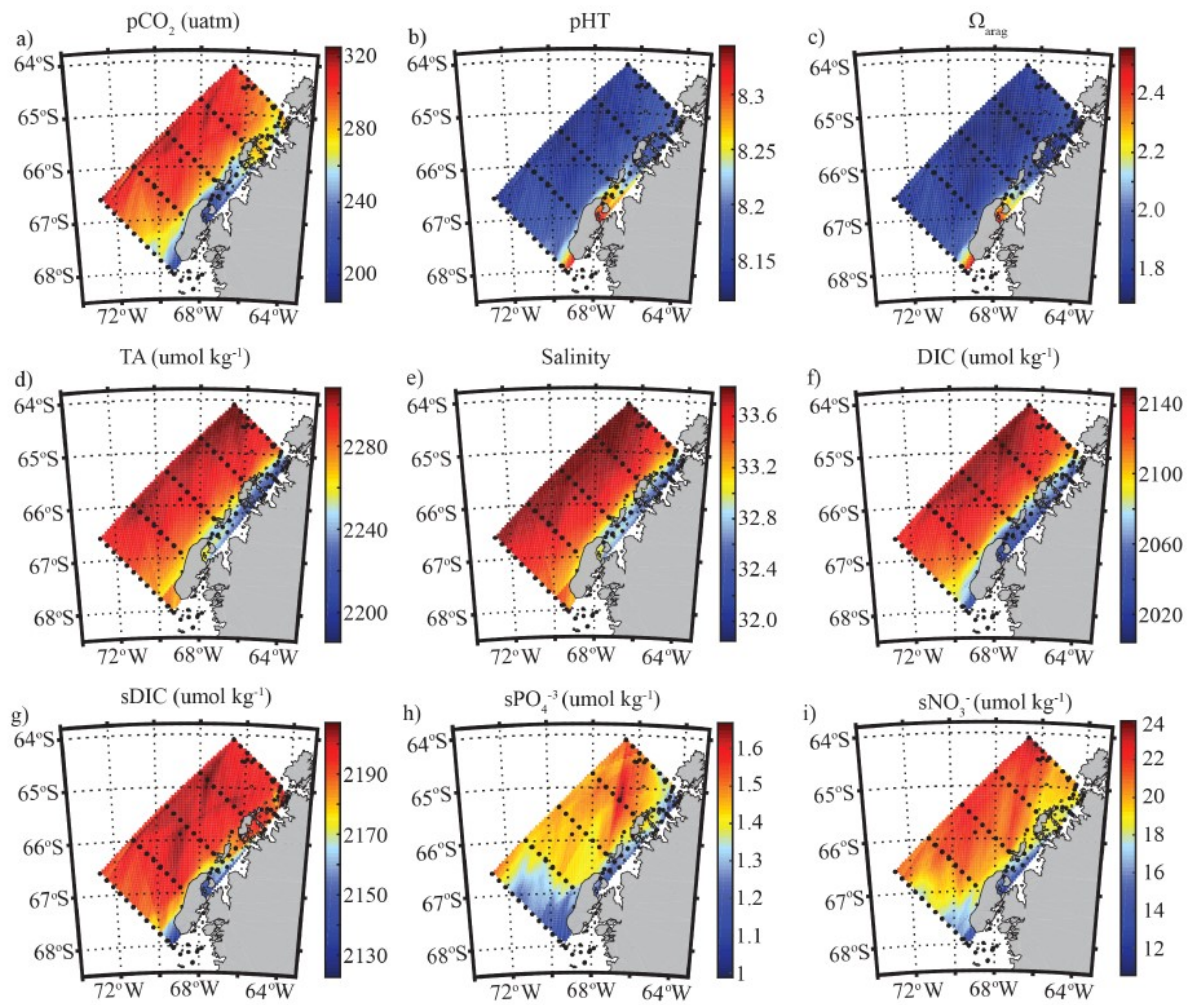
1402
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1404 Figure 8. Summertime distribution of inorganic carbon system and other biogeochemical parameters
1405 in surface water for the Palmer LTER grid for the period 1993 to 2012, showing onshore-offshore and
1406 north-south gradients in carbonate chemistry, salinity and inorganic nutrients. Reproduced with
1407 permission from Hauri et al. (2015).
