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A subsurface eddy associated with a submarine canyon increases availability and delivery of simulated Antarctic krill to penguin foraging regions

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ABSTRACT: The distribution of marine zooplankton depends on both ocean currents and swimming behavior. Many zooplankton perform diel vertical migration (DVM) between the surface and subsurface, which can have different current regimes. If concentration mechanisms, such as fronts or eddies, are present in the subsurface, they may impact zooplankton near-surface distributions when they migrate to near-surface waters. A subsurface, retentive eddy within Palmer Deep Canyon (PDC), a submarine canyon along the West Antarctic Peninsula (WAP), retains diurnal vertically migrating zooplankton in previous model simulations. Here, we tested the hypothesis that the presence of the PDC and its associated subsurface eddy increases the availability and delivery of simulated Antarctic krill to nearby penguin foraging regions with model simulations over a single austral summer. We found that the availability and delivery rates of simulated krill to penguin foraging areas adjacent to PDC were greater when the PDC was present compared to when PDC was absent, and when DVM was deepest. These results suggest that the eddy has potential to enhance krill availability to upper trophic level predators and suggests that retention may play a significant role in resource availability for predators in other similar systems along the WAP and in other systems with sustained subsurface eddies.

KEY WORDS: Krill · Resource availability · Diel vertical migration · Retention · Biological hotspot · Palmer Deep Canyon · Regional Ocean Modeling System · Penguins · Antarctica

1. INTRODUCTION

Zooplankton play critical ecological roles in the surface ocean both as grazers and potential prey for upper trophic levels (Banse 1995, Dam et al. 1995, Landry et al. 1997). The distributions of these critical species are driven by the interaction between ocean currents in their environment, swimming behaviors, and size. This relationship is defined by the Reynolds number, which is the ratio of inertial and viscous forces in flow (Falkowski & Oliver 2007). Based on the size of an organism and its swimming speed, this ratio defines whether the organism in that flow is governed by inertial or viscous forces (Koehl &

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Strickier 1981, Falkowski & Oliver 2007). Phytoplankton, classified as single-celled organisms with length scales less than 0.02 cm (Finkel et al. 2010), have small Reynolds numbers (~10^{-2}). Therefore, phytoplankton exist in a viscous environment and their distributions are driven by water currents. Zooplankton, however, due to their wide range of sizes (~0.1–6 cm) display an intermediate range of Reynolds numbers (~10^{-1} to 10^{3}) (Koehl & Strickier 1981, Price 1988), indicating that they can occupy both viscous and inertial environments (Koehl & Strickier 1981). These intermediate Reynolds numbers mean that both their swimming ability and ocean currents impact their distribution. This is especially true for macrozooplankton that generally occupy the upper limits of the zooplankton length scale (>2 cm) (Ross et al. 2008).

Zooplankton species throughout the world can perform diel vertical migration (DVM) (Brierley 2014), traveling out of the lighted ocean surface to depth at dawn to avoid visual predators. This migration is reversed at dusk, as they travel several hundred meters to feed in productive surface layers (Hays 2003, Brierley 2014). Through DVM, zooplankton potentially interact with different flow fields as they move across depths. For example, modeling studies within the Irish Sea have shown that simulated *Calanus* spp. copepods are more likely to be retained when they perform DVM, due to the presence of a subsurface eddy at depth (Emsley et al. 2005). Similarly, simulated juvenile euphausiids and other zooplankton are retained within Monterey Bay (USA) due to DVM behaviors within a modeled 2-layer system (Carr 2006). Therefore, the potential for subsurface concentrating flows to affect the surface distributions of vertically migrating zooplankton suggests that it could impact both top-down (zooplankton grazing on phytoplankton) and bottom-up (zooplankton being preyed upon by higher trophic levels) controls of the local food web. For example, the distribution of Antarctic krill *Euphausia superba* (henceforth referred to as krill), a keystone macrozooplankton along the West Antarctic Peninsula (WAP), could also be concentrated in these subsurface retentive flows. Since krill have been observed to perform DVM, their distributions, and therefore, their availability to predators, may be reflective of these subsurface concentration features.

One area where this may occur is Palmer Deep Canyon (PDC), a submarine canyon along the WAP. This region is considered a biological hotspot due to high local phytoplankton concentrations (Kavanaugh et al. 2015), high densities of krill (Bernard & Steinberg 2013, Bernard et al. 2017, Nardelli et al. 2021), and many upper trophic level predators supported by the region in the austral summer (Fraser & Trivelpiece 1996, Schofield et al. 2013). This includes central place foragers such as Adélie penguins *Pygoscelis adeliae* and gentoo penguins *P. papua*, whose chicks are dependent on local resources (Fraser & Trivelpiece 1996, Schofield et al. 2013). The presence of PDC, and similar canyons, is thought to facilitate the unique physical and biological processes responsible for the formation and persistence of biological hotspots in close proximity to the canyons (Fraser & Trivelpiece 1996, Schofield et al. 2013).

The high predator diversity and penguin foraging activity near PDC, and other Antarctic submarine canyons, suggests that prey resources are reliably abundant (Pickett et al. 2018, Oliver et al. 2019, Santora et al. 2020, Nardelli et al. 2021). However, the connection between PDC, prey distributions, and foraging activity is unclear. One possibility is the upwelling of warm, nutrient-rich Upper Circumpolar Deep Water (UCDW) facilitated by the canyon (Schofield et al. 2013, Kavanaugh et al. 2015). The upwelling of UCDW was hypothesized to increase sea surface temperatures, reduce sea ice coverage, and fuel phytoplankton blooms over PDC, which would in turn feed prey species such as krill (Schofield et al. 2013, Kavanaugh et al. 2015). Under this hypothesized mechanism, production would be localized and sustained by delivery of limiting nutrients to the surface waters over PDC. However, UCDW does not appear to be a major source of limiting nutrients to the surface (Sherrell et al. 2018, Carvalho et al. 2020). Furthermore, multi-year observations during the austral summer by underwater gliders, and annual CTD profiles collected as part of the Palmer Antarctica Long-Term Ecological Research (PAL-LTER) program annual cruise, suggested that upwelling of UCDW into the surface layer is rare in PDC (Carvalho et al. 2016, Hudson et al. 2019).

Alternatively, deep circulation related to PDC may promote retention that increases the residence time of macrozooplankton, such as Antarctic krill, in the region. Recent *in situ* observations and model simulations of the region have suggested that a persistent subsurface, retentive eddy is present over PDC during the austral summer (Hudson et al. 2021). Flow within this feature follows isobaths, suggesting that it is a feature that regularly occurs within PDC, and *in situ* observations from subsurface gliders confirm the presence of isopycnal doming over PDC, which suggests that flow follows isobaths within PDC (Hudson et al. 2021). Model-estimated residence times of non-

vertically migrating simulated particles increase with depth within this feature, ranging from ~20 d at 50 m to ~130 d at 300 m within the subsurface eddy (Hudson et al. 2021). Simulated zooplankton performing DVM from 10 to 300 m were retained for nearly 30 d within the canyon (Hudson et al. 2022). This suggests that this subsurface feature has the potential to retain critical food resources while penguins rear their chicks during the breeding season near PDC.

