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► **To cite this version:**

Daniel Jones, Filipe Ceia, Eugene Murphy, Karine Delord, Robert Furness, et al.. Untangling local and remote influences in two major petrel habitats in the oligotrophic Southern Ocean. *Global Change Biology*, 2021, 27 (5773-5785), 10.1111/gcb.15839 . hal-03330670

**HAL Id: hal-03330670**

**<https://hal.science/hal-03330670>**

Submitted on 24 May 2024

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Jones, D. C. et al. (2022) Untangling local and remote influences in two major petrel habitats in the oligotrophic Southern Ocean. *Global Change Biology*, 27(22), pp. 5773-5785.

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Deposited on: 24 April 2023

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**Untangling local and remote influences in two major petrel habitats in the oligotrophic Southern Ocean**

Journal:	<i>Global Change Biology</i>
Manuscript ID	Draft
Wiley - Manuscript type:	Primary Research Articles
Date Submitted by the Author:	n/a
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Keywords:	Antarctic Circumpolar Current (ACC), Biogeography, Conservation, High seas, Hotspot, Open ocean, Primary productivity, Seabirds
Abstract:	<p>Ocean circulation connects geographically distinct ecosystems across a wide range of spatial and temporal scales via exchanges of physical and biogeochemical properties. Remote oceanographic processes can be especially important for ecosystems in the Southern Ocean, where the Antarctic Circumpolar Current (ACC) transports properties across ocean basins through both advection and mixing. Recent tracking studies have indicated the existence of two large-scale, open ocean habitats in the Southern Ocean used by grey petrels (<i>Procellaria cinerea</i>) from two populations (i.e. Kerguelen and Antipodes islands) during their nonbreeding season for extended periods during austral summer (i.e. October to February). In this work, we use a novel combination of large-scale oceanographic observations, surface drifter data, satellite-derived primary productivity, numerical adjoint sensitivity experiments, and output from a biogeochemical state estimate to examine local and</p>

	<p>remote influences on these grey petrel habitats. Our aim is to understand the oceanographic features that control these isolated foraging areas and to evaluate their ecological value as oligotrophic open ocean habitats. We estimate the minimum local primary productivity required to support these populations to be much less than 1% of the estimated local primary productivity. The region in the southeast Indian Ocean used by the birds from Kerguelen is connected by circulation to the productive Kerguelen shelf. In contrast, the region in the south-central Pacific Ocean used by seabirds from the Antipodes is relatively isolated suggesting it is more influenced by local factors or the cumulative effects of many seasonal cycles. This work exemplifies the potential use of predator distributions and oceanographic data to highlight areas of the open ocean that may be more dynamic and productive than previously thought. Our results highlight the need to consider advective connections between ecosystems in the Southern Ocean and to re-evaluate the ecological relevance of oligotrophic Southern Ocean regions from a conservation perspective.</p>

# Untangling local and remote influences in two major petrel habitats in the oligotrophic Southern Ocean

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**Local and remote influences in the open ocean**

23

24 **Running head: Local and remote influences in the open ocean**

25 **Keywords: Antarctic Circumpolar Current (ACC), Biogeography, Conservation, Grey petrels,**

26 **High seas, Hotspot, Open ocean, Primary productivity, *Procellaria cinerea*, Seabirds**

27

For Review Only

**Local and remote influences in the open ocean**28 **ABSTRACT**

29 Ocean circulation connects geographically distinct ecosystems across a wide range of spatial  
30 and temporal scales via exchanges of physical and biogeochemical properties. Remote oceanographic  
31 processes can be especially important for ecosystems in the Southern Ocean, where the Antarctic  
32 Circumpolar Current (ACC) transports properties across ocean basins through both advection and  
33 mixing. Recent tracking studies have indicated the existence of two large-scale, open ocean habitats in  
34 the Southern Ocean used by grey petrels (*Procellaria cinerea*) from two populations (i.e. Kerguelen  
35 and Antipodes islands) during their nonbreeding season for extended periods during austral summer  
36 (i.e. October to February). In this work, we use a novel combination of large-scale oceanographic  
37 observations, surface drifter data, satellite-derived primary productivity, numerical adjoint sensitivity  
38 experiments, and output from a biogeochemical state estimate to examine local and remote influences  
39 on these grey petrel habitats. Our aim is to understand the oceanographic features that control these  
40 isolated foraging areas and to evaluate their ecological value as oligotrophic open ocean habitats. We  
41 estimate the minimum local primary productivity required to support these populations to be much less  
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43 the birds from Kerguelen is connected by circulation to the productive Kerguelen shelf. In contrast, the  
44 region in the south-central Pacific Ocean used by seabirds from the Antipodes is relatively isolated  
45 suggesting it is more influenced by local factors or the cumulative effects of many seasonal cycles.  
46 This work exemplifies the potential use of predator distributions and oceanographic data to highlight  
47 areas of the open ocean that may be more dynamic and productive than previously thought. Our results  
48 highlight the need to consider advective connections between ecosystems in the Southern Ocean and  
49 to re-evaluate the ecological relevance of oligotrophic Southern Ocean regions from a conservation  
50 perspective.

51

**Local and remote influences in the open ocean**52 **INTRODUCTION**

53           The Southern Ocean is a unique and important component of the Earth System. It provides a  
54 large fraction of the nutrients available to the global ocean (Sarmiento et al. 2004; Marinov et al.  
55 2008) and is an important site for anthropogenic carbon sequestration (Le Quéré et al. 2007).  
56 Southern Ocean circulation is dominated by the powerful Antarctic Circumpolar Current (ACC),  
57 which connects the ocean basins and spreads heat, carbon, and nutrients within those basins via both  
58 its dominant time-mean flow and its vigorous associated eddy circulation (Rintoul 2018). Partly  
59 because of the high level of connectivity enforced by the ACC, Southern Ocean ecosystems often  
60 cannot be considered as isolated systems, as they are connected across a wide range of spatial and  
61 temporal scales (Murphy et al. 2012).

62           In eutrophic coastal regions (e.g. areas of strong coastal upwelling) high primary production  
63 supports an abundant trophic pyramid and some of the largest fisheries in the world (Ryther 1969;  
64 Pauly & Christensen 1995; Chavez & Messié 2009). In contrast, in the oligotrophic open oceans, the  
65 food webs are generally characterized by a complex low-nutrient input system that exports little of its  
66 production and supports relatively few fisheries (Chavez et al. 2011). Numerous marine organisms,  
67 including seabirds, migrate between the highly productive upwelling regions in coastal areas through  
68 less-productive open ocean regions (Bolten 2003; Egevang et al. 2010; Block et al. 2011) and may  
69 have to feed regularly to survive in these poorly known regions. Although eddies, oceanic fronts, and  
70 small bathymetric features that present barriers to current flow (i.e. seamounts, islands and shelf  
71 breaks) may provide important hotspots in the open ocean and attract aggregations of predators (Bost  
72 et al. 2009; Godø et al. 2012; Young et al. 2015; Xavier et al. 2003; Xavier et al. 2004; Menkes et al.  
73 2002; Morato et al. 2010), little attention has been paid to less productive regions such as large  
74 oligotrophic regions in the upper layers of the ocean, and how they are essential to species survival.  
75 Large-scale patterns of upwelling and downwelling, trajectory drifts, and connections to productive



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76 shelf regions via ocean circulation may influence production and species distribution in the upper  
77 layers of the open Southern Ocean. For instance, the importance of advection in transferring krill or  
78 secondary production in maintaining food webs was regularly studied in coastal areas and hotspots in  
79 the Southern Ocean (e.g. Hofmann et al. 2004; Murphy et al. 1998, 2004, 2007), but not in the open  
80 oceans regions. These issues are particularly important for conservation, as marine protected areas  
81 mainly cover coastal areas (Allison et al. 1998; Game et al. 2009) due to the relative lack of  
82 information on large-scale open ocean regions.

83 Predator tracking data (e.g. for seabirds) can highlight unique hotspots for biodiversity,  
84 including open ocean areas that may have been neglected and warrant further investigation. A  
85 tracking study found that grey petrels (*Procellaria cinerea*, Gmelin, JF, 1789) from the Antipodes  
86 and Kerguelen Islands spend their nonbreeding period in pelagic regions, far away from their land-  
87 based breeding areas and any known areas of high productivity (Torres et al. 2015). The presence of  
88 these two petrel populations in ostensibly unsuitable areas of the open Southern Ocean suggests that  
89 our understanding of these areas is incomplete. In this study, we identify local and remote influences  
90 on these two distinct large-scale open ocean regions used by populations of grey petrels during the  
91 nonbreeding season (Torres et al. 2015) (i.e. austral summer, October to February). We focus on the  
92 potential connections between the nonbreeding areas and nearby ocean regions, including large-scale  
93 upstream upwelling and remote productive shelf seas. We use a novel combination of drifter  
94 trajectories, satellite-derived primary productivity, numerical adjoint sensitivity experiments, and  
95 output from a biogeochemical state estimate to highlight these connections. Our aims are to better  
96 understand the productivity within these open ocean areas able to support such large populations of  
97 seabirds, and their connections with the surrounding ocean regions. The productivity required to  
98 sustain the nonbreeding petrels does not need to be exceptionally high, but rather it needs to be  
99 *sufficient* to support the food web on which the petrels rely. Since the strong, mostly zonal flow of

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100 the ACC connects different parts of the Southern Ocean on monthly-to-yearly timescales, circulation  
101 and productivity upstream of the open ocean habitats may impact the suitability of these habitat areas  
102 for the petrel populations.

