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

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Abstract:	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 (Procellaria cinerea) 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

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.

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

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Keywords: Antarctic Circumpolar Current (ACC), Biogeography, Conservation, Grey petrels, High seas, Hotspot, Open ocean, Primary productivity, *Procellaria cinerea*, Seabirds

ABSTRACT

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 (*Procellaria cinerea*) 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 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.

INTRODUCTION

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

In eutrophic coastal regions (e.g. areas of strong coastal upwelling) high primary production supports an abundant trophic pyramid and some of the largest fisheries in the world (Ryther 1969; Pauly & Christensen 1995; Chavez & Messié 2009). In contrast, in the oligotrophic open oceans, the food webs are generally characterized by a complex low-nutrient input system that exports little of its production and supports relatively few fisheries (Chavez et al. 2011). Numerous marine organisms, including seabirds, migrate between the highly productive upwelling regions in coastal areas through less-productive open ocean regions (Bolten 2003; Egevang et al. 2010; Block et al. 2011) and may have to feed regularly to survive in these poorly known regions. Although eddies, oceanic fronts, and small bathymetric features that present barriers to current flow (i.e. seamounts, islands and shelf breaks) may provide important hotspots in the open ocean and attract aggregations of predators (Bost et al. 2009; Godø et al. 2012; Young et al. 2015; Xavier et al. 2003; Xavier et al. 2004; Menkes et al. 2002; Morato et al. 2010), little attention has been paid to less productive regions such as large oligotrophic regions in the upper layers of the ocean, and how they are essential to species survival. Large-scale patterns of upwelling and downwelling, trajectory drifts, and connections to productive shelf regions via ocean circulation may influence production and species distribution in the upper layers of the open Southern Ocean. For instance, the importance of advection in transferring krill or secondary production in maintaining food webs was regularly studied in coastal areas and hotspots in the Southern Ocean (e.g. Hofmann et al. 2004; Murphy et al. 1998, 2004, 2007), but not in the open oceans regions. These issues are particularly important for conservation, as marine protected areas mainly cover coastal areas (Allison et al. 1998; Game et al. 2009) due to the relative lack of information on large-scale open ocean regions.

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

METHODS

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

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

Satellite chlorophyll comes from algorithms designed to predict Southern Ocean chlorophyll concentrations more accurately from the MODIS and SeaWiFS products (Johnson et al. 2013). We use seasonal net primary productivity from the Oregon State University, Ocean Primary Productivity dataset, https://www.science.oregonstate.edu/ocean.productivity/. The standard product that we use is based on a Vertically Generated Production Model (VGPM) (Behrenfeld & Falkowski 1997a, 1997b). The VGPM is a chlorophyll-based model that estimates net primary production using a temperature-dependent description of chlorophyll-specific photosynthetic efficiency. For the VGPM, net primary production is a function of chlorophyll, available light, and the photosynthetic efficiency. The standard product uses MODIS chlorophyll and temperature data, SeaWiFS Photosynthetically Available Radiation (PAR), and model-derived estimates of euphotic zone depth based on chlorophyll concentration (Morel & Berthon 1989).

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

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

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

Local and remote influences in the open ocean

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

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

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

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

Local and remote influences in the open ocean

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

RESULTS

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

Two strong upwelling areas (greater than 150 m/yr) are found 20-30° in longitude upstream of each grey petrel habitat (Figure 1). The zonal flow of the ACC offers a horizontal circulation pathway between the upwelling areas and the petrel habitats. The two petrel habitats are both intersected by Polar Front and the Subantarctic Front on their southern edges, but they do extend 10-20° further northward in latitude relative to the fronts. Surface drifter data indicate that the mean surface circulation in and around both petrel habitats is strongly zonal, offering a clear circulation pathway between the upstream upwelling areas and their associated petrel habitats.

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

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

Considering the source waters of the SIO over the five-year timescale of our adjoint sensitivity runs, ECCOv4 shows that the highest sensitivity values extend from the northern half of the SIO to the west, connecting with Grand Terre, the main island of the Kerguelen group (Figure 3). The highest sensitivities are found in the top 5 m, but the sensitivity to interior values (100 m) is non-negligible. The SIO source waters are mostly found north of the Polar Front, as most of the sensitivity follows the path of the ACC. Similarly, the source waters of the CPO are mostly found along the ACC (Figure 3). For both the SIO and the CPO, the sensitivity fields suggest an advective connection between the relatively productive shelf environments associated with the breeding locations of the KIP and the AIP.