Here, we performed a modeling experiment to examine how the subsurface eddy within PDC could impact the concentration and delivery of simulated krill performing DVM to nearby penguin foraging areas. We tracked particles that performed DVM to mimic krill behavior in a numerical model with and without PDC. Using these simulated krill, we calculated residence times over the canyon, simulated krill concentrations, delivery rates, and delivery from the eddy region to nearby penguin foraging areas with and without PDC present in simulations. We hypothesized that residence times of simulated krill over PDC and within penguin foraging regions will be higher when PDC is present due to the presence of the subsurface eddy. In addition, we hypothesized that this increased retention will result in higher simulated krill concentrations, delivery rates to the foraging regions, and delivery from the subsurface eddy region to the foraging regions when PDC is present.

Results that support these hypotheses would suggest that the subsurface eddy could concentrate resources in and facilitate the delivery of resources to nearby penguin foraging areas, providing a different mechanistic explanation for the canyon hypothesis, and for the existence of this biological hotspot. Recent analysis of penguin colony locations throughout Antarctica has illustrated that the correlation between submarine canyons and biological hotspots is not unique to the WAP, but holds true throughout the Southern Ocean (Santora et al. 2020). Therefore, the mechanisms driving the biological hotspot within PDC may be applicable to other biological hotspots throughout the Southern Ocean.

2. METHODS

2.1. Penguin colony locations and foraging regions

Adélie and gentoo penguin foraging regions were identified using satellite tag data from PAL-LTER (Fig. 1; Nardelli et al. 2021). Adélie penguins were tagged on Humble and Torgersen Islands, and gentoo penguins were tagged at Biscoe Island (Fig. 1). Satellite tag data were collected from 2009 to 2018, and tagging protocols are described in Pickett et al. (2018). Foraging locations were identified using dive profiles as described by Cimino et al. (2016). Locations were used to generate foraging regions based on 2-dimensional kernel density estimation (KDE) techniques following the methods of Pickett et al. (2018) across all tagging years. The 90% KDE was

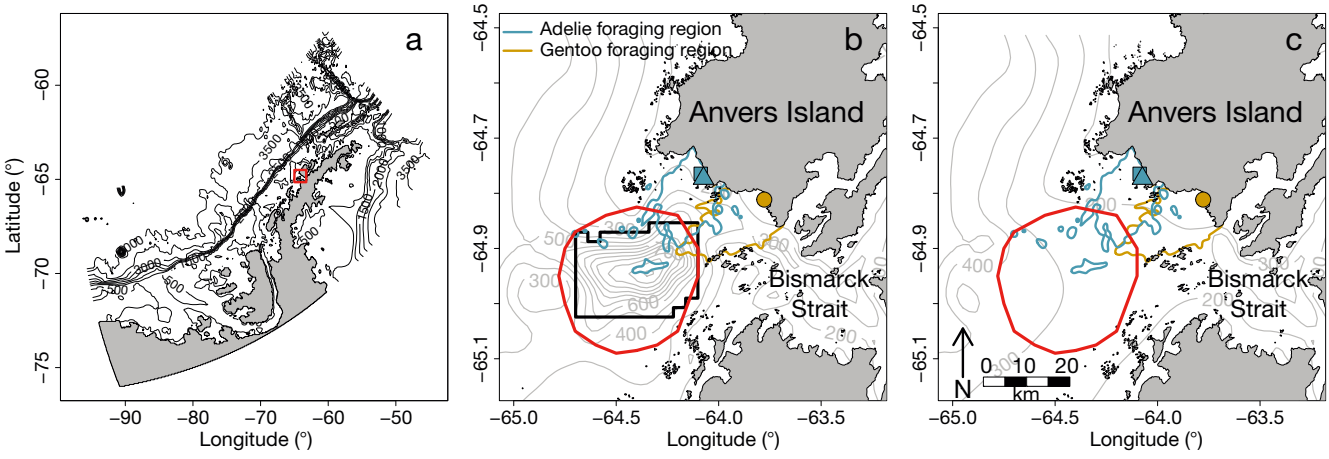

Fig. 1. (a) Bathymetry of the Regional Ocean Modeling System domain (ROMS) used in these experiments. The red box illustrates the areas plotted in panels b and c. (b) Bathymetry of Palmer Deep Canyon (PDC) and the surrounding shelf area. The black box illustrates the region defined as PDC for residence time calculations. Bathymetry is from ROMS. (c) Bathymetry of the same region, with the canyon removed. In panels b and c, the blue and yellow lines represent the Adélie and gentoo penguin foraging regions as defined by the 90% kernel density estimation (KDE); the red line outlines the eddy region; the blue square and triangle indicate the colonies on Humble and Torgerson Islands where Adélie penguins were tagged; and the yellow circle represents the colony on Biscoe Island where gentoo penguins were tagged

used to define the consistent foraging areas utilized over the entire austral summer across sampling years. While preliminary data suggest there can be within-season variability in foraging grounds, we did not consider any within-summer variation here in producing our foraging regions. This foraging region was previously published in Nardelli et al. (2021). The Adélie foraging region had an area of 221 km^2, and 25% of this region overlapped with the eddy region. The gentoo foraging region had an area of 224 km^2 with only 5% overlapping with the eddy region (Fig. 1b,c).

2.2. Regional Ocean Modeling System

We used the Regional Ocean Modeling System (ROMS; Haidvogel et al. 2008) to examine how simulated krill performing DVM are transported into the penguin foraging areas with and without PDC (Fig. 1a). The model bathymetry with and without PDC is illustrated in Fig. 1b,c. PDC was removed by limiting the depth of the region to 500 m, then using a Shapiro filter over the region to smooth the bathymetry (Shapiro 1970).

The version of ROMS used here had a 1.5 km horizontal resolution with 24 terrain-following vertical layers (Graham et al. 2016, Hudson et al. 2021) with greater resolution near the top and bottom ocean surfaces. For example, the vertical resolution of the model from the surface to 1400 m depth of PDC ranged from 10.7 to 115 m. The model included atmospheric forcing from the Antarctic Mesoscale Prediction System (Powers et al. 2012), tidal forcing from the CATS2008 regional Antarctic tidal model (Padman et al. 2002), dynamic sea ice (Budgell 2005), and interactions between floating ice shelves and the waters beneath (Holland & Jenkins 1999, Dinniman et al. 2011). Forces and initializations were kept the same between the simulations with and without PDC. In simulations without PDC, the model quickly corrected for the different bathymetry. Simulations ran from 1 November 2008 to 30 May 2009, but analysis focused on the austral summer (1 December 2008 to 28 February 2009). The 2008–2009 austral summer was chosen based on forcing data availability at the time of the experiment. Modeled potential temperature, salinity, and density (σ_θ) were averaged over the austral summer along 3 transects over PDC (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m702p105_supp/).