103

**104 METHODS**

105 Tracking data show that the population of grey petrels that breeds on the Kerguelen Islands,  
106 hereafter referred to as KIP, spent their nonbreeding season in a remote region of the southeast Indian  
107 Ocean (Figure 1, top). For convenience, we refer to this region as the SIO. The grey petrels that breed  
108 on the Antipodes Islands, hereafter referred to as AIP, spent their nonbreeding season in a remote  
109 region of the central Pacific Ocean (Figure 1, bottom). For convenience, we refer to this region as the  
110 CPO. We use the 90% contour of the population density kernel (UD90) from Torres et al. (2015),  
111 during the nonbreeding season of grey petrels from KIP and AIP.

112 We use surface drifter data to estimate circulation timescales between study regions and  
113 upstream regions in the surface Southern Ocean. Surface drifter data is from the National Oceanic  
114 and Atmospheric Administration (NOAA) Atlantic Oceanographic Meteorological Laboratory  
115 (AOML) Global Drifter Data Assembly Center, <http://www.aoml.noaa.gov/phod/dac/dacdata.php>,  
116 plotted using JLAB, <http://www.jmlilly.net>. We selected the drifters that were tracked through both  
117 (i.) the middle of the Kerguelen habitat and its associated Kerguelen shelf and (ii.) the middle of the  
118 Antipodes habitat and the southern edge of the Campbell shelf to get an estimate of the circulation  
119 timescale between the plateau areas and the open ocean petrel habitats.

120 Satellite chlorophyll comes from algorithms designed to predict Southern Ocean chlorophyll  
121 concentrations more accurately from the MODIS and SeaWiFS products (Johnson et al. 2013). We

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122 use seasonal net primary productivity from the Oregon State University, Ocean Primary Productivity  
 123 dataset, <https://www.science.oregonstate.edu/ocean.productivity/>. The standard product that we use is  
 124 based on a Vertically Generated Production Model (VGPM) (Behrenfeld & Falkowski 1997a,  
 125 1997b). The VGPM is a chlorophyll-based model that estimates net primary production using a  
 126 temperature-dependent description of chlorophyll-specific photosynthetic efficiency. For the VGPM,  
 127 net primary production is a function of chlorophyll, available light, and the photosynthetic efficiency.  
 128 The standard product uses MODIS chlorophyll and temperature data, SeaWiFS Photosynthetically  
 129 Available Radiation (PAR), and model-derived estimates of euphotic zone depth based on  
 130 chlorophyll concentration (Morel & Berthon 1989).

131 We estimate the minimum amount of primary productivity needed to sustain the petrel  
 132 populations and compare that with local values (i.e. within the UD90). The nutrients and energy  
 133 associated with local productivity are immediately available to the local food web, and ultimately a  
 134 small fraction is available to the top predators in the region, including at the KIP and AIP. A rough  
 135 estimate of the minimum level of productivity required to sustain both petrel populations is given by:

$$136 \quad P_{min} = \frac{p_{carbon} N_{petrels} E_{min}}{r A C_{assim} E_{prey}}, \text{(Equation 1)}$$

137 where  $P_{min}$  has units of g[C]/m<sup>2</sup>; the factors and their values are summarized in Table 1. We use the  
 138 estimate of 53,000 breeding pairs at Antipodes Island (Bell 2002) and 5,000 breeding pairs on the  
 139 Kerguelen Islands (Barbraud et al. 2009). Following Carneiro et al. (2020), we used a ratio of five  
 140 based on available demographic data for grey petrels or related species, to convert the number of  
 141 breeding pairs estimated at each site to the total population, accounting for sabbatical (deferring)  
 142 adults and immatures. The combined estimate (from both sites) is 290,000 individual petrels, and we  
 143 assumed that immatures travel to the same areas as the nonbreeding adults.

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144 The calculation of source waters was partially based on the approach of Song et al. (2016).  
145 We used the ECCOv4 global ocean state estimate (Forget et al. 2015), which is an observationally-  
146 constrained global ocean model. This state estimate was constructed by bringing an instance of the  
147 MITgcm model, available via <http://mitgcm.org>, into consistency with a suite of observational data,  
148 including ship-based hydrographic profiles, autonomous float profiles, and satellite observations of  
149 sea surface height. This was accomplished by iteratively adjusting the initial conditions and surface  
150 forcing in order to minimize a measure of model-data misfit. The result is an ocean model with  
151 realistic, well-constrained hydrography and circulation that covers the period 1992-2011 at roughly  
152 1° horizontal resolution. ECCOv4 uses a GGL mixed layer turbulence closure scheme for mixing and  
153 the Gent-McWilliams scheme to parameterize unresolved transport (Gaspar et al. 1990; Gent &  
154 McWilliams 1990). The ECCOv4 model setup is available at <https://github.com/gaelforget/ECCOv4>.

155 Using an ocean adjoint model based on the ECCOv4 setup, we calculate the source waters of  
156 the SIO and CPO, with a specific focus on the source waters that can influence the SIO and CPO  
157 during the nonbreeding season (October to February). We define our quantity of interest as the  
158 October-to-February mean passive tracer concentration:

$$159 \quad J = \iint_{Oct}^{Feb} \phi(\mathbf{r}, t) dt dV, \quad (\text{Equation 2})$$

160 where the integrand is the passive tracer concentration, which depends on both position  $\mathbf{r}$  and time  $t$ ,  
161 and the volume integral over either the SIO or the CPO. We use our adjoint model setup to calculate  
162 the linear sensitivities of the mean passive tracer concentration to the tracer value in every grid cell at  
163 each time step, i.e.  $\partial J / \partial \phi(\mathbf{r}, t)$ . This can be thought of as a source water calculation, in that we  
164 calculate the potential impact of each grid cell on the integral  $J$ . We calculate the sensitivities over a  
165 five-year period, so a lead time of five years is the longest considered in this study.

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166 In order to understand the seasonal cycles of various biogeochemical tracers in the grey petrel  
167 non-breeding areas and respective Kerguelen and Campbell shelves, we use the biogeochemical  
168 Southern Ocean state estimate (B-SOSE), produced by Verdy & Mazloff (2017). Much like  
169 ECCOv4, B-SOSE is constrained by a suite of observations, including biogeochemical Argo float  
170 profiles. It differs from ECCOv4 in that B-SOSE is a regional model, with an analysis domain that  
171 extends from 30°S to the Antarctic shelf sea, with higher horizontal resolution ( $1/3^\circ$ ). B-SOSE covers  
172 the period 2008-2012, and it represents biogeochemical cycles, including iron, light, nutrients, and  
173 air-sea gas exchange using an evolved version of the BLING model (Galbraith et al. 2010). The  
174 seasonal cycles of net primary production (NPP) and net community production (NCP) were also  
175 assessed. NPP describes the net fixation of inorganic carbon by autotrophic organisms, i.e. the  
176 difference between gross primary production and autotrophic respiration. Part of this organic material  
177 is respired locally, and the difference between NPP and this heterotrophic respiration is termed net  
178 community production (NCP) (Brix et al. 2006).

179

**180 RESULTS**

181 The northern margin of the Kerguelen shelf is connected to the SIO by the circulation of the  
182 ACC. Similarly, the ACC connects the southern margin of the Campbell Plateau to the CPO,  
183 although comparatively further away. Based on 182 surface drifters, we estimate the mean surface  
184 transit time between the Kerguelen shelf and the middle of the SIO to be  $3.7 \pm 2.1$  months (Figure 1,  
185 top). Surface drifter trajectories also show a clear circulation connection between the southern edge  
186 of the Campbell Plateau and the CPO, with a mean transit time of  $7.0 \pm 1.4$  months (Figure 1, bottom).

187 Two strong upwelling areas (greater than 150 m/yr) are found 20-30° in longitude upstream of  
188 each grey petrel habitat (Figure 1). The zonal flow of the ACC offers a horizontal circulation

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189 pathway between the upwelling areas and the petrel habitats. The two petrel habitats are both  
190 intersected by Polar Front and the Subantarctic Front on their southern edges, but they do extend  
191 10-20° further northward in latitude relative to the fronts. Surface drifter data indicate that the mean  
192 surface circulation in and around both petrel habitats is strongly zonal, offering a clear circulation  
193 pathway between the upstream upwelling areas and their associated petrel habitats.