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

Local and remote influences in the open ocean

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

Next, we consider the Kerguelen plateau and SIO. As with the Campbell plateau, to first order the DIC concentration is increased by mixing and decreased by biological production minus remineralization (Figure 5c). Advection and surface processes also enhance DIC on the plateau. However, the DIC budget in the SIO is unique relative to the other three cases. Mixing, air-sea gas exchange, and dilution from evaporation all play leading roles in enhancing DIC concentration in the SIO; biological production still tends to decrease DIC concentration there (Figure 5d). The increased role of advection in the SIO is consistent with a connection between the Kerugelen plateau and the SIO, which is physically possible in light of the shorter transit times between the two regions. As with the Campbell-CPO system, the iron budget is still largely a balance between mixing and biological production (Figure 5g and 5h). These budget results strengthen the hypothesis that the shelf and habitat are more connected in the Kerguelen-SIO system than they are in the Campbell-CPO system, in which the two regions evolve largely independently.

DISCUSSION

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

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

The connection between oceanic features and seabird distributions has been an intense area of research in recent years (Scales et al. 2018; McDuie et al. 2018; Pistorius et al. 2017; McDuie & Congdon 2016; Yoda et al. 2014; Jaquemet et al. 2014; De Monte et al. 2012; Wakefield et al. 2011). One mechanism that may help to support the productivity in the two petrel habitats is large-scale upwelling. A region of exceptionally strong upwelling is located between the Kerguelen Islands and the SIO, largely set by rapid lateral changes in mixed layer depth (Sallée et al. 2010) (Figure 1, top). Similarly, an area of strong upwelling is located between the Campbell Plateau and the CPO, although it is relatively small in areal extent compared with the SIO (Figure 1, bottom). Although primary production is relatively low in the upwelling areas when compared with adjacent coastal shelves, they still can have a crucial role in supporting the biological activity in the petrel foraging habitats. In addition to the transport of volume, heat, salt, and nutrients across the base of the mixed layer, strong upwelling currents, combined with the zonal flow of ACC, may also help keep organic matter near the surface, far downstream of where the organic matter originated (e.g. organic matter produced in a coastal region may be subsequently advected to an open ocean upwelling area). Similarly, Hyrenbach et al. (2006) showed that great-winged petrels (*Pterodroma macroptera*) in the Indian Ocean, north of the Subtropical Convergence Zone, were widely distributed and their presence was heavily influenced by large-scale oceanographic conditions. However, both regions used by nonbreeding grey petrels considered in our study are located in regions of moderately high sea surface height variability (Mazloff et al. 2010). Thus, mesoscale and sub-mesoscale eddies may also influence local surface nutrient distributions and thereby the primary productivity (Bertrand et al. 2014). The relative importance of large-scale oceanographic features, smaller scale features, and the associated trophic level dynamics in setting seabird distributions remains an active area of investigation (Bost et al. 2009; Young et al. 2015; Grecian et al. 2016).

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

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

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

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

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

This work is an example of how top predator distributions and oceanographic data can potentially highlight areas of the open ocean that may be more dynamic and productive than previously thought, and able to support greater predator abundance. It was here illustrated the importance of advection for connecting different parts of the ocean ecosystem, especially in the relatively well-mixed Southern Ocean. The presence of fast and far-traveling seabirds such as grey petrels can indicate hotspot areas that need to be better studied. Furthermore, there may be similar areas in the open ocean where predator distributions (including seabirds, cetaceans and large pelagic fish) can indicate regions that require further study. Marine protected areas have only very recently been established in eutrophic coastal regions of the Southern Ocean (CCAMLR 2012; Grant et al. 2013), and open ocean conservation efforts are becoming increasingly important (Delord et al. 2014; Hindell et al. 2020). The conservation relevance of open ocean areas may have been overlooked. It may be useful to generally supplement existing physical and biogeochemical oceanographic data with top predator data to understand species distributions in oligotrophic regions and guide conservation management plans in the changing environment of the Southern Ocean (Rintoul et al. 2018; Xavier et al. 2016)

CONCLUSIONS

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

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CONFLICT OF INTEREST

The authors declare no competing interests.

AUTHOR CONTRIBUTION

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

DATA AVAILABILITY STATEMENT

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

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

Factor	Value	Source
Mass fraction of carbon in chlorophyll ($pcarbon$)	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 ($Emin$)	700 kJ/day	(Ellis & Gabrielsen 2002)
Trophic level transfer coefficient (r)	1.2×10^{-4}	(Priddle et al. 1998)
Surface area of SIO + CPO (A)	3.95×10^{13} 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)