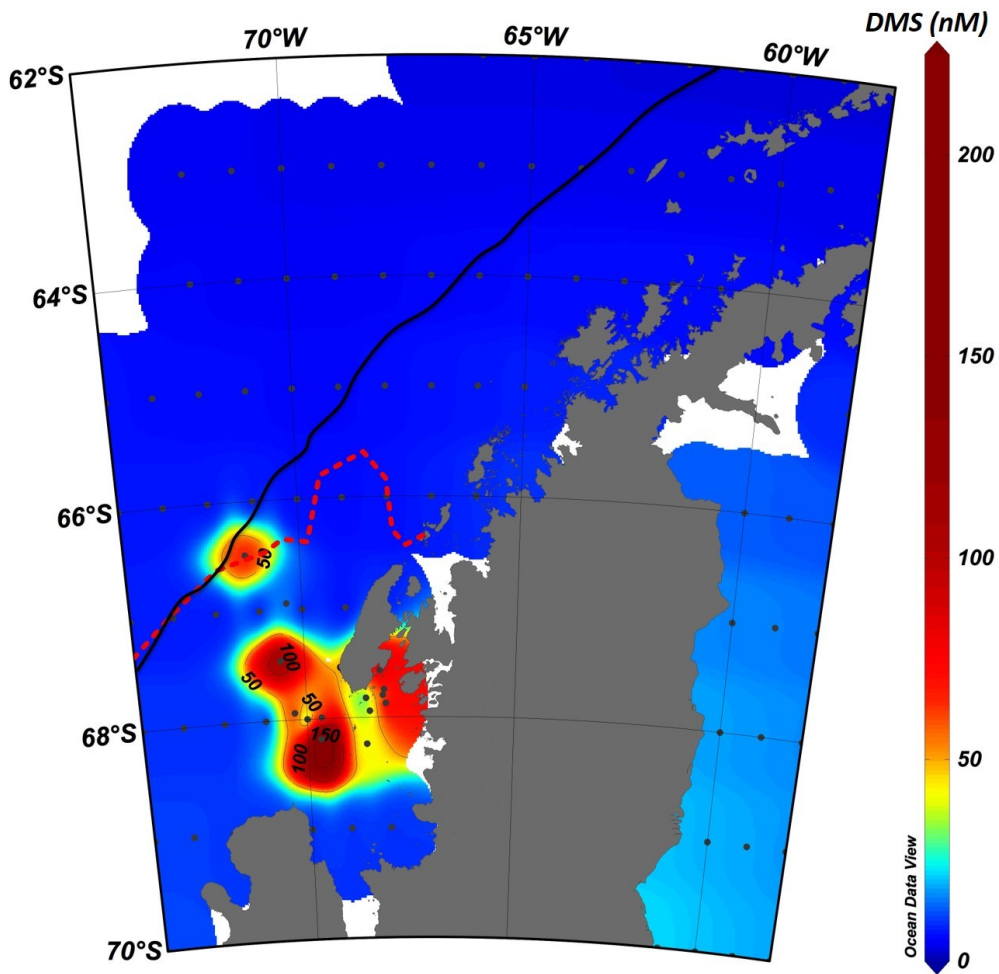
Figure 9. Surface DMS concentrations during cruise JR307 in January 2015 plotted on top of the 1x1 gridded January DMS climatology (Lana et al. 2011). JR307 data were calculated from filtered DMS(P) values (Stefels et al. 2018). The black line depicts the shelf edge; the red dotted line indicates the approximate position of the northern edge of the marginal ice zone during the second half of December 2014, immediately preceding the cruise.