194 Both the SIO and the CPO are characterized by relatively low primary productivity throughout  
195 the whole year compared with the more productive shelf seas (Figure 2). The highest values of  
196 chlorophyll are found from October to December in regions that cut through the habitat-upwelling  
197 systems. Net primary production in the Kerguelen habitat ranges from 430 mg[C]/(m<sup>2</sup> day) in  
198 January to below 200 mg[C]/(m<sup>2</sup> day) in June. The Antipodes habitat displays a slightly lower  
199 average production, from 400 mg[C]/(m<sup>2</sup> day) in January to 150 mg[C]/(m<sup>2</sup> day) in June. The  
200 seasonal variation in productivity matches the transition between the breeding season (austral winter)  
201 and the non-breeding season (austral summer) for both petrel populations, with an increase in the  
202 spring and subsequent decrease in austral autumn.

203 We estimate a minimum required level of primary productivity to support the petrel  
204 populations (both KIP and AIP) to be of order 10<sup>-5</sup> mg[C]/(m<sup>2</sup> day). The productivity in these regions  
205 range from roughly 150-430 mg[C]/(m<sup>2</sup> day) in the SIO and the CPO through the year (Arrigo et al.  
206 2008), which is many orders of magnitude larger than this minimum required productivity to support  
207 both petrel populations. Our estimate of minimum required productivity is consistent with the  
208 hypothesis that there is enough local productivity to support the KIP and AIP populations within the  
209 SIO and CPO.

210 Considering the source waters of the SIO over the five-year timescale of our adjoint sensitivity  
211 runs, ECCOv4 shows that the highest sensitivity values extend from the northern half of the SIO to

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212 the west, connecting with Grand Terre, the main island of the Kerguelen group (Figure 3). The  
213 highest sensitivities are found in the top 5 m, but the sensitivity to interior values (100 m) is non-  
214 negligible. The SIO source waters are mostly found north of the Polar Front, as most of the  
215 sensitivity follows the path of the ACC. Similarly, the source waters of the CPO are mostly found  
216 along the ACC (Figure 3). For both the SIO and the CPO, the sensitivity fields suggest an advective  
217 connection between the relatively productive shelf environments associated with the breeding  
218 locations of the KIP and the AIP.

219 The seasonal cycles of biogeochemical tracers in the Southern Ocean (using B-SOSE) present  
220 very similar patterns in both non-breeding areas of KIP and AIP, and respective Kerguelen and  
221 Campbell shelves, although with a delay in the non-breeding habitats (Figure 4). The nutrients  
222 nitrate, phosphate and iron increase at roughly the same time in both the Kerguelen shelf seas and in  
223 the SIO, although the values peak in the shelf seas roughly one month before those in the SIO (Figure  
224 4). Specifically, from January to July, net community production (NCP) and net primary production  
225 (NPP) in the Kerguelen shelf seas leads production in the SIO, with a delay of roughly one month.  
226 This one-month delay is on the low end of the transit timescales of  $3.7 \pm 2.1$  months, suggesting that  
227 productivity in the SIO is influenced by both local and nonlocal factors. On the other hand, the CPO  
228 is relatively isolated compared with the SIO. Time series analysis indicates that nitrate, phosphate  
229 and iron in the nonbreeding region peak roughly 1-2 months after peaking in the Campbell shelf seas  
230 (Figure 4). Similarly, net community production and net primary productivity in the CPO peak  
231 roughly two months after peaking on Campbell shelf. These 1-2 months delay is much less than the  
232 transit timescale between the shelf and the habitat of  $7.0 \pm 1.4$  months, suggesting that the productivity  
233 in the CPO is strongly influenced by local factors and/or the cumulative effects of many seasonal  
234 cycles.

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235 In the minimum productivity estimate above, we used carbon, modified by scaling factors  
236 related to energy efficiency and transmission between trophic levels, as an approximate indicator of  
237 available biomass for the top predators. As such, the properties of the local carbon budget are  
238 relevant for our study. To better understand the factors driving the available carbon in the relevant  
239 regions, we examine monthly budget climatologies derived from B-SOSE (Figure 5). We also  
240 examine the drivers of iron, which is a limiting micronutrient for primary productivity. First, we will  
241 consider the Campbell plateau and CPO. In the lead-up to the non-breeding season (October through  
242 February), in both the shelf region and the CPO, the leading-order balance is between mixing, which  
243 tends to increase DIC, and biological production (minus remineralization), which tends to decrease  
244 DIC (Figure 5a and 5b). Mixing brings nutrients to the surface, such as the limiting micronutrient  
245 iron, which enables productivity (Figure 5e and 5f). Air-sea gas exchange plays a secondary role in  
246 the plateau region (Figure 5a), while both air-sea gas exchange and advection increase DIC in the  
247 CPO (Figure 5b). Notably, the mixing of DIC peaks in September in both the plateau region and the  
248 CPO, indicating that the two regions evolve largely independently, especially considering the long  
249 transit time between the regions. This is consistent with more local control of DIC in the CPO region,  
250 driven mostly by mixing and enhanced by both advection and air-sea gas exchange.

251 Next, we consider the Kerguelen plateau and SIO. As with the Campbell plateau, to first order  
252 the DIC concentration is increased by mixing and decreased by biological production minus  
253 remineralization (Figure 5c). Advection and surface processes also enhance DIC on the plateau.  
254 However, the DIC budget in the SIO is unique relative to the other three cases. Mixing, air-sea gas  
255 exchange, and dilution from evaporation all play leading roles in enhancing DIC concentration in the  
256 SIO; biological production still tends to decrease DIC concentration there (Figure 5d). The increased  
257 role of advection in the SIO is consistent with a connection between the Kerguelen plateau and the  
258 SIO, which is physically possible in light of the shorter transit times between the two regions. As



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259 with the Campbell-CPO system, the iron budget is still largely a balance between mixing and  
260 biological production (Figure 5g and 5h). These budget results strengthen the hypothesis that the  
261 shelf and habitat are more connected in the Kerguelen-SIO system than they are in the Campbell-  
262 CPO system, in which the two regions evolve largely independently.

263

**264 DISCUSSION**

265 In this work, we show how several large-scale physical and biogeochemical metrics influence  
266 availability of nutrients and energy in two oligotrophic open ocean regions used by nonbreeding grey  
267 petrels during the austral summer. We have illustrated that the southeast Indian Ocean (SIO) and  
268 central Pacific Ocean (CPO) are both connected to upstream upwelling areas and productive shelf  
269 regions via ocean circulation. Local and remote oceanographic features allow necessary productivity  
270 in these oligotrophic areas to support the food web in which large populations of grey petrels rely.  
271 The areas of strongest productivity are found immediately around the Kerguelen Islands and  
272 Campbell Plateau. However, the circulation timescales between the productive shelves and the  
273 nonbreeding habitats are on the order of 4-7 months, which allows for some lag between primary  
274 production, consumption of species at lower trophic levels, and predation by the petrels. We find an  
275 area of strong upwelling upstream of each petrel habitat, and the upwelling areas are closely  
276 connected to the habitats by the strong zonal flow of the ACC. This study highlights the importance  
277 of such oligotrophic areas in the Southern Ocean, considering local and remote effects (e.g. adjacent  
278 upwelling areas and production on a remote shelf) and the time lag between primary production and  
279 consumption on the distribution of top predators.

280 In general, ocean currents can transport both primary producers (e.g. phytoplankton) and  
281 secondary producers (e.g. zooplankton). In terms of connecting spatially separated ocean ecosystems,

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282 the relative importance of the transport of primary producers versus the transport of secondary  
283 producers remains an active area of investigation. As biomass moves up the food web (i.e. to higher  
284 trophic levels), organisms tend to live longer and hence can act as vectors for energy transport,  
285 connecting separate ecosystems in space and time (Murphy et al. 1998). Secondary production can  
286 also be advected, so the peak productivity of higher trophic levels lags behind the peak productivity  
287 of lower levels (Murphy et al. 2007). Budget calculations that include the advection of secondary  
288 producers would be a useful addition to the study of the petrel habitats considered here.