Figure captions

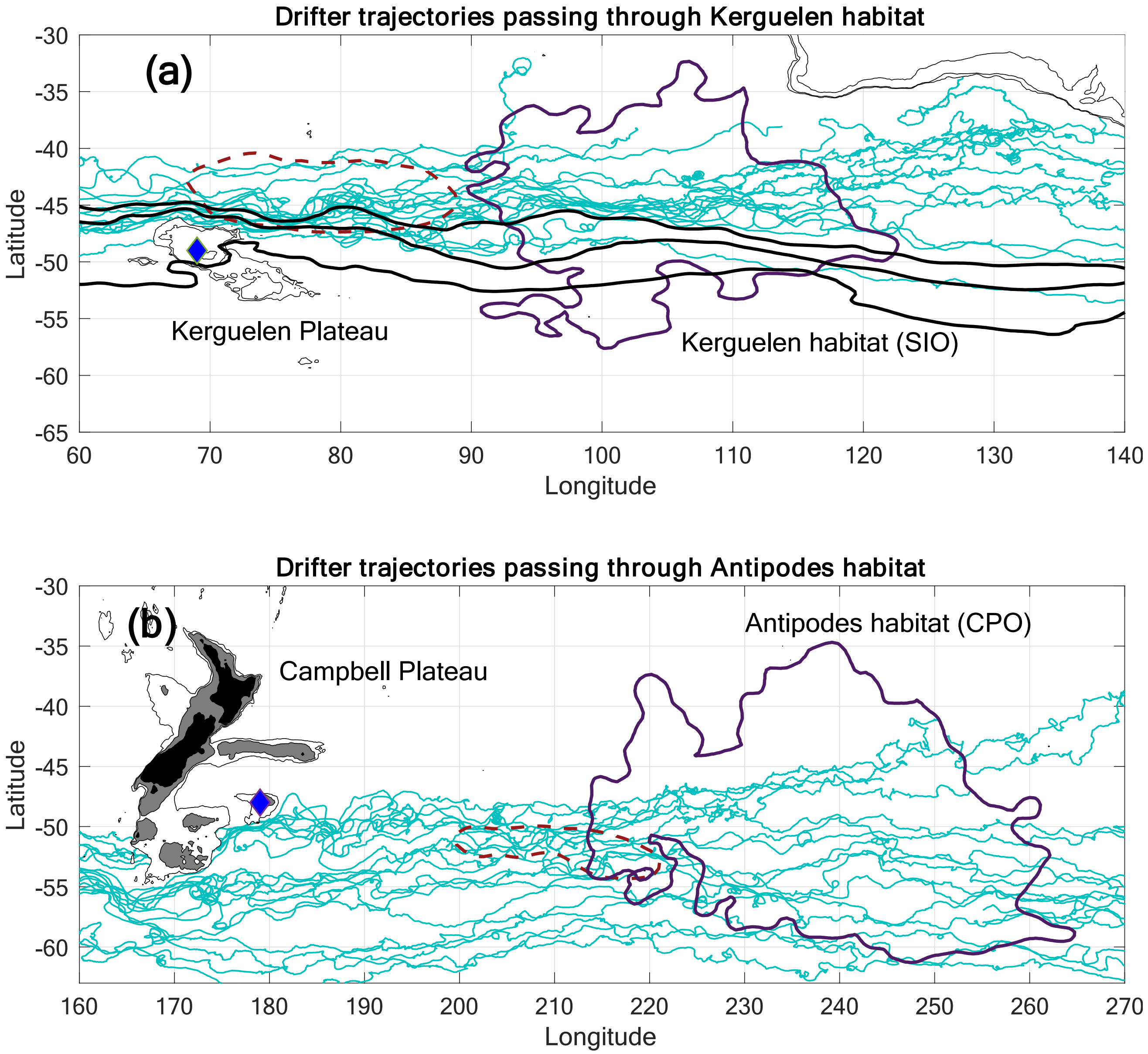


Figure 1. Distribution of nonbreeding grey petrels tracked using geolocators from (top) Kerguelen Islands and (bottom) Antipodes Islands, overlaid on a total of 182 surface drifter tracks. The 90% density contours during the petrel nonbreeding season (October to February; Torres et al. 2015) are shown 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).