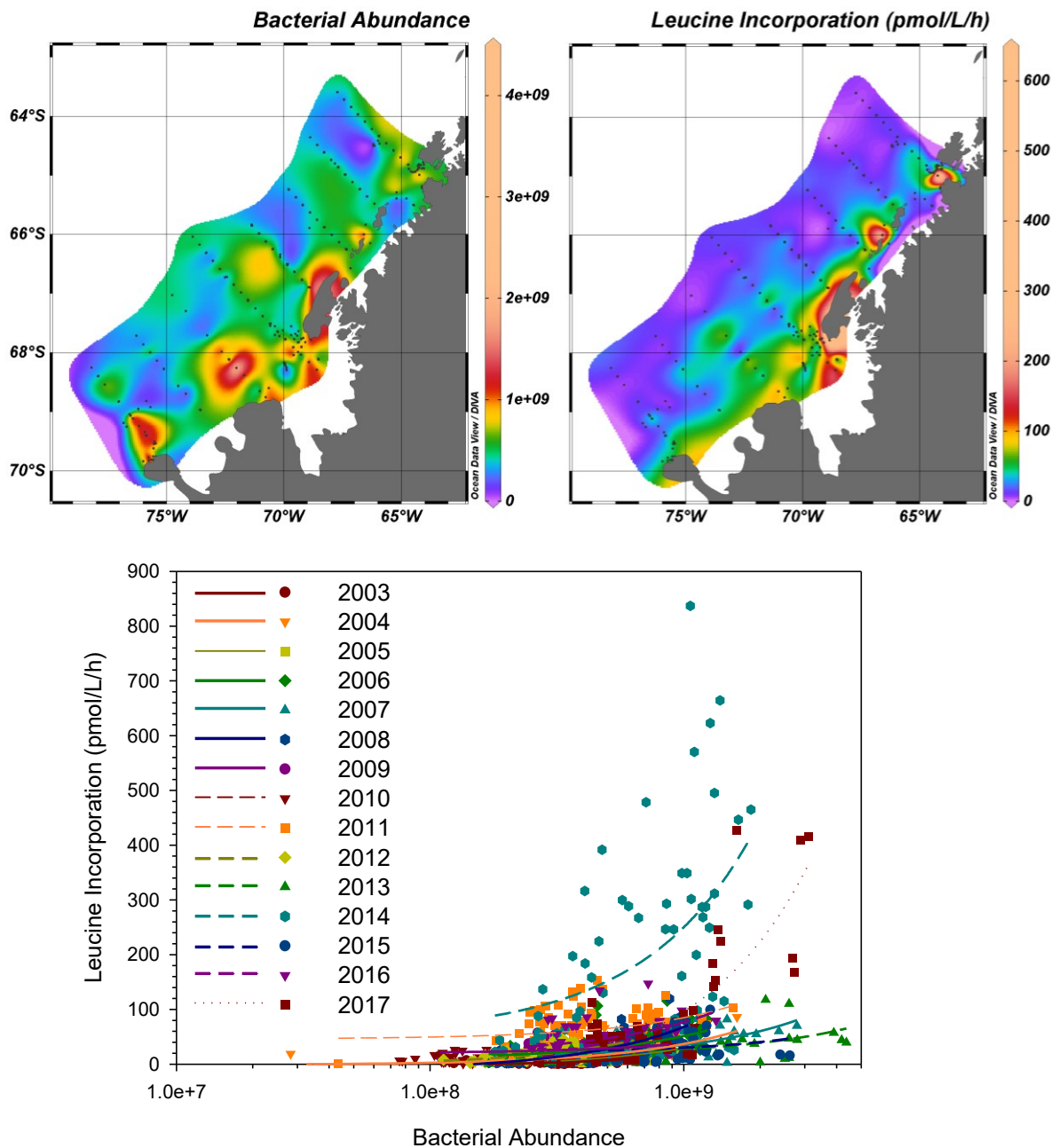
Figure 10. Long-term averages (2003-2017) for January of both bacterial abundance (top left) and production (top right) in the surface ocean (maximum depth 10 m), showing intense spatial heterogeneity with higher abundance and production in inshore regions, and higher abundance further south. Lower panel shows strong variability in bacterial production with abundance for 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 Ducklow et al. (2012a).