289 The connection between oceanic features and seabird distributions has been an intense area of  
290 research in recent years (Scales et al. 2018; McDuie et al. 2018; Pistorius et al. 2017; McDuie &  
291 Congdon 2016; Yoda et al. 2014; Jaquemet et al. 2014; De Monte et al. 2012; Wakefield et al. 2011).  
292 One mechanism that may help to support the productivity in the two petrel habitats is large-scale  
293 upwelling. A region of exceptionally strong upwelling is located between the Kerguelen Islands and  
294 the SIO, largely set by rapid lateral changes in mixed layer depth (Sallée et al. 2010) (Figure 1, top).  
295 Similarly, an area of strong upwelling is located between the Campbell Plateau and the CPO,  
296 although it is relatively small in areal extent compared with the SIO (Figure 1, bottom). Although  
297 primary production is relatively low in the upwelling areas when compared with adjacent coastal  
298 shelves, they still can have a crucial role in supporting the biological activity in the petrel foraging  
299 habitats. In addition to the transport of volume, heat, salt, and nutrients across the base of the mixed  
300 layer, strong upwelling currents, combined with the zonal flow of ACC, may also help keep organic  
301 matter near the surface, far downstream of where the organic matter originated (e.g. organic matter  
302 produced in a coastal region may be subsequently advected to an open ocean upwelling area).  
303 Similarly, Hyrenbach et al. (2006) showed that great-winged petrels (*Pterodroma macroptera*) in the  
304 Indian Ocean, north of the Subtropical Convergence Zone, were widely distributed and their presence  
305 was heavily influenced by large-scale oceanographic conditions. However, both regions used by

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306 nonbreeding grey petrels considered in our study are located in regions of moderately high sea  
307 surface height variability (Mazloff et al. 2010). Thus, mesoscale and sub-mesoscale eddies may also  
308 influence local surface nutrient distributions and thereby the primary productivity (Bertrand et al.  
309 2014). The relative importance of large-scale oceanographic features, smaller scale features, and the  
310 associated trophic level dynamics in setting seabird distributions remains an active area of  
311 investigation (Bost et al. 2009; Young et al. 2015; Grecian et al. 2016).

312         The ecosystems that support both open ocean petrel populations during their nonbreeding  
313 seasons must ultimately be supported by primary production. A commonly used proxy for  
314 photosynthetic activity is the presence of chlorophyll, which is now routinely remotely sampled by  
315 satellite-mounted instruments (e.g. MODIS, SeaWiFS). Compared with the productive shelf  
316 environments (e.g. around Kerguelen Islands and Campbell Plateau), primary production is relatively  
317 low in the regions used by the nonbreeding grey petrels. The source water calculations further  
318 suggest that the CPO is more isolated than the SIO and thus more sensitive to changes in local  
319 conditions than to changes in the upstream ACC, at least on annual timescales. This result is  
320 supported by biogeochemical time series from an observationally constrained state estimate (B-  
321 SOSE). However, the shelf regions have very large areal extends, so total export production can be  
322 large and endure for long periods. The petrels do not necessarily require a high level of productivity,  
323 but only a *sufficient* level of productivity to support (1) the food web on which they rely and (2) the  
324 other top predators with which they compete. They survive in relatively low productivity  
325 environments, but sufficiently robust to support these populations of seabirds (i.e. much less than 1%  
326 of the estimated local primary productivity) and the respective food webs, as well as potential  
327 competitors. On sufficiently long timescales, there is also input of production from outside  
328 nonbreeding habitats. Some fraction of the energy and nutrients associated with this productivity may  
329 ultimately become available for use by top predators, including that related to advection and

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330 movement of crustaceans, fish, and squid into these oligotrophic areas. Still, the ability of the grey  
331 petrels to acquire energy and nutrients may be limited by spatiotemporal variability in productivity  
332 and prey availability, as well as competition with other predators.

333         Contrary to the most subantarctic seabirds, the grey petrel breeds during the austral winter and  
334 the nonbreeding season is austral summer when primary productivity (and presumably secondary  
335 productivity) is higher in Southern Ocean. It has presumably adapted to survive in an ecological  
336 niche and exploit areas of sufficient productivity where the competitive pressure during its non-  
337 breeding season is low, i.e. they are more successful in these particular areas than in relatively more  
338 productive ones (Torres et al. 2015). It is possible that the upwelling features play a role in the direct  
339 delivery of prey to the petrel populations themselves, i.e. ocean circulation is more relevant for  
340 influencing prey distributions (Chavez & Messié 2009), which is an issue that cannot currently be  
341 addressed, given our lack of knowledge of the distributions of the prey and of other predators in these  
342 regions. However, as birds do not feed directly on primary productivity, it is reasonable to conclude  
343 that the respective food webs in these areas are sufficiently robust to sustain large populations of grey  
344 petrels. The actual presence of the petrels, and the long duration of their stay in the open ocean,  
345 indicates that there must be enough production to support relatively healthy trophic webs in these  
346 broad habitat areas.

347         In parallel with continued observational efforts, studies such as this one must rely on proxies  
348 and our current understanding of how large-scale oceanic processes impact the surface nutrient  
349 distribution. Nutrient upwelling can encourage biological activity at the surface, as long as there is a  
350 sufficient concentration of iron and other micronutrients. Productivity in the Southern Ocean is  
351 limited by iron availability, and iron can be introduced to the surface waters via atmospheric dust  
352 deposition (Jickells & Moore 2015; Jickells & Baker 2016; Pollard et al. 2009). Atmospheric dust  
353 deposition is especially low in the regions used by the nonbreeding petrels, based on maps in Jickells

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354 & Moore (2015), but it is relatively high upstream; nonlocal dust deposition may be more important  
355 than local dust deposition in this case. This is also consistent with the iron budgets shown in this  
356 study, wherein the atmospheric dust deposition is negligible in our target regions. In fact, upwelling  
357 of iron from the interior and sediment release associated with shelves is partially responsible for the  
358 strong productivity found on the shelves of the Kerguelen Islands and Campbell Plateau (Pollard et  
359 al. 2009). Our study found that upwelling of iron is a dominant process for increasing iron  
360 concentration in both the shelf environments and the open ocean environments. At present, few  
361 observational estimates of nutrient upwelling exist, and those estimates tend to focus on the wind-  
362 driven component that is most relevant near the Antarctic continent. Additional sampling is needed to  
363 address the effect of lateral induction and mesoscale eddies on surface nutrient delivery.

364 A complete understanding of the large-scale distribution of any particular species requires  
365 detailed knowledge of a wide range of physical (e.g. temperature, sea surface height),  
366 biogeochemical (e.g. nutrient distributions), and ecological factors (e.g. the availability of prey, the  
367 presence or absence of other competitive species). Despite considerable and ongoing efforts, the food  
368 web structure of the Southern Ocean remains poorly sampled, making a full characterization of  
369 ecosystem dynamics and species distributions difficult (Griffiths 2010). More prey data is needed in  
370 order to address the competitive pressure and transfers of energy and nutrients through trophic levels  
371 in the nonbreeding regions and source water regions. However, we can still relate large-scale oceanic  
372 features (e.g. areas of upwelling, chlorophyll maxima) to large-scale species distributions in a  
373 consistent way using existing and emerging physical and biogeochemical data products.

374 This work is an example of how top predator distributions and oceanographic data can  
375 potentially highlight areas of the open ocean that may be more dynamic and productive than  
376 previously thought, and able to support greater predator abundance. It was here illustrated the  
377 importance of advection for connecting different parts of the ocean ecosystem, especially in the

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378 relatively well-mixed Southern Ocean. The presence of fast and far-traveling seabirds such as grey  
379 petrels can indicate hotspot areas that need to be better studied. Furthermore, there may be similar  
380 areas in the open ocean where predator distributions (including seabirds, cetaceans and large pelagic  
381 fish) can indicate regions that require further study. Marine protected areas have only very recently  
382 been established in eutrophic coastal regions of the Southern Ocean (CCAMLR 2012; Grant et al.  
383 2013), and open ocean conservation efforts are becoming increasingly important (Delord et al. 2014;  
384 Hindell et al. 2020). The conservation relevance of open ocean areas may have been overlooked. It  
385 may be useful to generally supplement existing physical and biogeochemical oceanographic data  
386 with top predator data to understand species distributions in oligotrophic regions and guide  
387 conservation management plans in the changing environment of the Southern Ocean (Rintoul et al.  
388 2018; Xavier et al. 2016)

389

**390 CONCLUSIONS**

391 In this work, we considered potential local and remote sources of influence on two open ocean  
392 regions occupied by grey petrels during their nonbreeding season. Our results indicate that both local  
393 and remote processes drive enough productivity to support large populations of seabirds and  
394 potentially other top predators, and their respective food webs. The minimum required productivity  
395 to support grey petrel populations was estimated to be many orders of magnitude smaller than the  
396 observed local productivity in these oligotrophic areas of the Southern Ocean. Both regions are  
397 situated in similar physical environments (i.e. connected to the nutrient rich shelf waters and  
398 upstream upwelling areas via the Antarctic Circumpolar Current). However, the source water  
399 calculations suggest that the CPO is more isolated than the SIO, and is thus more sensitive to changes  
400 in local conditions than to remote changes in the upstream ACC. Thus, our study highlights the

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401 importance of both local and remote oceanographic influences in the productivity of pelagic  
402 oligotrophic areas of the Southern Ocean. Such large open areas in the ocean are indubitably  
403 important in sustaining marine biodiversity, providing sanctuaries for top predators such as grey  
404 petrels.