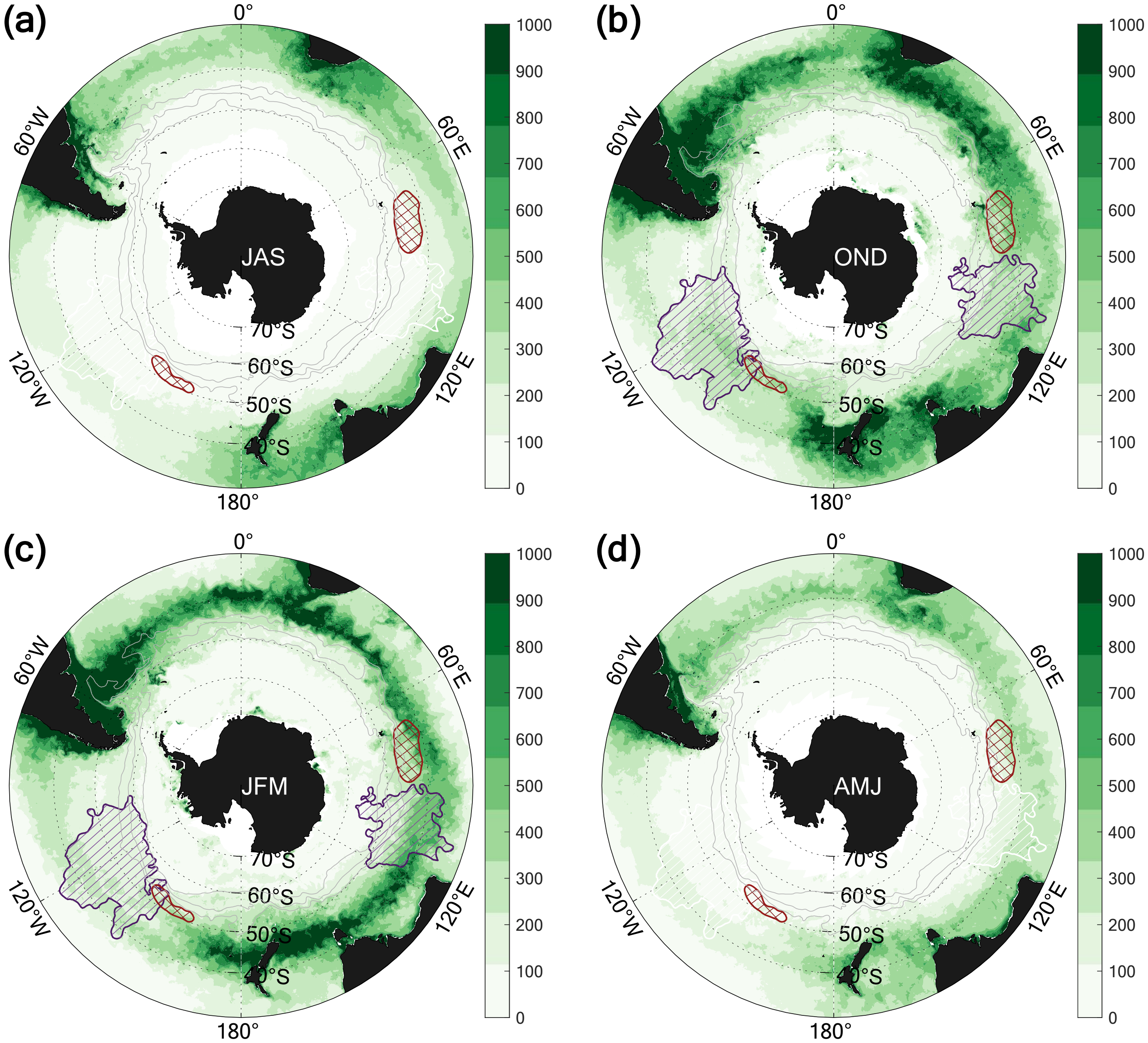


Figure 2. Seasonal net primary productivity (mg[C]/m^2) from the Oregon State University Ocean Primary Productivity dataset. The grey contours mark the positions of the Polar Front (innermost) and Subantarctic Fronts (SAF and SAF-N) (Sallée et al. 2010). The purple hatches indicate the 90% distribution 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 m/yr. Shown are values