Particles performing DVM were released on an approximately 4 km grid around PDC every 2 d from 1 November 2008 to 30 April 2009 to simulate krill behavior (Fig. S1). Particles were released every 2 d to account for surface residence times over PDC, which suggest that particles are only retained over PDC for ~2 d before they are advected out of the region (Kohut et al. 2018). One particle was released per release location (pink points in Fig. S1) at 20 m, after which particles followed assigned DVM behaviors (see below). Particles were advected within the model at every time step (50 s) and were tracked for at least 30 d and for as long as 210 d. Advection included modeled horizontal and vertical velocities as well as vertical random walk to mimic the transport effect of vertical turbulence, which is parameterized in the model (Hunter et al. 1993, Visser 1997). The vertical random walk was implemented following Hunter et al. (1993), and the value of the random walk was normally distributed around zero. Horizontal diffusion was not considered, since previous studies with this model have illustrated that it can resolve mesoscale eddies on the continental shelf of the WAP (Graham et al. 2016) and we are not concerned with finer-scale horizontal motions. Particle positions were saved hourly.

Since we examined the impact of the subsurface eddy on resource availability for local penguin populations, we used the particles as proxies for Antarctic krill, which make up a majority of penguin diets in this region (Pickett et al. 2018). Henceforth, we will refer to the particles in the model as 'simulated krill'. In doing so, we made the following assumptions: (1) krill are readily available within our study site; (2) krill are passive drifters in the horizontal; (3) their only active swimming behavior is DVM. By seeding simulated krill on a regular grid within our study area, we are inherently assuming that krill are available in this region in the simulated time frame. Krill distributions around PDC and the WAP are known to be heterogeneous (Atkinson et al. 2008, Bernard & Steinberg 2013, Steinberg et al. 2015, Cimino et al. 2016, Bernard et al. 2017, Tarling et al. 2018, Oliver et al. 2019, Nardelli et al. 2021). Therefore, the simulated krill metrics we calculate should be considered as potential simulated krill counts and delivery rates, not absolute values.

While krill are capable of swimming in the horizontal to form swarms (Tarling & Fielding 2016), and perform inshore migrations in the austral fall and winter (Lascara et al. 1999, Nicol 2006, Atkinson et al. 2008, Cleary et al. 2016), we did not model this horizontal movement because (1) no horizontal movement model for krill exists on the horizontal scale of ROMS (1.5 km) within our study region; and

(2) our focus is on the effects of DVM on local residence times and distributions. Krill swimming speeds are known, but turning angles are not. Therefore, a model of krill horizontal movement would be a Brownian motion model, where every swimming direction is equally likely. On average, a Brownian motion model produces no net horizontal movement. Therefore, even though we acknowledge that krill are not passive, the lack of a krill swimming direction model leads us to treat them as net passive drifters. Previous studies have also assumed that krill are passive drifters in the horizontal (for example, Hofmann et al. 1998, Hofmann & Murphy 2004, Murphy et al. 2004, Thorpe et al. 2004, Piñones et al. 2013) and have argued that currents are a major driver of macrozooplankton distributions within the Southern Ocean (Hofmann et al. 1998, Hofmann & Murphy 2004, Murphy et al. 2004, Thorpe et al. 2004, Cleary et al. 2016).

DVM timing was based on local solar angle, which was above the horizon from 15 to 21 h over the austral summer. Upward velocities were added to the simulated krill when the sun was below the horizon and the krill were below the defined upper migration depth. Downward velocities were added when the sun was above the horizon and the krill were above the defined lower migration depth. DVM depths and swimming speeds of migrating krill were based on previously published observations and acoustic observations of krill DVM (Kils 1981, Nowacek et al. 2011, Espinasse et al. 2012, Kane et al. 2018). Based on these observations, DVM was simulated for migrations between 10 and 50, 10 and 150, and 10 and 300 m at a vertical swimming speed of 0.03 m s^{-1}. Previous simulations illustrated that swimming speed had little to no effect on residence times of vertically migrating simulated zooplankton (Hudson et al. 2022), so only 1 vertical swimming speed was considered here.

2.3. Residence time and krill distribution metrics

Residence times of simulated krill were calculated using the e-folding time method, defined as the time required for the initial concentration of simulated krill over an area to decrease through passive horizontal advection out of the defined regions to 1/e (~37%) after release (Piñones et al. 2011). Residence times were calculated over PDC (Fig. 1b) and in each of the foraging areas using R version 4.0.5 (R Core Team 2021; Fig. 1). Calculated residence times were averaged from December to February to cover the chick-rearing period. Residence times for simulated zooplankton performing DVM within PDC have been reported previously (Hudson et al. 2022). Since this previous study also assumed that zooplankton are passive in the horizontal and only swim in the vertical, we assume that these particle simulations also represent simulated krill. Therefore, the residence times presented by Hudson et al. (2022) are the same for our simulated krill, and we present these data here for comparison to residence times in the absence of PDC. We extend the findings of Hudson et al. (2022) by calculating the simulated krill distribution metrics described below within known penguin foraging regions.

Three krill distribution metrics were calculated for each of the foraging regions: simulated krill counts, overall delivery rates to the foraging region, and delivery rates from the subsurface eddy region to the foraging region. Simulated krill were counted in individual model grid cells across the study region (Fig. S1) and within each of the foraging regions. The numbers of unique simulated krill individuals were counted on a 1.5 km grid (same as the ROMS model) for each day of the austral summer for a total of 90 d. The differences between runs with and without PDC were calculated daily and then averaged over the 90 d of the austral summer. Simulated krill were counted once daily in each grid cell to avoid counting the same simulated krill in the same grid cell multiple times. For example, if a krill started the day in model cell A, moved into adjacent cell B, and then back into cell A over a single day, the krill would only be counted in cells A and B once for that day and the count would reset the next day. Similarly, if a krill remained in a single cell for an entire day, it would only count as 1 unique krill in that grid cell for that day. This method was also used to count the number of unique krill observed per day within the foraging areas, using the 'point.in.polygon' function in the R package 'sp' version 1.4-5 (Pebesma & Bivand 2005, Bivand et al. 2013). Simulated krill were not counted until 5 d after they were released, so counts were not influenced by release locations. This 5 d advection period was used for all metrics, including delivery rates.

To examine how the presence of the canyon affects simulated krill delivery to the foraging regions, we calculated 2 different delivery metrics: (1) the number of overall simulated krill that entered each foraging area (i.e. overall delivery rates), and (2) the number of simulated krill that interacted with the eddy region (Fig. 1b,c) before entering a foraging area (i.e. delivery rates from the subsurface eddy region only).