405

**406 ACKNOWLEDGMENTS**

407 We would like to thank Norman Ratcliffe for discussions that improved this work. DJ is supported by  
408 grants from the Natural Environment Research Council, including ACSIS [grant NE/N018028/1] and  
409 a UKRI Future Leaders Fellowship [grant MR/T020822/1]. [RP] This study represents a contribution  
410 to the Ecosystems component of the British Antarctic Survey Polar Science for Planet Earth  
411 Programme, funded by The Natural Environment Research Council. [LT] Funding for the grey petrel  
412 work was the New Zealand Ministry for Primary Industries (PRO2006–01). [KD] Funding and  
413 support for the study in French Southern Territories was provided by the Institut Polaire Français  
414 Paul-Emile Victor (IPEV, programme no. 109, HW), the Prince Albert II de Monaco Foundation,  
415 Program ANR Biodiversité 2005–11 REMIGE, Program ANR 07 Biodiv ‘Glides’, and the Zones  
416 Atelier Antarctique (ZATA-LTSER France, CNRS-INEE). This study benefited from the strategic  
417 program of MARE (MARE - UID/MAR/04292/2020) and the transitory norm contract DL57/2016 to  
418 FRC (DL57/2016/CP1370/CT90) at the University of Coimbra, financed by the Foundation for  
419 Science and Technology (FCT; Portugal).

420

**421 CONFLICT OF INTEREST**

422 The authors declare no competing interests.

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423

424 **AUTHOR CONTRIBUTION**

425 JX, DJ and LT conceived of the initial study. DJ and FC led the writing of the manuscript. DJ carried  
426 out the analysis. JX contributed to the manuscript text, particularly in the introduction and discussion  
427 sections. All authors reviewed the manuscript. RF provided critical information for the minimum  
428 primary productivity calculation. BS prepared Figure 4. PU provided input on the primary  
429 productivity calculation. LT provided the petrel tracking data, with input from RP, DT, PS, KD, and  
430 HW. JS provided ACC front positions and upwelling data. AV and MM provided the budget data.  
431 EM provided conceptual guidance and offered feedback throughout the project.

432

433 **DATA AVAILABILITY STATEMENT**

434 Surface drifter data is from the National Oceanic and Atmospheric Administration (NOAA) Atlantic  
435 Oceanographic Meteorological Laboratory (AOML) Global Drifter Data Assembly Center,  
436 <http://www.aoml.noaa.gov/phod/dac/dacdata.php>, plotted using JLAB, <http://www.jmlilly.net>. We  
437 use seasonal net primary productivity from the Oregon State University, Ocean Primary Productivity  
438 dataset, <https://www.science.oregonstate.edu/ocean.productivity/>. The ECCOv4 model setup is  
439 available at <https://github.com/gaelforget/ECCOv4>. B-SOSE is available at  
440 [http://sose.ucsd.edu/bsose\\_solution\\_Iter105.html](http://sose.ucsd.edu/bsose_solution_Iter105.html).

441

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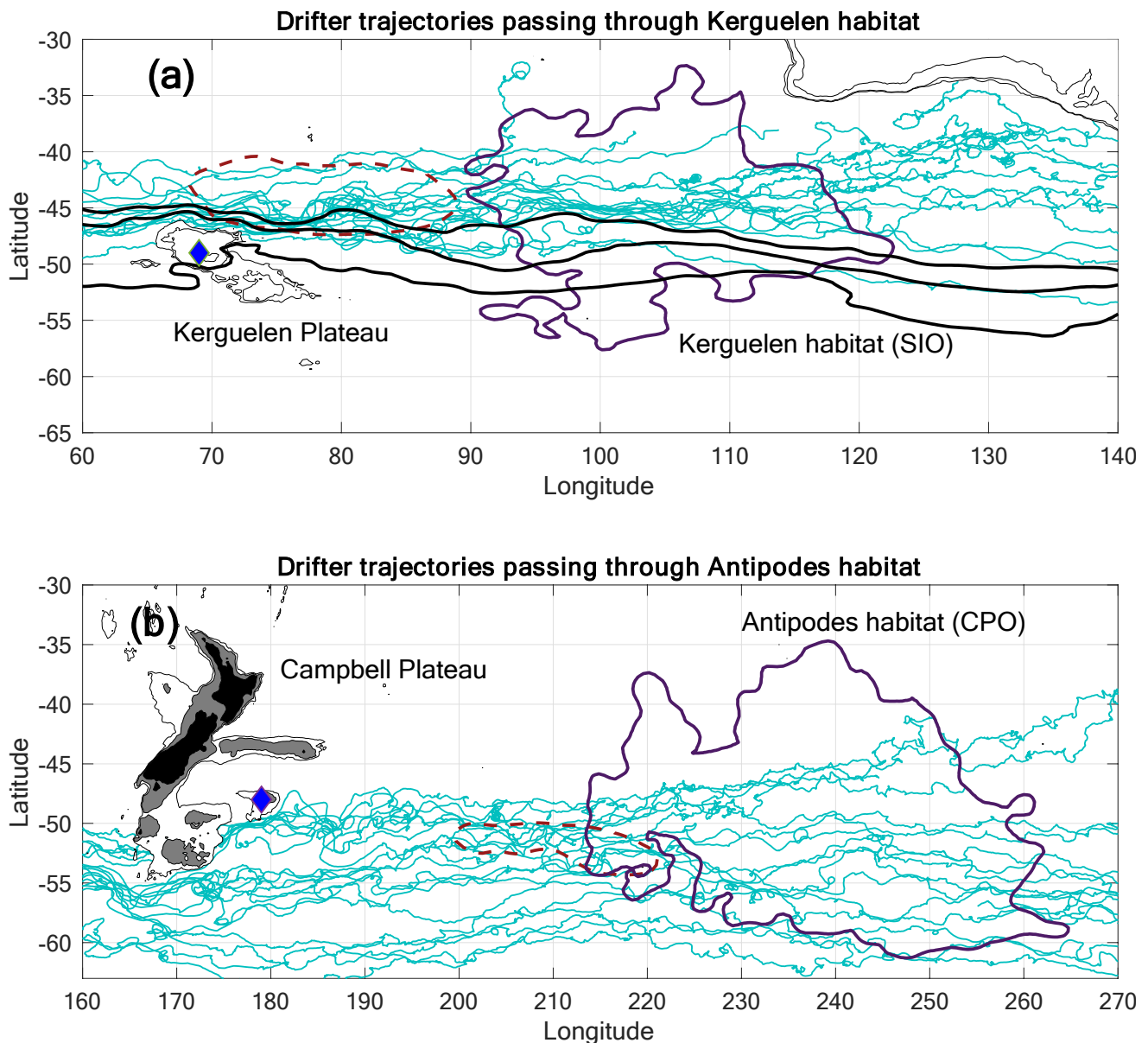
646 **Table 1.** Parameter definitions, values, and sources for the terms in Equation 1, used to define the  
 647 minimum productivity estimate (units g[C]/m<sup>2</sup>).

Factor	Value	Source
Mass fraction of carbon in chlorophyll ( $p_{carbon}$ )	0.544 gC/g	(Williams & Follows 2011)
Number of grey petrels in regions ( $N_{petrels}$ )	290 000	(Torres et al. 2015)
Minimum energy required by single grey petrel ( $E_{min}$ )	700 kJ/day	(Ellis & Gabrielsen 2002)
Trophic level transfer coefficient ( $r$ )	$1.2 \times 10^{-4}$	(Priddle et al. 1998)
Surface area of SIO + CPO ( $A$ )	$3.95 \times 10^{13} \text{ m}^2$	(Torres et al. 2015)
Assimilation efficiency ( $c_{assim}$ )	0.75	(Jackson 1986)
Energy density of prey ( $E_{prey}$ )	3 kJ/g	(Eder & Lewis 2005; Sinclair et al. 2015; Thompson 1992)