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

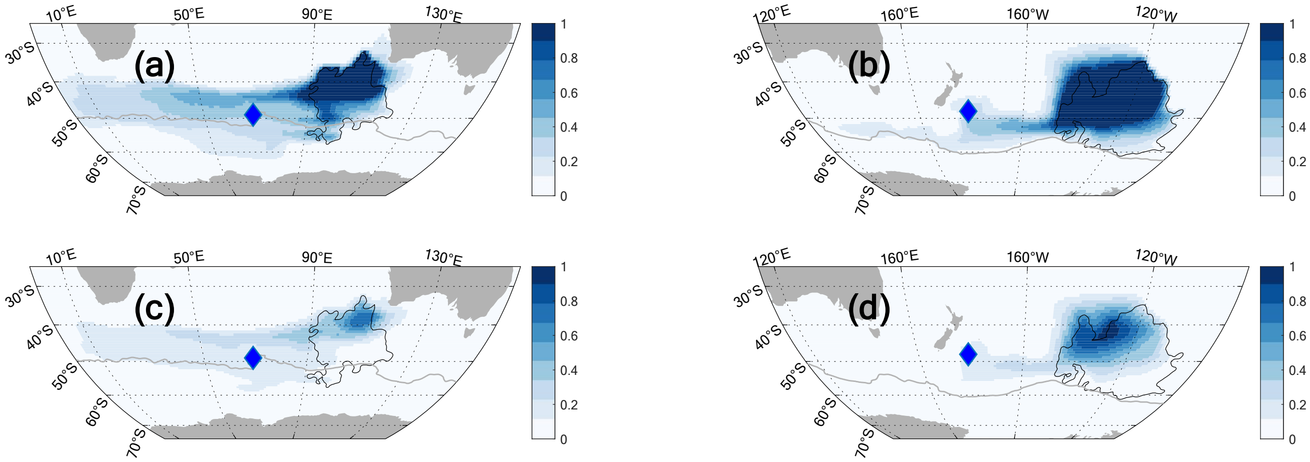


Figure 3. Source waters of the SIO (left) and CPO (right) over a five-year timescale. Shown are the source water contributions from the 5 m (top) and 100 m (bottom) depth levels, shown as the scaled sensitivity per unit meter. The Polar Front is shown as a thin grey line, and the breeding colony locations 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).

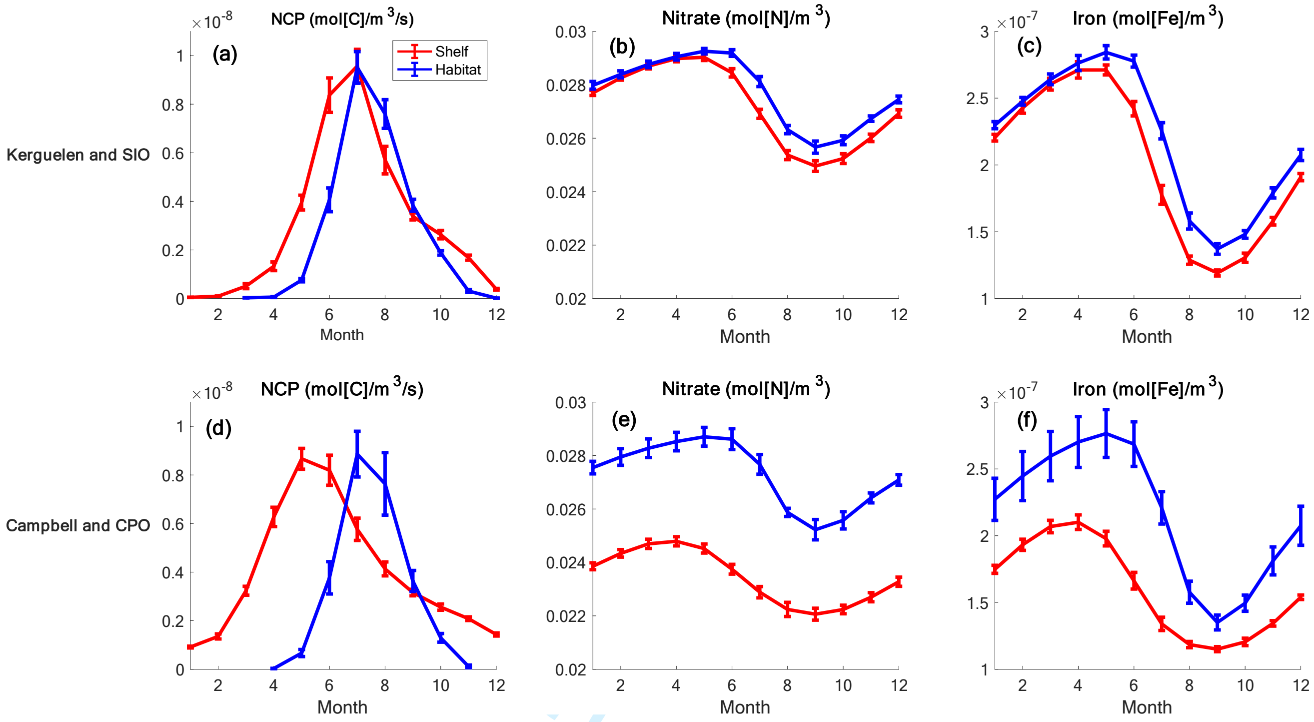


Figure 4. Monthly mean time series of productivity and nutrients from 2008 to 2012 from B-SOSE iteration 122. Solid lines indicate monthly climatological values, and the error bars indicate one standard deviation in the monthly mean values. Net community production (NCP) is similar in its seasonal cycle 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.