The eddy region was determined by visually inspecting mean circulation at 50 m to determine the horizontal extent of the feature. We chose to differentiate overall krill delivery and delivery from the eddy region to determine the direct effect of PDC and the resulting subsurface eddy on simulated krill delivery. Only simulated krill that entered the eddy area (Fig. 1b,c) within 1 wk of entering the foraging regions were considered for this metric. This time frame was selected to determine the direct impacts of the subsurface eddy and to avoid counting simulated krill that could have interacted with the eddy, exited onto the continental shelf, and then were transported back to the penguin foraging regions at a later time, a trajectory that was observed in some simulated krill but took much longer than 7 d. This time frame was only considered for the delivery from the eddy region metric and is independent of the 5 d advection period between simulated krill release and the beginning of tracking for count and delivery metrics. Both delivery metrics were calculated daily.

Since these metrics, including residence times, were calculated from simulated data, any p-values in a statistical analysis of our metrics, or metrics from any other simulated dataset, could be manipulated simply by increasing the number of simulations. Therefore, we instead focused on the differences between metrics when PDC was present and absent from model simulations. Differences are presented as percent differences with respect to metrics when PDC was absent. Positive values of percent change indicate when metrics were higher in the presence of PDC, while negative values indicate when metrics were higher in the absence of PDC. Percent changes were then $\log_{10}$ transformed to be properly visualized. To transform negative percent changes, the $\log_{10}$ of the absolute value of the percent change was calculated and then multiplied by negative one.

3. RESULTS

3.1. Comparing physical oceanography in the presence and absence of PDC

In the presence of PDC, flow below the mixed layer (~50 m; Hudson et al. 2021, 2022) has a strong barotropic component, with flow following isobaths around the canyon, forming a closed, recirculating eddy (Fig. 2a–e; Hudson et al. 2021). Summer averaged current velocities within the canyon were between ~10 and 20 cm s^{-1}, with speeds generally slower on the outer rim of the eddy, over the rim of PDC, and faster in the center (Fig. 2a–e). Current velocities in the eddy and over the rim of PDC were relatively consistent with depth (Fig. 2a–e). Isopycnal doming was observed over PDC when the feature was present, indicating the presence of a small baroclinic component to the flow (Fig. S2a,c,e; Hudson et al. 2021). A component of the flow also moved shoreward from the subsurface eddy (Fig. 2a–e). This was likely driven by the head of the canyon and the resulting barotropic flow following the isobaths towards shore. Daily averaged currents at 100 m illustrate that current velocities at this depth are relatively consistent within the subsurface eddy from late December to late February (Video S1). In early December, currents are more variable over PDC, with current velocities of over 20 cm s^{-1} over the canyon moving waters inshore towards the penguin foraging regions before the subsurface eddy forms at the end of the month (Video S1).

Flow generally moved from east to west along the coast of Anvers Island, with waters generally moving ~5 cm s^{-1} (Fig. 2a–c). Currents were fastest as waters moved into the Bismarck Strait, as fast as ~20 cm s^{-1} at shallower (0–100 m) depths (Fig. 2a–e). A strong (~20 cm s^{-1}) coastal current was also present along the western coast of Anvers Island to the north of PDC, which may be the seasonally influenced Antarctic Peninsula Coastal Current that is present along much of the west coast of the WAP (Moffat et al. 2008). This current was strongest at the surface, and velocities decreased with depth (Fig. 2a–d). Along the continental shelf to the west of PDC, current velocities were on the order of ~10–15 cm s^{-1} and moved southward, following isobaths (Fig. 2a–e). Mean current conditions indicate that waters often moved from this continental shelf current into PDC (Fig. 2a–d). At 100 m, there was some variability in these features in early December and at the end of the austral summer (late February–March), but they were relatively consistent through the austral summer (Video S1).

In the absence of PDC, flow in the top 150 m was dominated by a strong jet to the south of Anvers Island moving from southeast to northwest (Fig. 2f–i). This flow was strongest at the surface (~20 cm s^{-1}), and velocities decreased with depth (~5–10 cm s^{-1}) (Fig. 2f–i). This feature dominated the eastern flank of the basin and eventually pushed water into the Bismarck Strait (Fig. 2f–i). On the western side of the basin, flow generally moved towards shore and to the northwest. These currents were no more than 5 cm s^{-1} (Fig. 2f–i). The isopycnal doming over PDC was noticeably absent when PDC was removed from