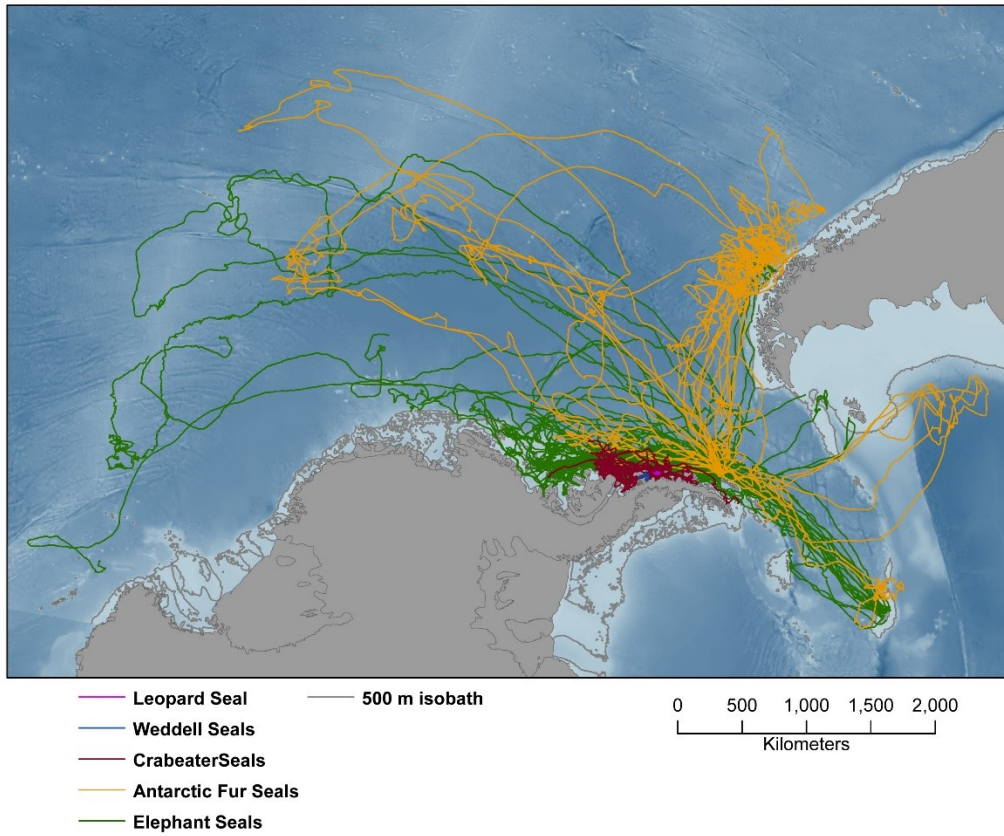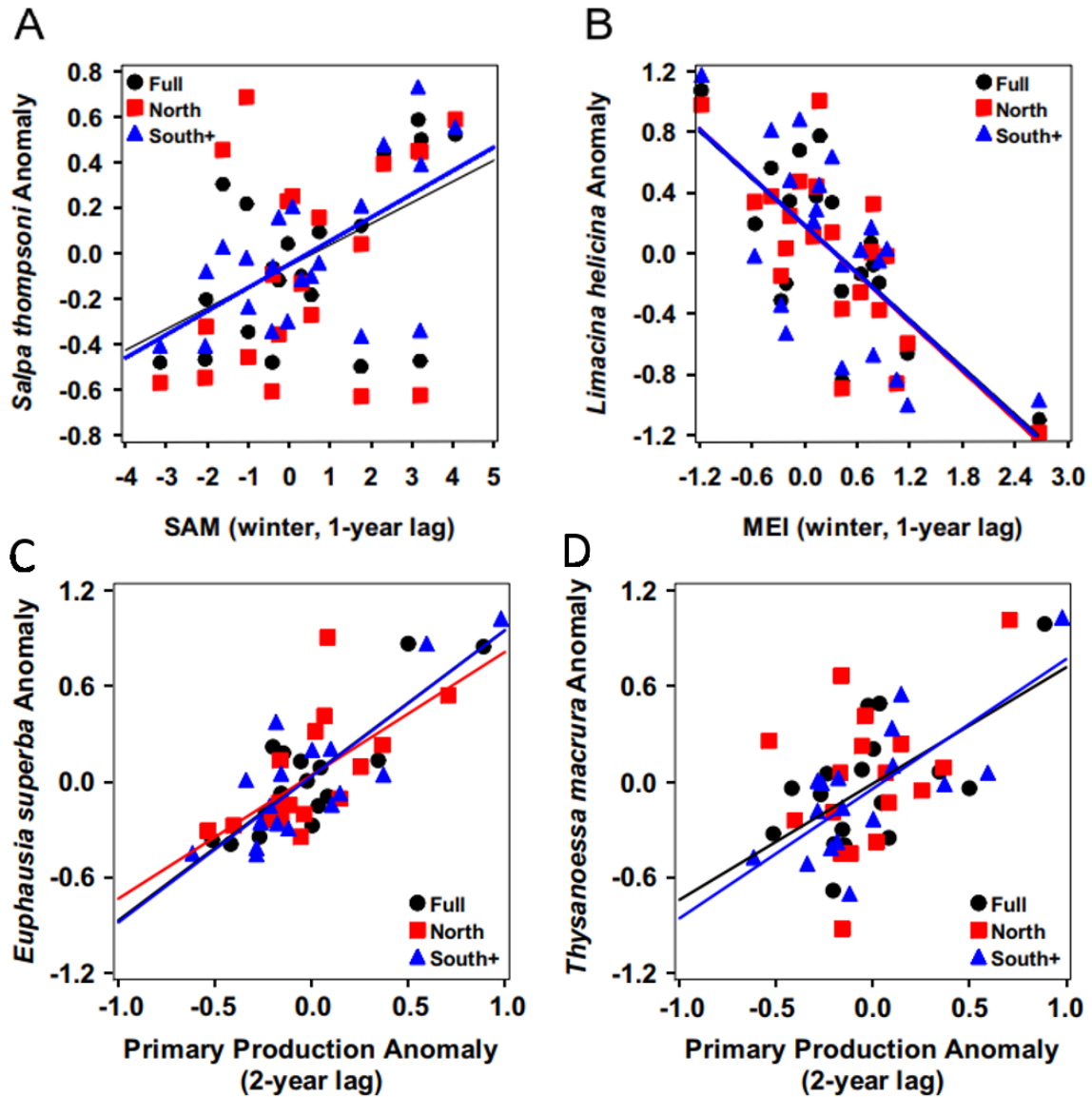
Figure 11. Tracks of crabeater seals (dark red) (Burns et al. 2004), elephant seals (green) (Huckstadt et al. 2012b), Weddell seals (blue), leopard seals (purple) (Costa et al. 2010), and fur seals (yellow) (Arthur et al. 2017) over an annual cycle from animal tracking tags.