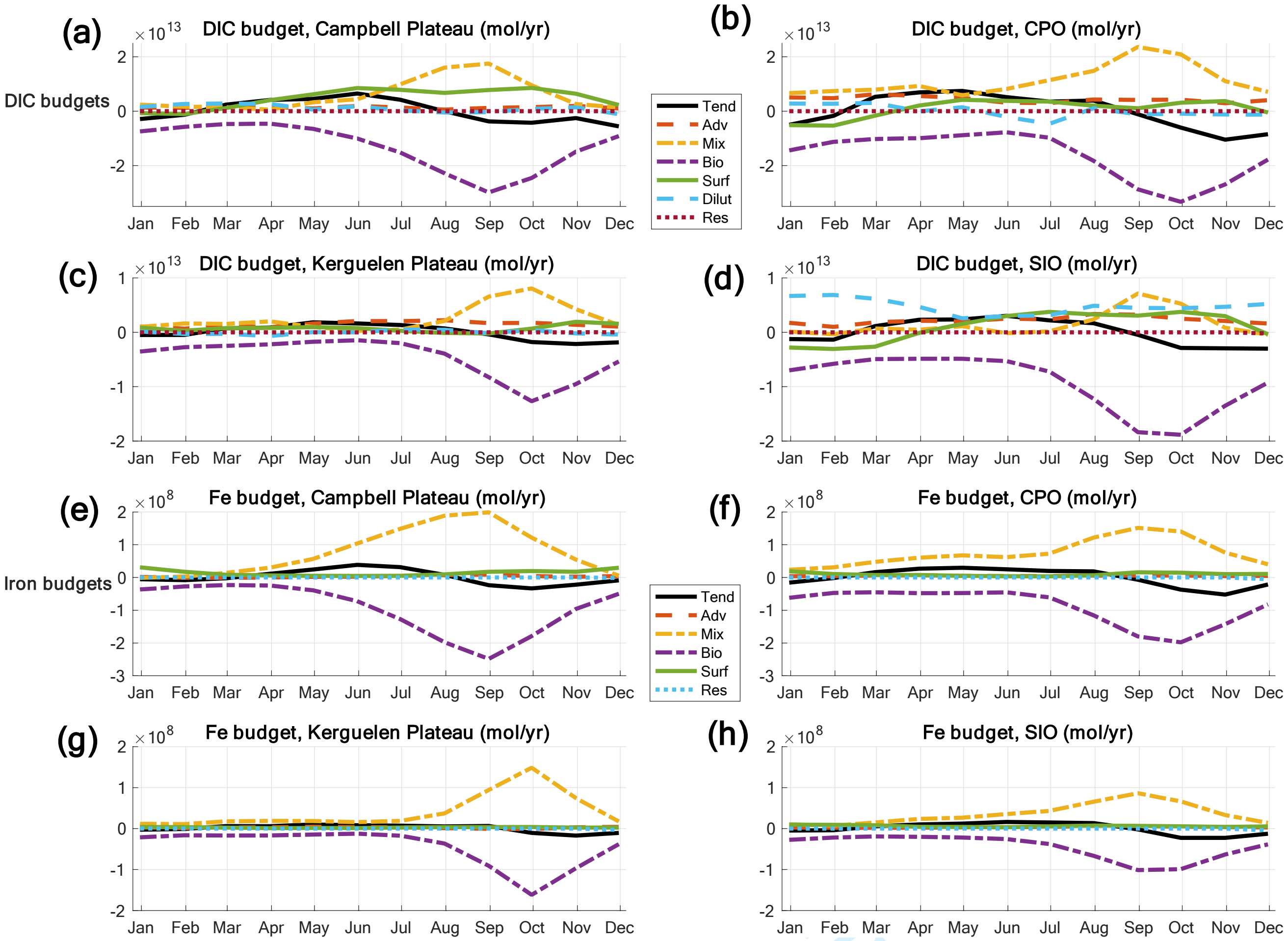


Figure 5. Climatological DIC and iron budgets integrated over the top 15 m of the indicated control volumes. Data from B-SOSE iteration 122. (a)-(d) Terms for the DIC budget include the total tendency (Tend), combined horizontal and vertical advection (Adv), combined horizontal and vertical mixing (Mix), 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.