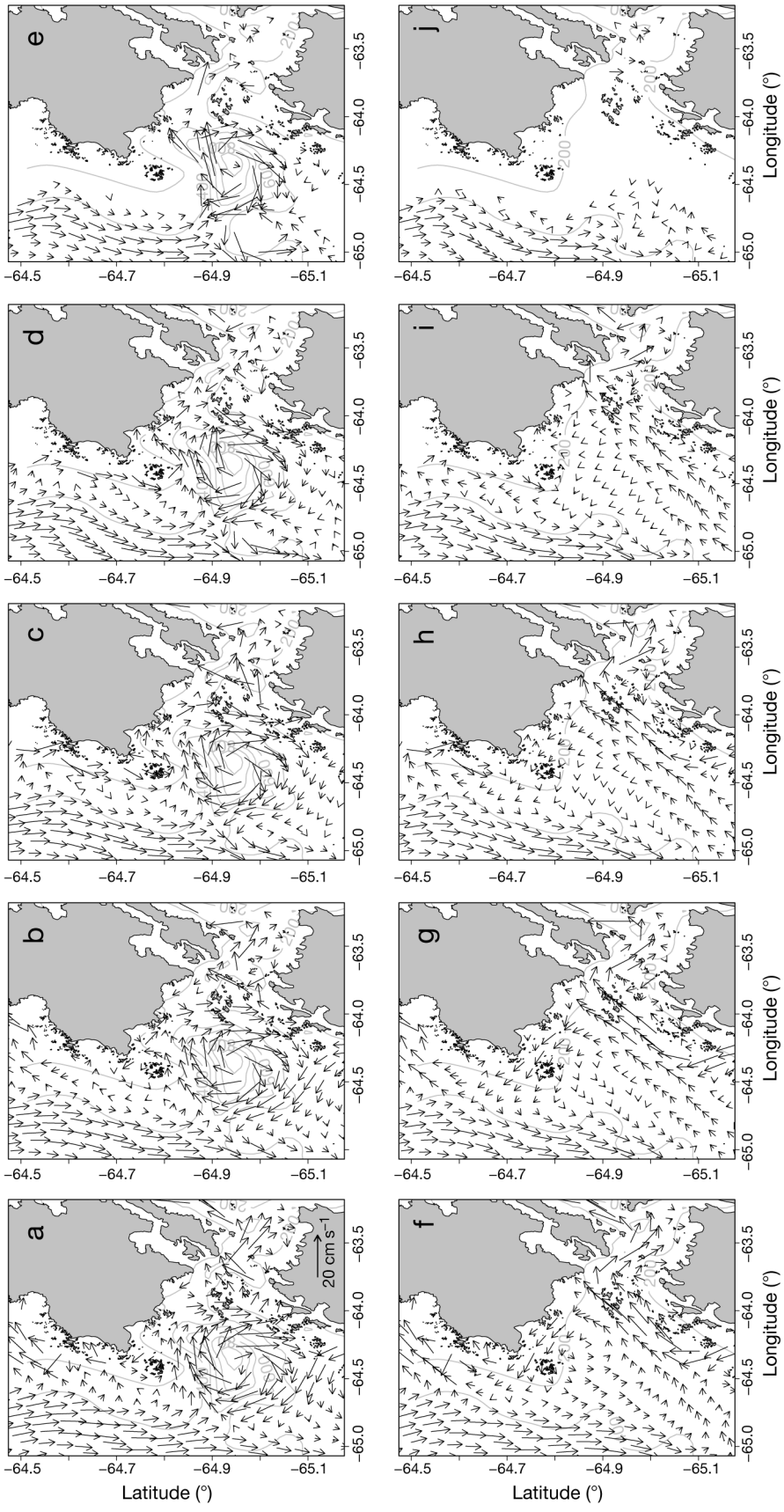

Fig. 2. Mean current velocities (a,f) at the surface and at (b,g) 50, (c,h) 100, (d,i) 150, and (e,j) 300 m with (a–e) and without (f–j) Palmer Deep Canyon. Velocities were averaged from December to February. A 20 cm s^{-1} scale bar is shown in panel a

model simulations (Fig. S2b,d,f). Changes in σ_θ were driven primarily by salinity changes, rather than temperature changes in the absence of PDC (Figs. S3 & S4). The recirculating eddy was also absent from mean velocity fields when PDC was not present in model simulations (Fig. 2; Video S2), indicating that PDC was responsible for the formation of this feature. Daily average currents at 100 m through the austral summer confirm this, illustrating that the current flowing northeast dominates for most of the austral summer (Video S2). Elsewhere in the region, current velocities and movement patterns on the continental shelf and in the coastal current on the western flank of Anvers Island were nearly the same in comparison to when PDC was present in model simulations (Fig. 2).

3.2. Residence times

Median residence times of simulated krill over PDC were higher when PDC was present (Fig. 3a), and residence time increased with depth of DVM (Fig. 3a). When PDC was removed, residence times were never greater than 10 d (Fig. 3a). With PDC present in the model, residence times were ~2 times higher for simulated krill migrating to 50 m (i.e. 5 vs. 10 d), and about ~3.6 times higher when migrating to 300 m (i.e. ~9 vs. 32 d).

Residence times were less than 5 d, regardless of migration depth or the presence of PDC in the Adélie and gentoo penguin foraging regions (Fig. 3b,c). In the Adélie penguin foraging region, residence times were consistent regardless of migration depth in the presence of PDC, while residence times increased with migration depth when PDC was absent, albeit only by a few days (Fig. 3b). When simulated krill migrated to 300 m, residence times were approximately 2 times greater when PDC was absent in comparison to when it was present (i.e. 1.5 vs. 3 d; Fig. 3b). In the gentoo foraging region, residence times were between 2 and 4 d, and did not differ with and without PDC (Fig. 3c).

3.3. Simulated krill distribution metrics

When PDC was present in model simulations, the number of simulated krill in the Adelie foraging region increased with DVM depth (Fig. S5). The number of simulated krill increased throughout the austral summer, reaching as high as 1500 simulated krill present in the Adélie foraging region when migrations occurred to 300 m and PDC was present in model simulations (Fig. S5). In the gentoo foraging region, simulated krill counts reached a maximum of ~1000 individuals in the presence of PDC when migrations occurred to 150 m (Fig. S5b). When PDC was absent from simulations, the number of simulated krill in the foraging regions remained relatively stable, or increased slightly, through the austral summer, remaining at or below 500 simulated krill in the foraging regions (Fig. S5). These continuous increases in the number of simulated krill within the foraging regions were likely in part due to the retention of continuously seeded krill in the simulation.

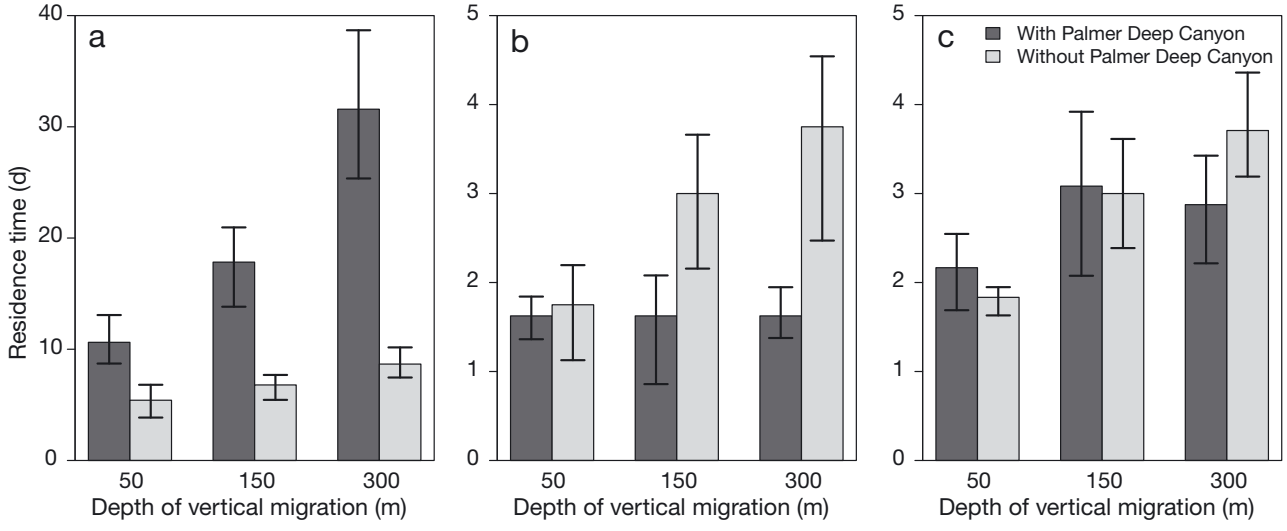

Fig. 3. Median residence times in days with the 3 diel vertical migration depths (a) over Palmer Deep Canyon and in (b) Adélie and (c) gentoo penguin foraging regions. Note that the *y*-axis in panel a differs from those in panels b and c. Error bars represent bootstrapped 95% confidence intervals