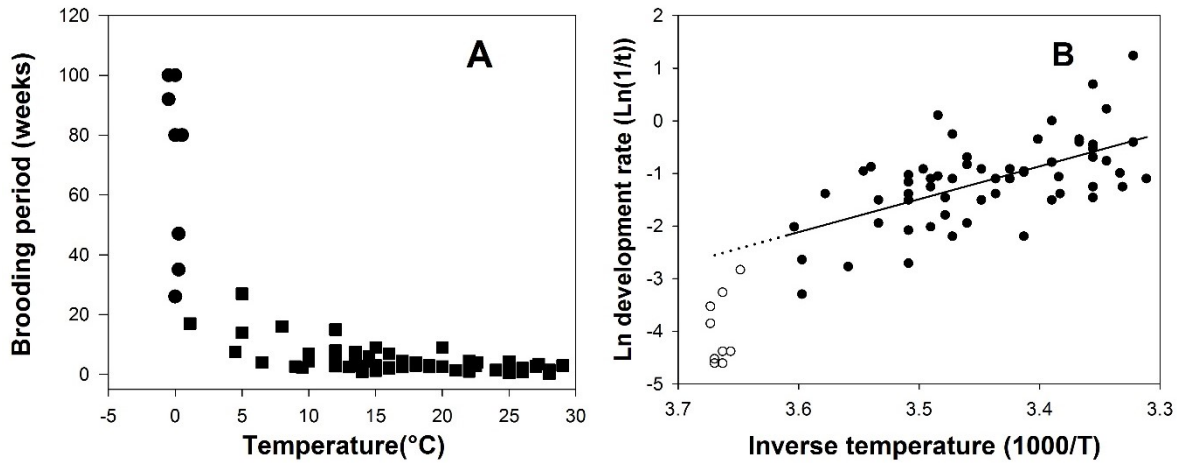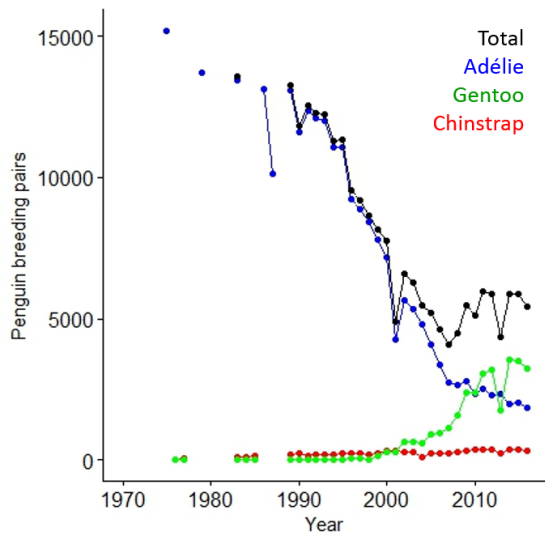
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1429 Figure 12. Brooding period and development rates of brooding marine gastropod snails at ambient
1430 temperatures for tropical to polar species. (a) Time from brood initiation to release (1/development
1431 rate) versus ambient temperature. In most cases, release is of crawling juveniles, but for two
1432 Antarctic species, release is of veliger larvae and development time to juvenile is approximately
1433 double that of brooding per se (Peck et al. 2006b). Data for 68 gastropod species, nine of which live
1434 at temperatures around 0°C, show the full development period to juvenile. (b) Arrhenius plot of Ln
1435 developmental rate to juvenile stage for brooding gastropod molluscs. Fitted line is for temperate
1436 and tropical species (filled circles; brooding rate (1/weeks) = 20.37 - 6.25 1000/T; r^2 = 0.36, F = 32.4,
1437 58 df, p <0.001); Antarctic species fall significantly below. Reproduced from Peck (2018).