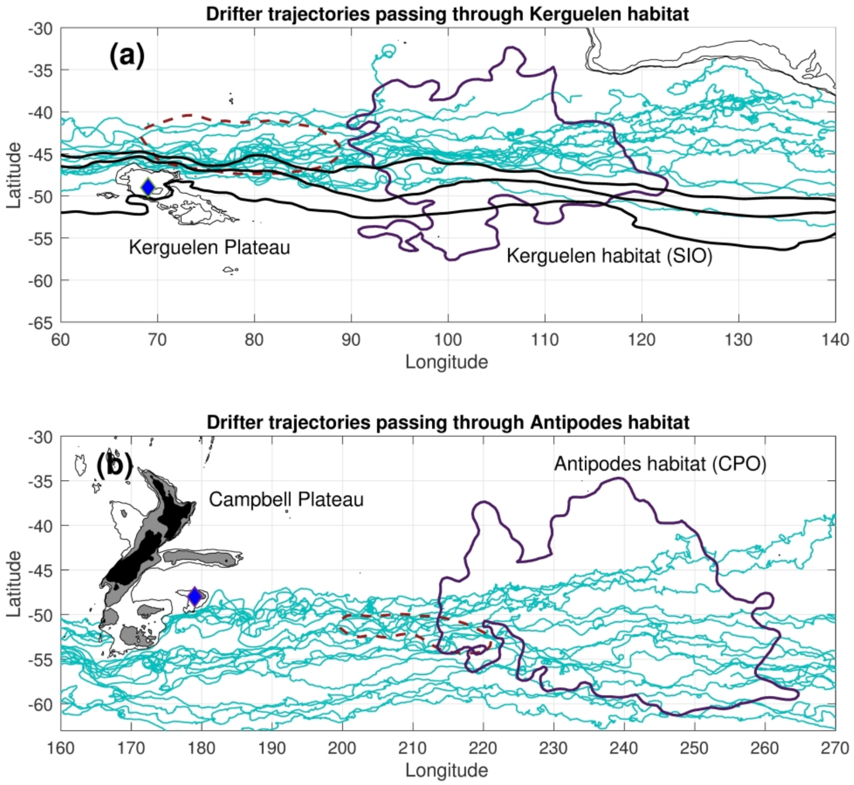


Figure 1. Distribution of nonbreeding grey petrels tracked using geolocators from (top) Kerguelen Islands and (bottom) Antipodes Islands, overlaid on a total of 182 surface drifter tracks. The 90% density contours during the petrel nonbreeding season (October to February; Torres et al. 2015) are shown 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)

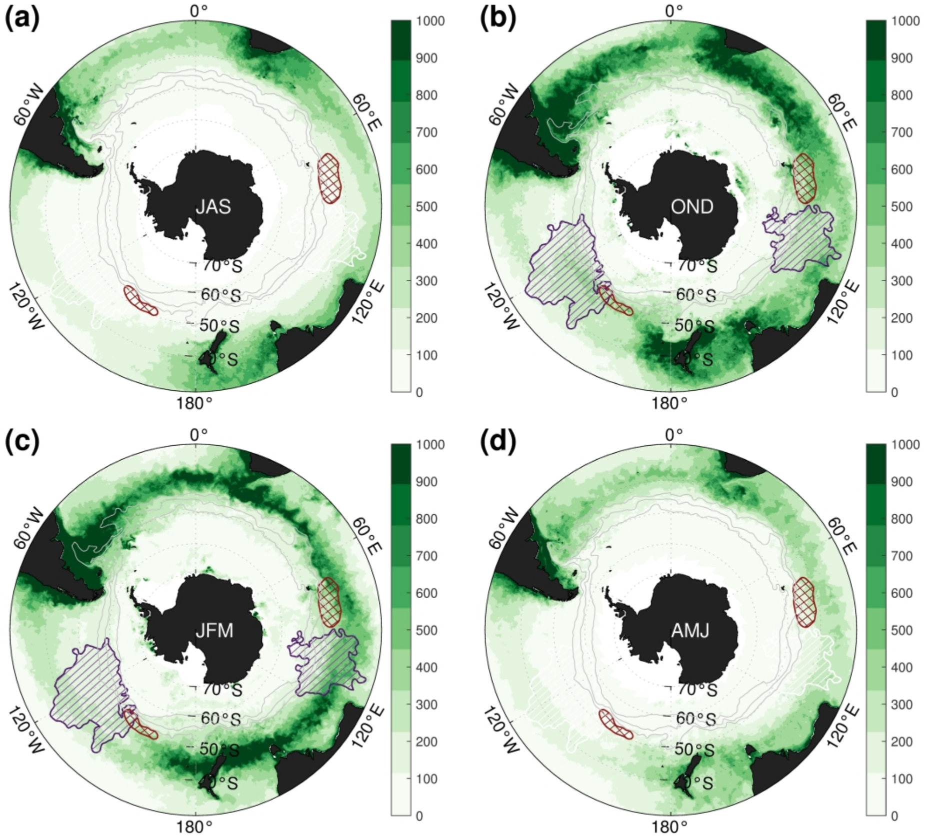


Figure 2. Seasonal net primary productivity (mg[C]/m2) from the Oregon State University Ocean Primary Productivity dataset. The grey contours mark the positions of the Polar Front (innermost) and Subantarctic Fronts (SAF and SAF-N) (Sallée et al. 2010). The purple hatches indicate the 90% distribution 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 m/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)