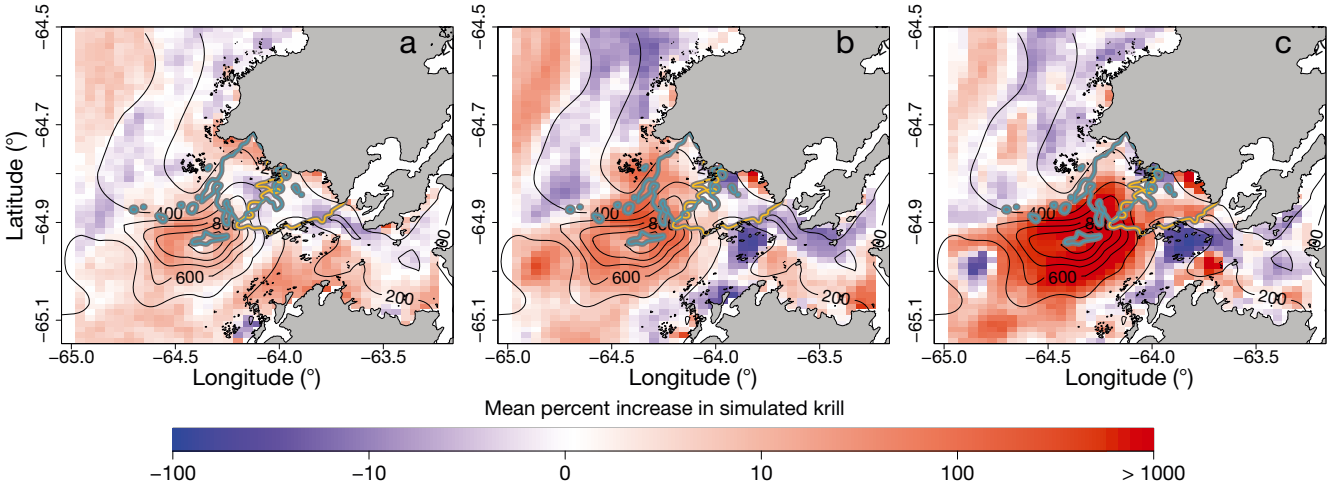

Fig. 4. Mean percent increase in the number of unique simulated krill in each grid cell with and without the presence of Palmer Deep Canyon (PDC) for simulated krill migrating to (a) 50, (b) 150, and (c) 300 m. Percent increases were calculated with respect to simulations without PDC and were $\log_{10}$ transformed to increase visibility. Negative values (blue) indicate that more simulated krill were present when PDC was absent. Positive values (red) indicate an increase in simulated krill when PDC was present. The blue and yellow shapes represent the Adélie and gentoo penguin foraging areas as shown in Fig. 1

When PDC was present, more simulated krill were present at all migration depths over PDC (Fig. 4). When DVM occurred to 50 m, the average number of simulated krill over PDC was ~10% greater when PDC was present (Fig. 4a). This difference increased to ~100% when DVM occurred to 150 m, and to 1000% when DVM occurred to 300 m (Fig. 4b,c). When PDC was not present in model simulations, there were ~10–30% more simulated krill to the north of PDC along the western coast of Anvers Island across all migration depths (Fig. 4). To the east of PDC, there was a similar area at the mouth of the Bismarck Strait that had as much as ~60% more simulated krill present when PDC was absent, and these differences were greatest when migrations were deepest (Fig. 4). These regions where more simulated krill were present in the absence of PDC indicate that few simulated krill were present in these areas when PDC was present.

Within the penguin foraging regions, differences in the number of simulated krill were small when migrations were shallowest (Fig. 4a). Inshore in both the Adélie and gentoo foraging regions, there was a slight increase (~5%) in the number of simulated krill when PDC was present (Fig. 4a). There were also areas in both foraging regions where ~5% more simulated krill were present in the absence of PDC near the head of PDC and near the mouth of the Bismarck Strait to the east (Fig. 4a). When vertical migrations deepened to 150 and 300 m, ~10% more simulated krill were present along the southern coast of Anvers Island around where the 2 foraging regions overlapped (Fig. 4b,c). There was also a small area along the coast of Anvers Island within the gentoo foraging region where there was a ~1000% increase in simulated krill when the canyon was present (Fig. 4b,c).

The median percent increase in simulated krill counts when migrations occurred to 50 m was 10% (interquartile range: –6 to 28%) greater when PDC was present in the Adélie foraging region and ~2% (–26 to 24%) greater when PDC was absent in the gentoo foraging region (Fig. 5a). When migrations deepened to 150 m, median percent increases were 28% (4–64%) and 21% (–16 to 59%) greater when PDC was present in the Adélie and gentoo foraging regions, respectively (Fig. 5a). Median percent increases were greatest when migrations occurred to 300 m, with 120% (62–239%) and 82% (44–175%) more simulated krill present in the Adélie and gentoo foraging regions, respectively, when PDC was present (Fig. 5a).

Time series of percent change illustrate that these trends were most consistent through the austral summer when migrations were deepest (i.e. 100% increase; Fig. 5b–d). When migrations occurred to 50 m, patterns were highly variable, ranging from a 100% increase to a 100% decrease (Fig. 5b). There were alternating periods when simulated krill were greater in the presence of PDC versus when PDC was absent (Fig. 5b). When migrations occurred to 150 m, the percent change was highly variable at the beginning and end of the austral summer, but somewhat consistent from late December to early February, with occasional, but large, declines in the percent change of simulated krill counts (Fig. 5c). When migrations deepened to 300 m, the percent change of