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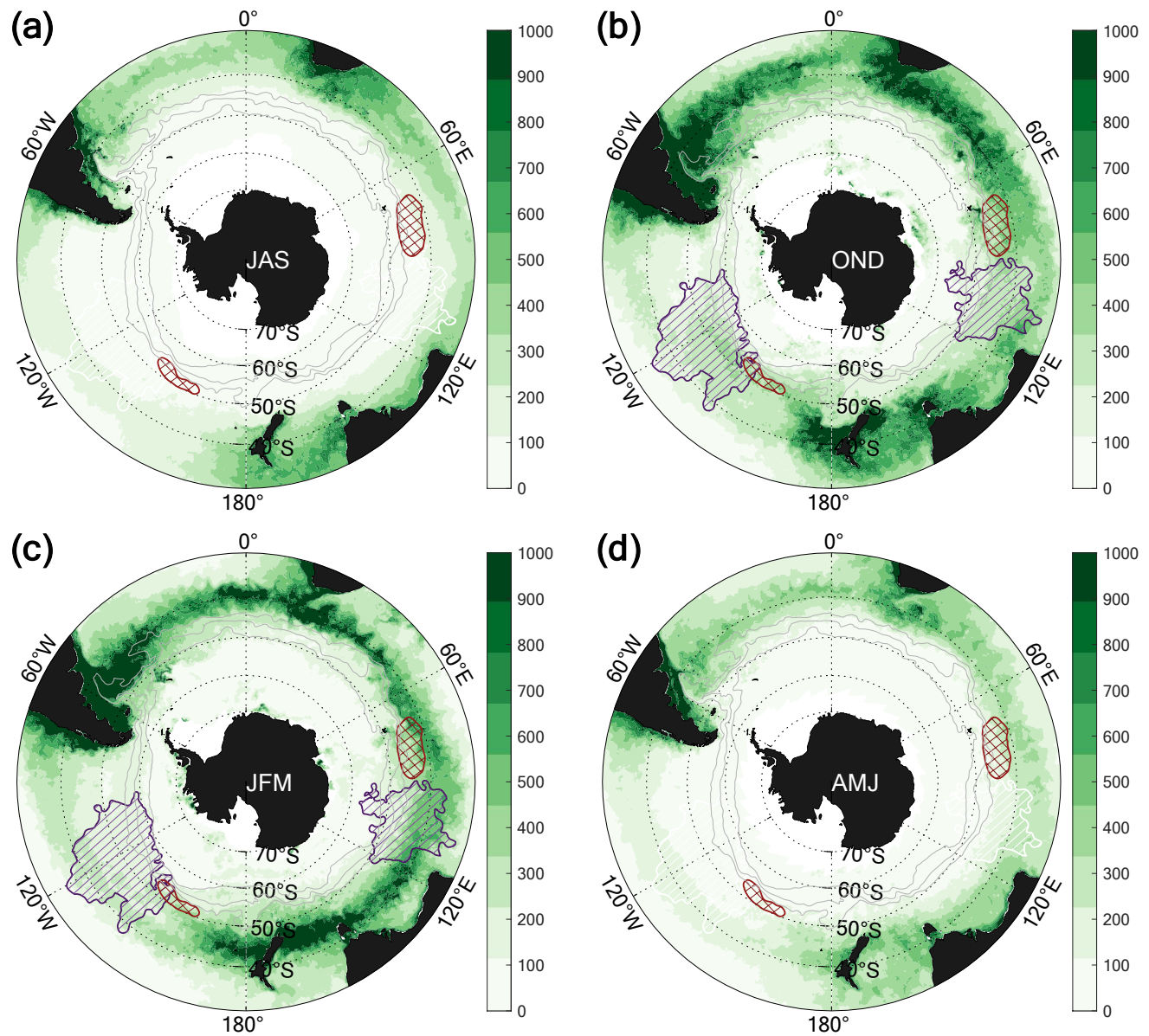
650 **Figure captions**

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652 **Figure 1.** Distribution of nonbreeding grey petrels tracked using geolocators from (top) Kerguelen  
 653 Islands and (bottom) Antipodes Islands, overlaid on a total of 182 surface drifter tracks. The 90%  
 654 density contours during the petrel nonbreeding season (October to February; Torres et al. 2015) are  
 655 shown as solid purple lines, and the surface drifter tracks are solid light blue lines. The breeding  
 656 colonies are indicated by blue diamonds. The dashed red lines indicate 150 m/yr upwelling contours  
 657 derived from Argo float data (Sallée et al. 2010).

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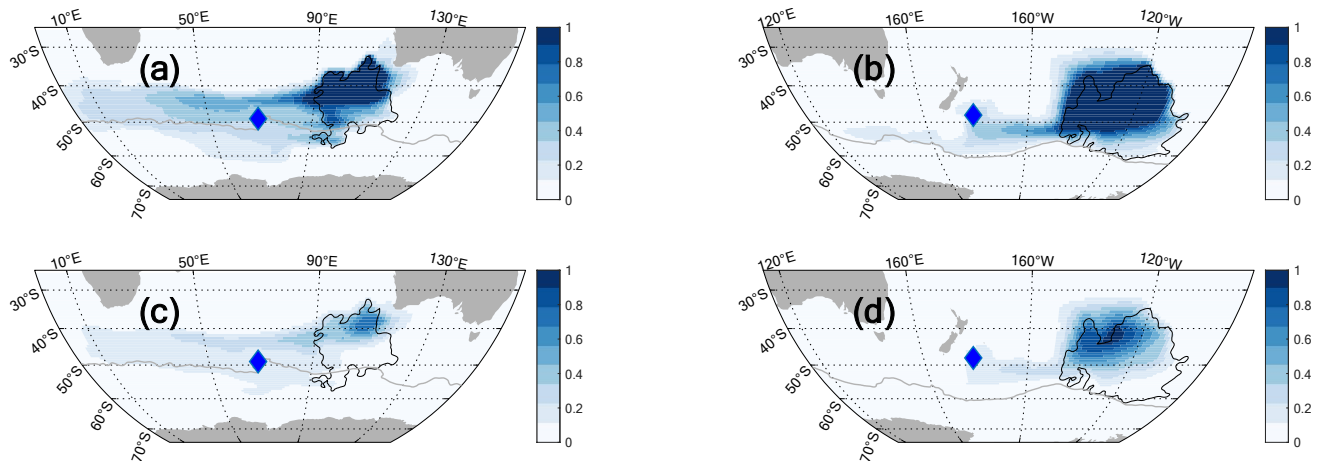
660 **Figure 2.** Seasonal net primary productivity ( $\text{mg}[\text{C}]/\text{m}^2$ ) from the Oregon State University Ocean  
 661 Primary Productivity dataset. The grey contours mark the positions of the Polar Front (innermost)  
 662 and Subantarctic Fronts (SAF and SAF-N) (Sallée et al. 2010). The purple hatches indicate the 90%  
 663 distribution contours of grey petrels tracked during the nonbreeding season (Torres et al. 2015). The  
 664 same contours are shown in white during JAS and AMJ, when the petrels are largely absent from the  
 665 habitats. The red cross-hatched area mark areas of upwelling greater than 150 m/yr. Shown are values

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666 averaged over July-August-September [JAS], October-November-December [OND], January-  
667 February-March [JFM], and April-May-June [AMJ].

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671 **Figure 3.** Source waters of the SIO (left) and CPO (right) over a five-year timescale. Shown are the  
672 source water contributions from the 5 m (top) and 100 m (bottom) depth levels, shown as the scaled  
673 sensitivity per unit meter. The Polar Front is shown as a thin grey line, and the breeding colony  
674 locations are marked by blue diamonds. All four panels have been scaled by the same maximum  
675 value as to indicate relative sensitivity. Front data is from Sallée et al. (2010).

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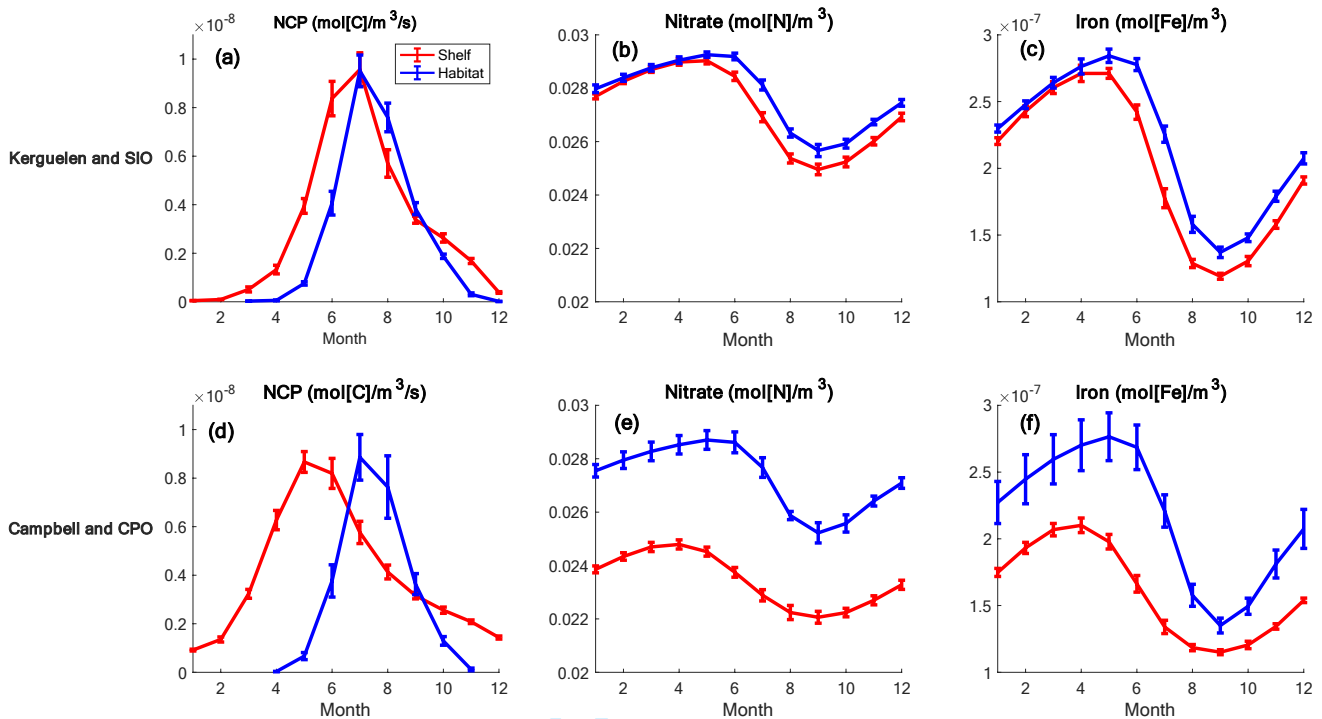
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## Local and remote influences in the open ocean

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683 **Figure 4.** Monthly mean time series of productivity and nutrients from 2008 to 2012 from B-SOSE  
 684 iteration 122. Solid lines indicate monthly climatological values, and the error bars indicate one  
 685 standard deviation in the monthly mean values. Net community production (NCP) is similar in its  
 686 seasonal cycle to net primary production (not shown), and nitrate is similar in its seasonal cycle to  
 687 phosphate (not shown), although the values are different. The months progress from 1=January to  
 688 12=December.