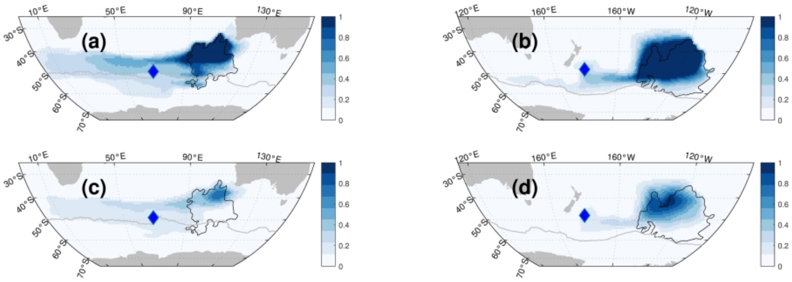
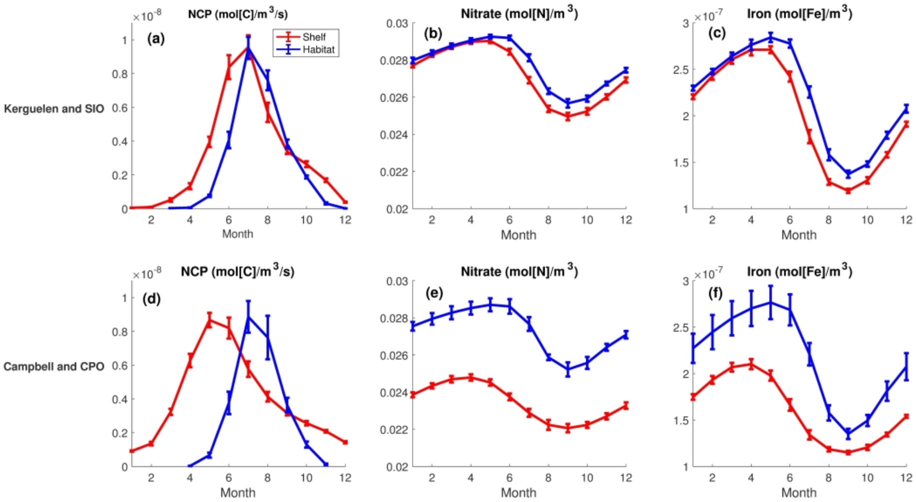


Figure 3. Source waters of the SIO (left) and CPO (right) over a five-year timescale. Shown are the source water contributions from the 5 m (top) and 100 m (bottom) depth levels, shown as the scaled sensitivity per unit meter. The Polar Front is shown as a thin grey line, and the breeding colony locations 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)



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439x239mm (300 x 300 DPI)

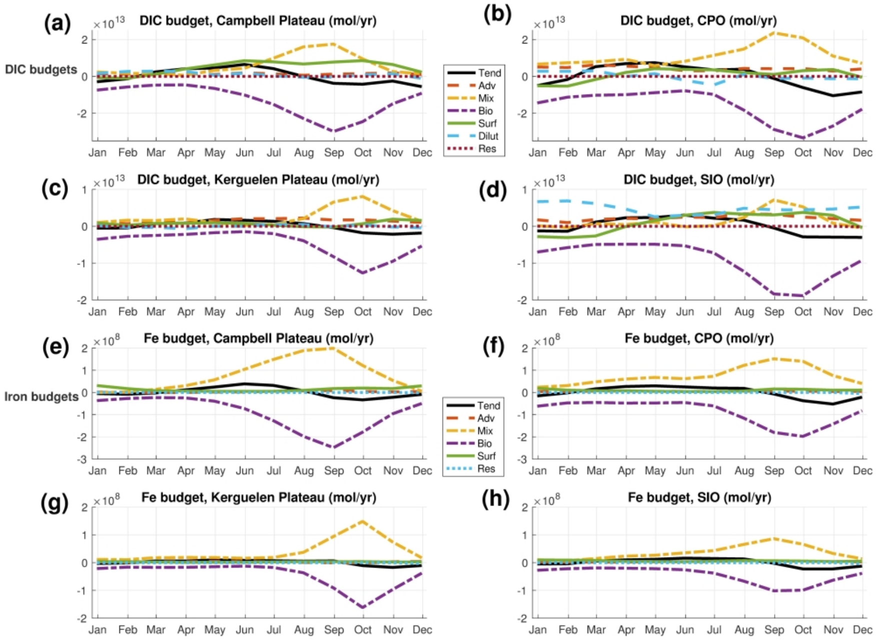

Figure 5. Climatological DIC and iron budgets integrated over the top 15 m of the indicated control volumes. Data from B-SOSE iteration 122. (a)-(d) Terms for the DIC budget include the total tendency (Tend), combined horizontal and vertical advection (Adv), combined horizontal and vertical mixing (Mix), 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)