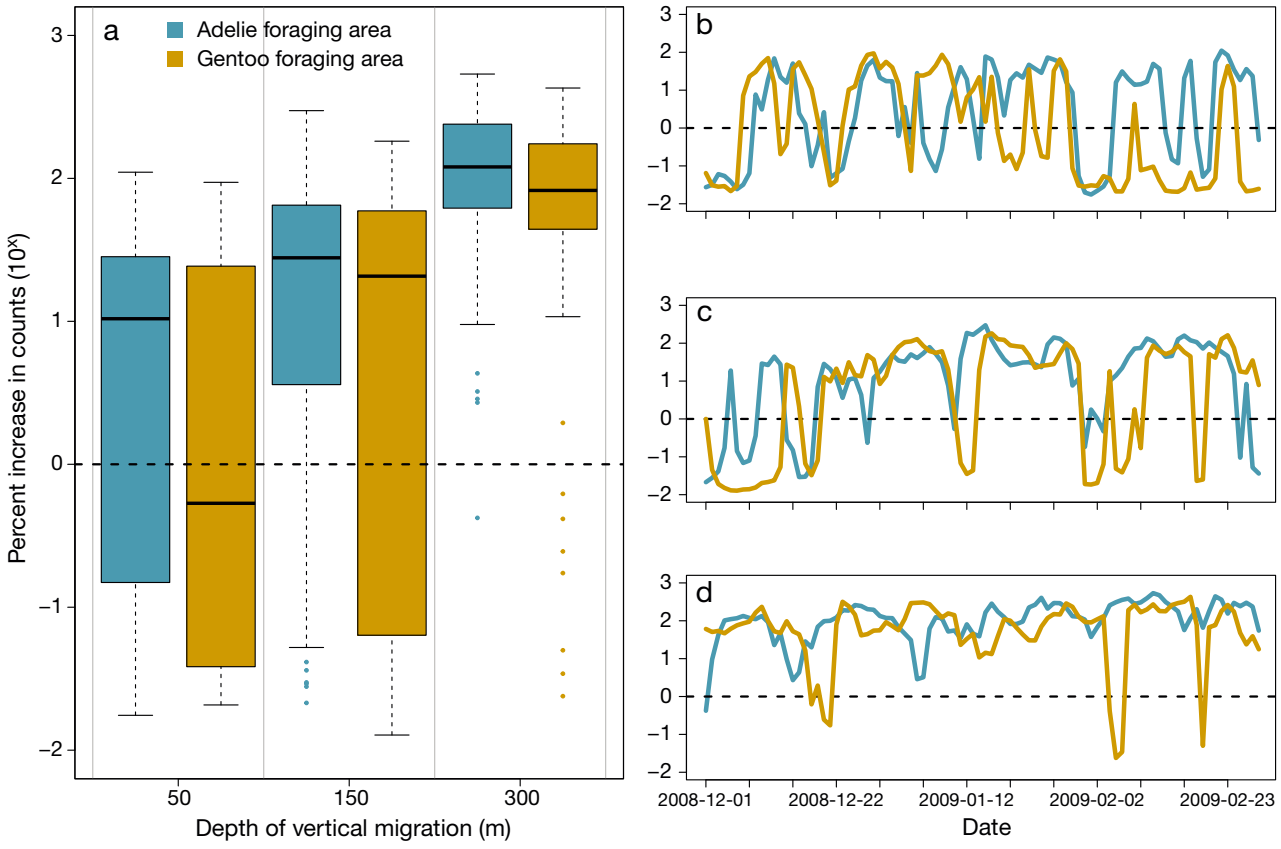

Fig. 5. (a) Distribution of percent differences in unique simulated krill counts over the austral summer within Adélie and gentoo penguin foraging regions for each of the migration depths simulated. Percent increases were calculated with respect to simulations without Palmer Deep Canyon (PDC) and were log transformed such that a value of 1 is equal to a 10% increase when PDC was present and −1 is equal to a 10% increase when PDC was absent. Horizontal bar: median; box: interquartile range (IQR; whiskers: first and third quantiles ±1.5× the IQR; points: outliers. (b–d) Log_{10} transformed time series of the percent changes in the number of simulated krill present within the foraging regions when migrations occurred to 50, 150, and 300 m, respectively

simulated krill counts was more consistent through the austral summer, with occasional large declines in the gentoo foraging region (Fig. 5d).

Overall simulated krill delivery rates were relatively similar through mid-January, regardless of migration depth (Fig. S6). In the Adélie penguin foraging region, 100–200 simulated krill entered the foraging region per day in the first half of the austral summer while delivery rates were closer to 40–100 in the gentoo penguin foraging region when PDC was present in model simulations (Fig. S6). After mid-January, the variability in delivery rates to both foraging regions increased across all migration depths, with a maximum of 700 and 400 simulated krill delivered to the Adélie and gentoo foraging areas, respectively, in the second half of the austral summer when PDC was present (Fig. S6). When PDC was absent from model simulations, delivery rates to both foraging regions decreased as migrations deepened, but still saw occasional spikes as high as ~400 simulated krill delivered per day, especially late in the austral summer (Fig. S6).

Patterns in the percent change of simulated krill delivery rates were similar to those found in the relative change of simulated krill counts (Figs. 5 & 6). When migrations occurred to 50 m, the median percent changes in the daily delivery of simulated krill were 25% (−19 to 96%) and −9% (−50 to 88%) for the Adélie and gentoo foraging regions, respectively (Fig. 6a). At this migration depth, more simulated krill were present in the Adélie foraging region when PDC was present, but more simulated krill were present in the gentoo foraging region when PDC was absent (Fig. 6a). In the Adélie foraging region, these medians increased to 69% (20–134%) and 188% (95–339%) more simulated krill delivered to the area daily when migrations deepened to 150 and 300 m, respectively (Fig. 6a). In the gentoo foraging region, the median percent increase in simulated krill daily delivery increased from 17% (−33 to 68%) to 179%

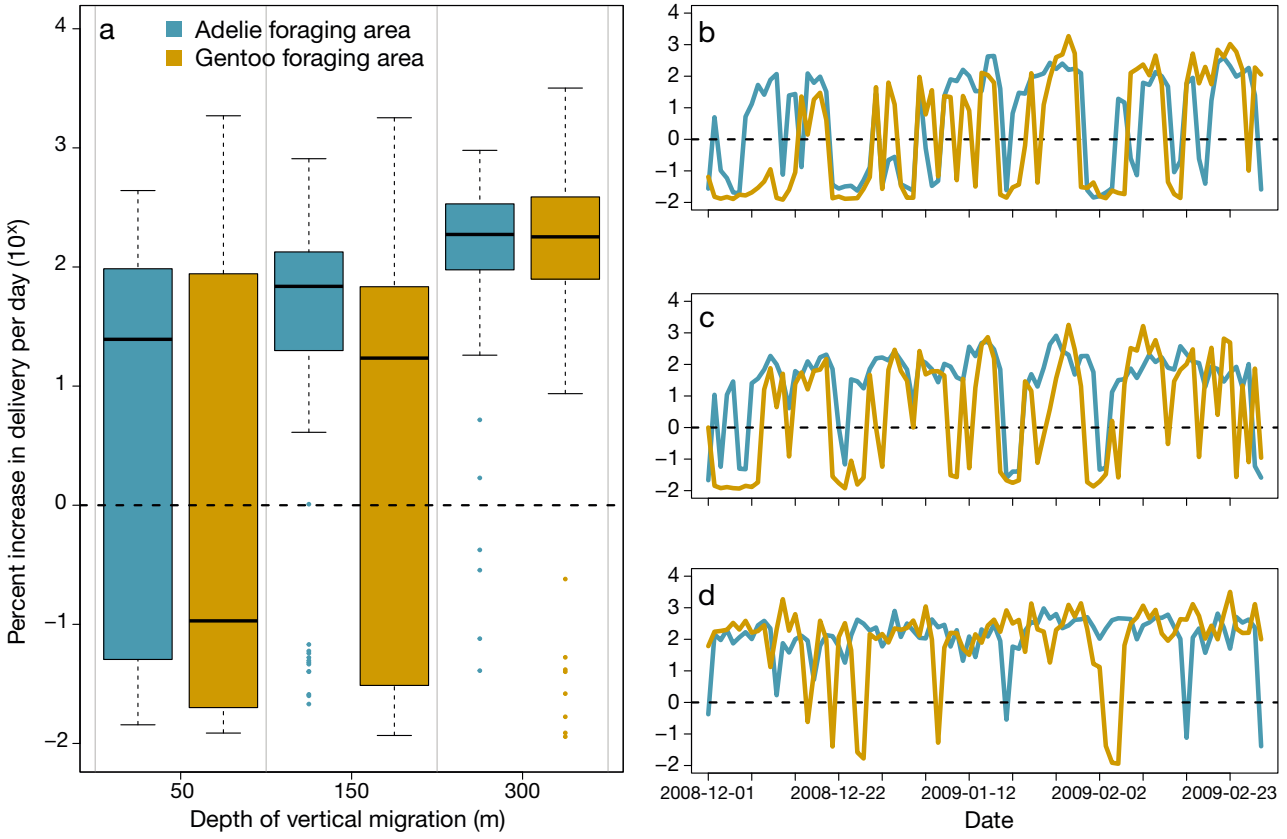

Fig. 6. As in Fig. 5, but with the delivery of simulated krill per day to the penguin foraging areas