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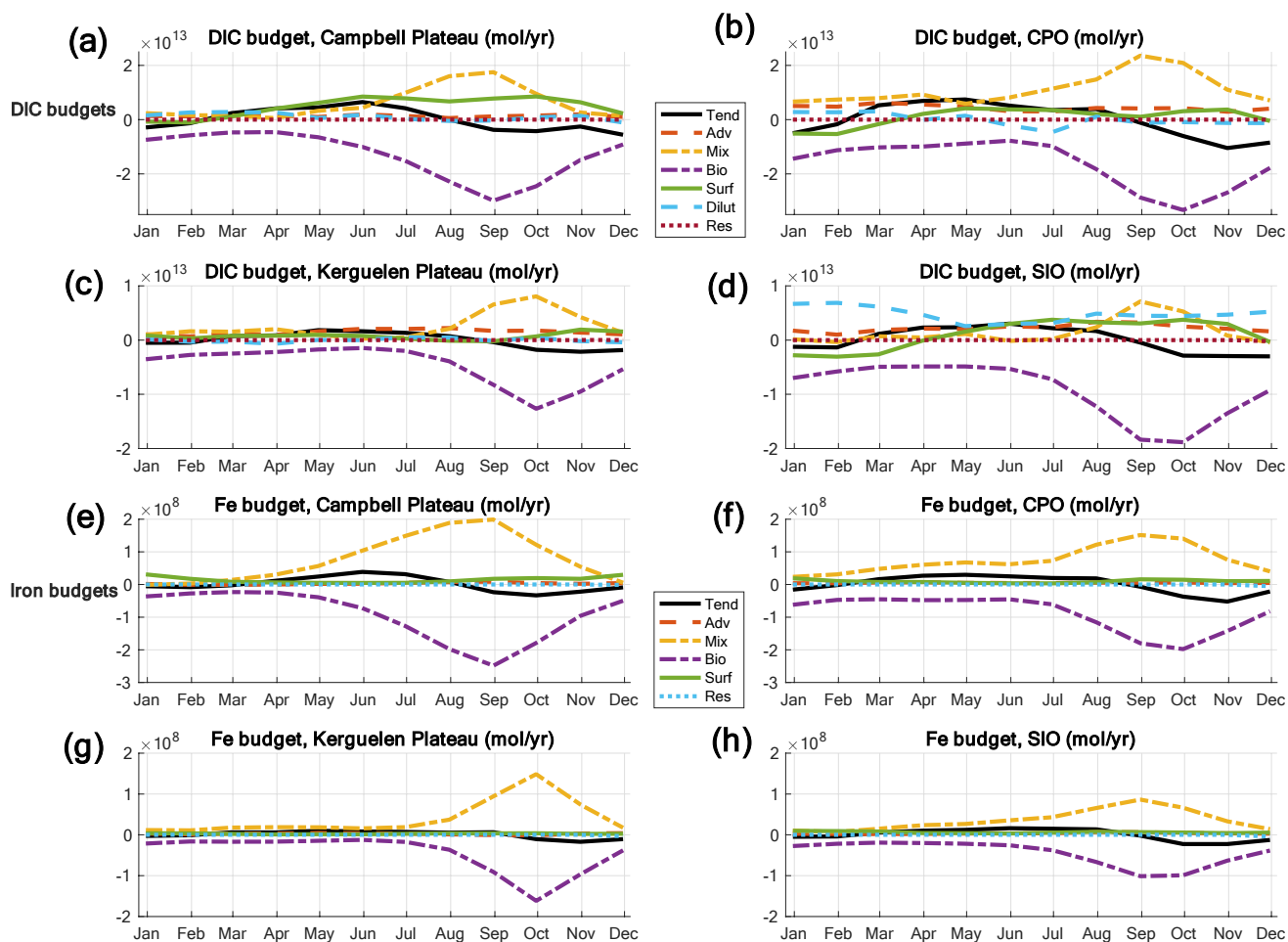
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## Local and remote influences in the open ocean

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696 **Figure 5.** Climatological DIC and iron budgets integrated over the top 15 m of the indicated control  
 697 volumes. Data from B-SOSE iteration 122. (a)-(d) Terms for the DIC budget include the total  
 698 tendency (Tend), combined horizontal and vertical advection (Adv), combined horizontal and vertical  
 699 mixing (Mix), biological uptake minus remineralization (Bio), surface processes, such as air-sea gas  
 700 exchange (Surf), and dilution (Dilut). The residual (Res) is small, indicating that the budget is closed.  
 701 (e)-(h) Terms for the iron budget are mostly the same as for the DIC budget, except the surface term  
 702 represents dust deposition (Surf) and dilution is not included.



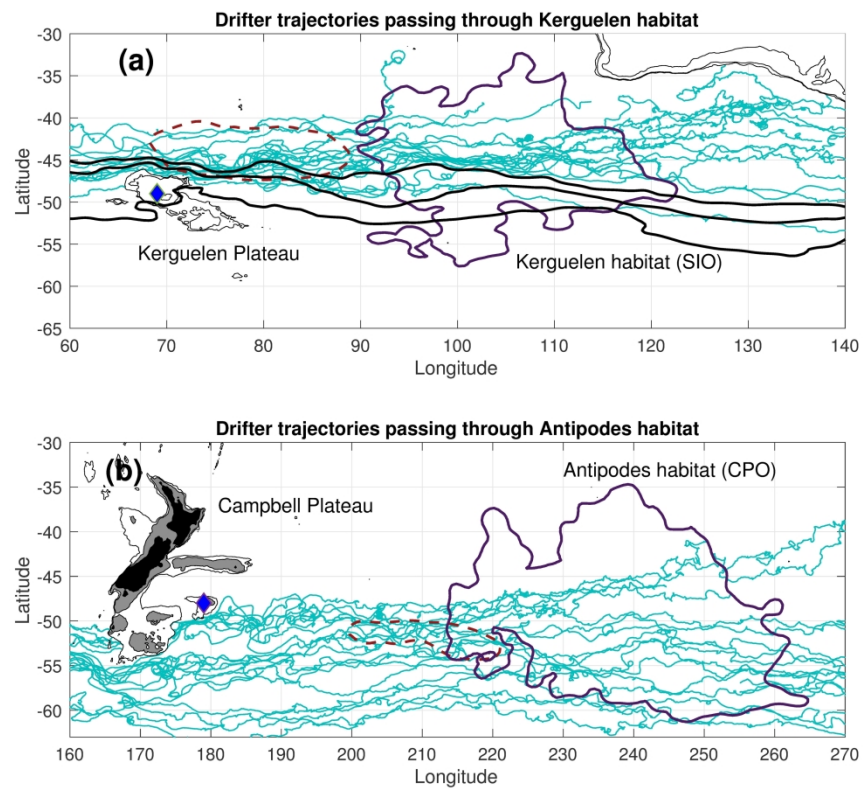


Figure 1. Distribution of nonbreeding grey petrels tracked using geolocators from (top) Kerguelen Islands and (bottom) Antipodes Islands, overlaid on a total of 182 surface drifter tracks. The 90% density contours during the petrel nonbreeding season (October to February; Torres et al. 2015) are shown as solid purple lines, and the surface drifter tracks are solid light blue lines. The breeding colonies are indicated by blue diamonds. The dashed red lines indicate 150 m/yr upwelling contours derived from Argo float data (Sallée et al. 2010).