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1451 Figure 14. Population census data for Adélie, chinstrap and gentoo penguins in the Palmer Station
1452 region, 1975-2016. Updated from Ducklow et al. (2013).

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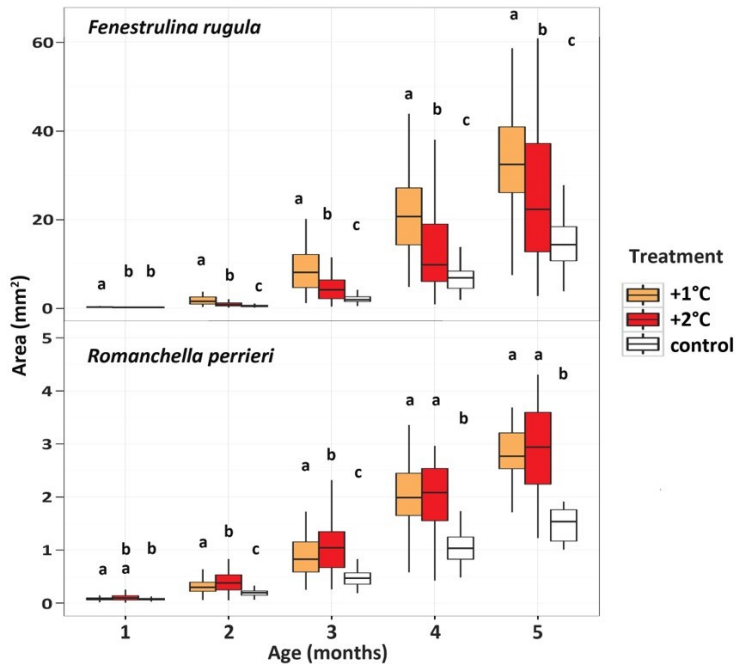
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Figure 15. Effects of *in situ* warming on the growth of common epifaunal marine invertebrates on Rothera Point, Adelaide Island. Panels show area covered by the spatially dominant bryozoan (*Fenestrulina rugula*) and spirorbid (*Romanchella perrieri*)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

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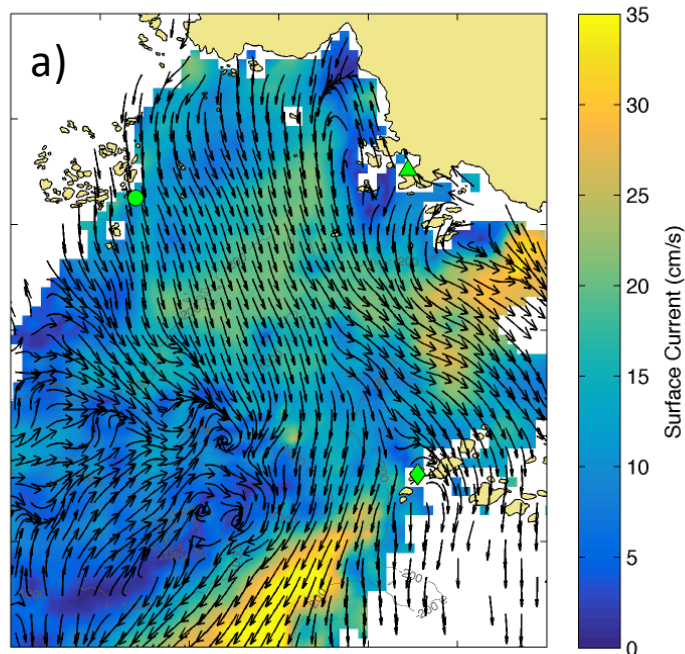
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Figure 16. Hourly surface current map for the Palmer Station region for January 27, 08:00 GMT, 2015. The HF radar sites located at Palmer Station (green triangle) and the Wauwermans (green diamond) and Joubin (green circle) island groups are also shown.

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