286x246mm (300 x 300 DPI)

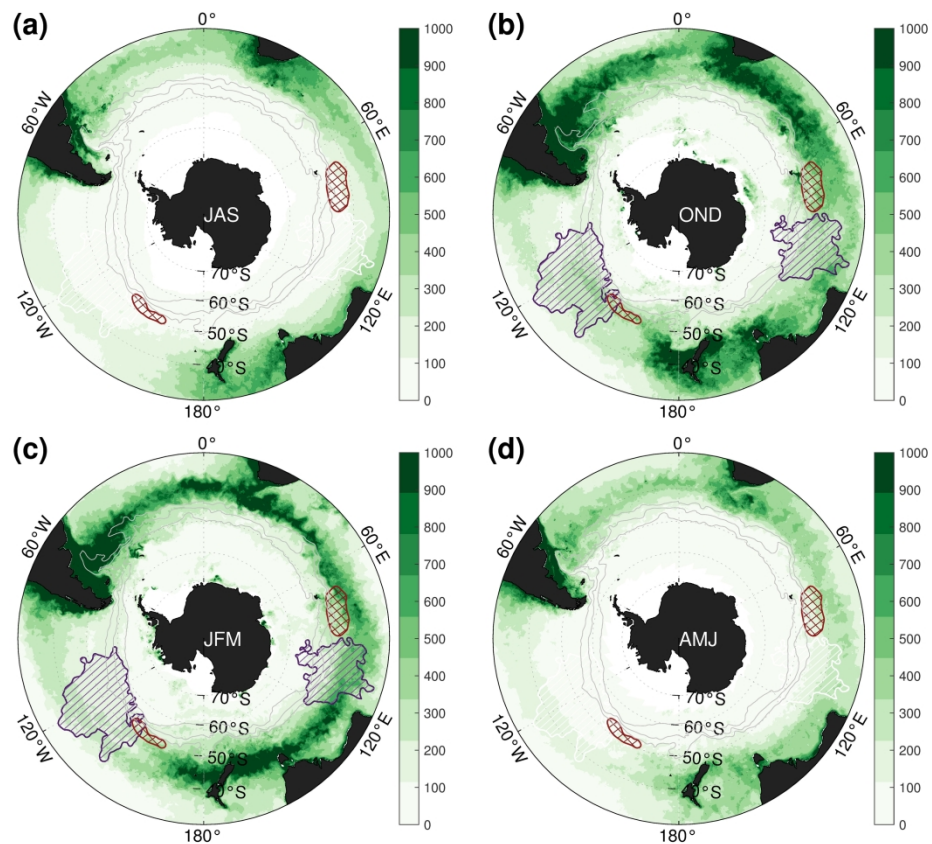


Figure 2. Seasonal net primary productivity ( $\text{mg}[\text{C}]/\text{m}^2$ ) from the Oregon State University Ocean Primary Productivity dataset. The grey contours mark the positions of the Polar Front (innermost) and Subantarctic Fronts (SAF and SAF-N) (Sallée et al. 2010). The purple hatches indicate the 90% distribution contours of grey petrels tracked during the nonbreeding season (Torres et al. 2015). The same contours are shown in white during JAS and AMJ, when the petrels are largely absent from the habitats. The red cross-hatched area mark areas of upwelling greater than 150  $\text{m}/\text{yr}$ . Shown are values averaged over July-August-September [JAS], October-November-December [OND], January-February-March [JFM], and April-May-June [AMJ].

290x248mm (300 x 300 DPI)

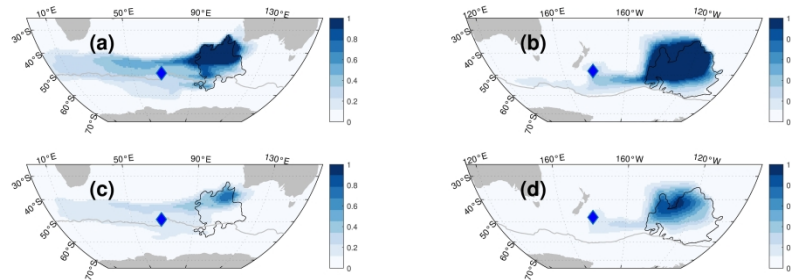


Figure 3. Source waters of the SIO (left) and CPO (right) over a five-year timescale. Shown are the source water contributions from the 5 m (top) and 100 m (bottom) depth levels, shown as the scaled sensitivity per unit meter. The Polar Front is shown as a thin grey line, and the breeding colony locations are marked by blue diamonds. All four panels have been scaled by the same maximum value as to indicate relative sensitivity. Front data is from Sallée et al. (2010).

408x126mm (300 x 300 DPI)

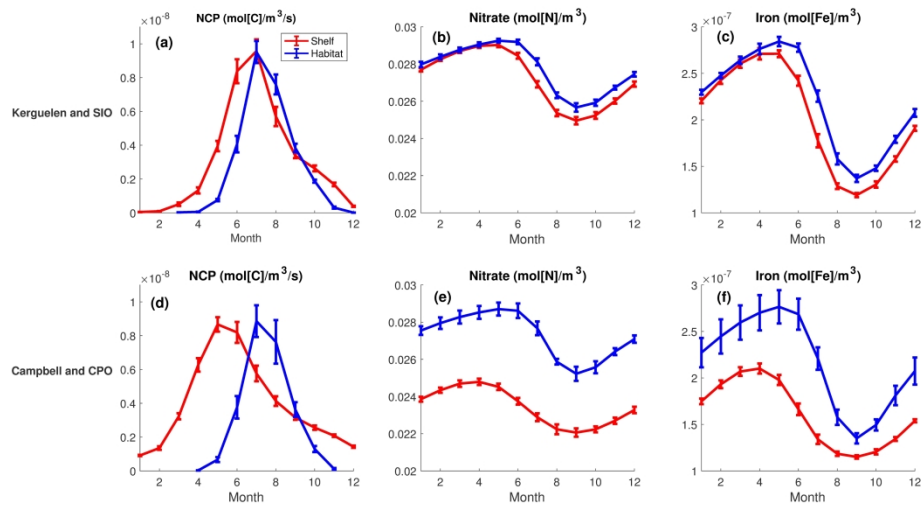


Figure 4. Monthly mean time series of productivity and nutrients from 2008 to 2012 from B-SOSE iteration 122. Solid lines indicate monthly climatological values, and the error bars indicate one standard deviation in the monthly mean values. Net community production (NCP) is similar in its seasonal cycle to net primary production (not shown), and nitrate is similar in its seasonal cycle to phosphate (not shown), although the values are different. The months progress from 1=January to 12=December.

439x239mm (300 x 300 DPI)

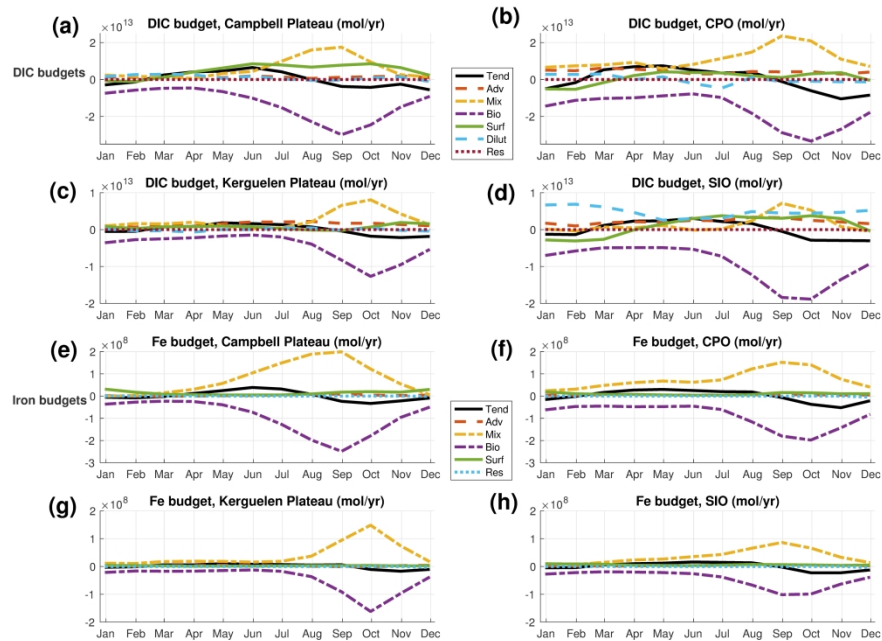


Figure 5. Climatological DIC and iron budgets integrated over the top 15 m of the indicated control volumes.

Data from B-SOSE iteration 122. (a)-(d) Terms for the DIC budget include the total tendency (Tend), combined horizontal and vertical advection (Adv), combined horizontal and vertical mixing (Mix), biological uptake minus remineralization (Bio), surface processes such as air-sea gas exchange (Surf), and dilution (Dilut). The residual (Res) is small, indicating that the budget is closed. (e)-(h) Terms for the iron budget are mostly the same as for the DIC budget, except the surface term represents dust deposition (Surf) and dilution is not included.

378x274mm (300 x 300 DPI)