(79 to 388%) over the same migration depths (Fig. 6a) when PDC was present.

The percent change of overall delivery rates through the austral summer was highly variable, especially when simulated krill had shallower migrations (Fig. 6b–d). When migrations occurred to 50 m, percent changes in overall simulated krill delivery rates within both foraging regions were periodic (Fig. 6b). There were periods where the percent increase in delivery rates was greater in the presence of PDC and in the absence of PDC of nearly identical magnitude (Fig. 6b). When simulated krill performed a deeper migration, delivery rates were greater in the presence of the canyon more often (Fig. 6c). When migrations occurred to 300 m, similar to simulated krill counts, overall delivery rates were consistently higher when the canyon was present by ~100% in both foraging regions (Fig. 6d). There were periodic declines in the percent change in both foraging regions, but they were more common in the gentoo foraging region (Fig. 6d).

Delivery rates from the eddy region (Fig. 1b) were calculated to determine the direct impact of the subsurface eddy on resource availability within the foraging regions. Delivery rates from the eddy region increased with migration depth when PDC was present in model simulations (Fig. S7). As migrations deepened, variability in delivery rates from the eddy region increased, especially late in the austral summer, similar to overall delivery rates (Fig. S7). Delivery rates from the eddy region generally ranged from 100 to 300 and from 50 to 150 simulated krill entering the Adélie and gentoo penguin foraging regions, respectively (Fig. S7). However, as many as 600 and 200 simulated krill entered the foraging regions in a single day when PDC was present in model simulations (Fig. S7). When PDC was absent, delivery rates from the eddy region to both foraging regions were below 100 simulated krill per day (Fig. S7).

As with the other metrics, the percent change in simulated krill delivery rates from the eddy region increased with migration depth (Fig. 7). When simulated krill migrated to 50 m, median percent differences in delivery rates from the eddy were 12% (–29 to 68%) higher in the Adélie foraging region when PDC was present (Fig. 7a). In the gentoo foraging region, delivery rates from the eddy were 30% (–71 to 76%) greater when PDC was absent from simula-

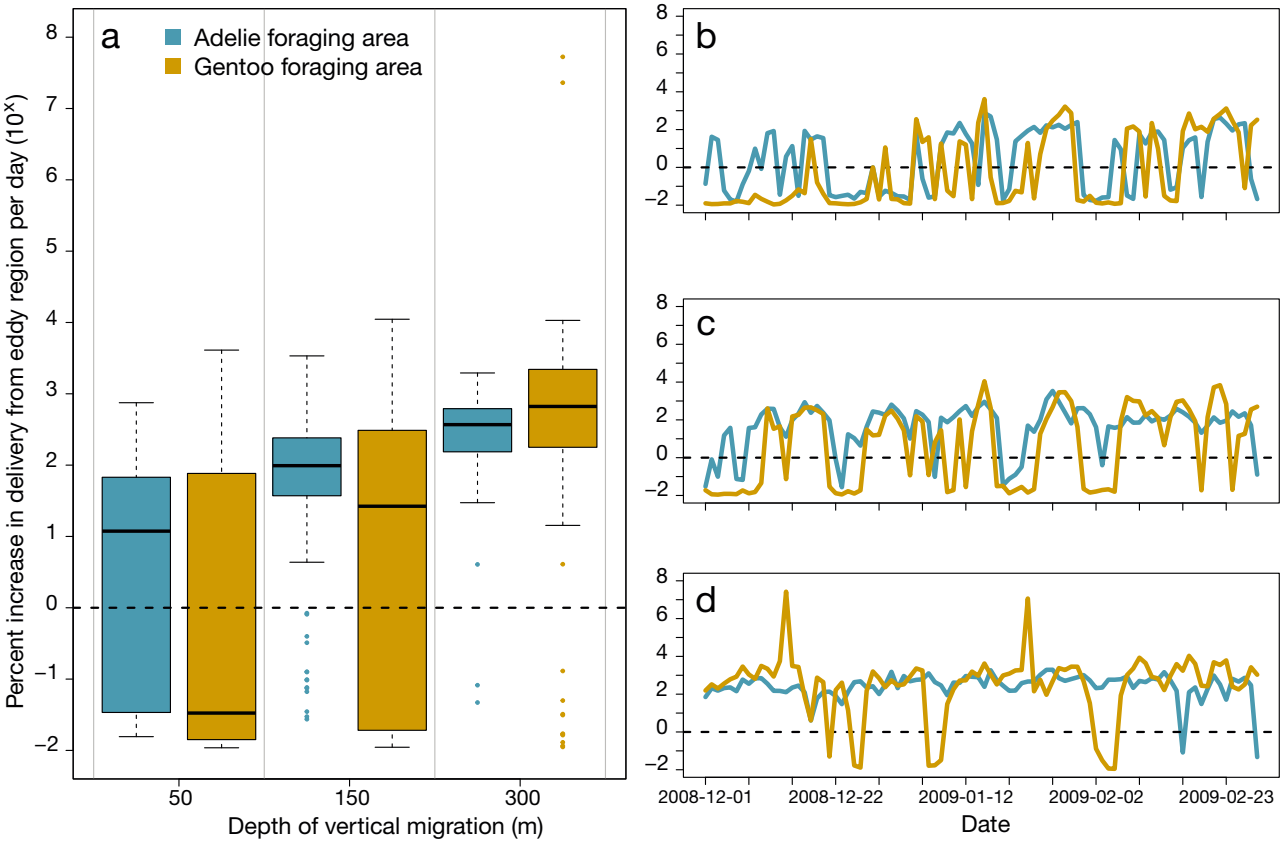

Fig. 7. As in Fig. 5, but with the delivery of simulated krill per day from the eddy region

tions (Fig. 7a). As migrations deepened to 150 m, simulated krill delivery rates were 98% (27–241%) and 27% (–52 to 307%) greater when PDC was present in the Adélie and gentoo penguin foraging regions (Fig. 7a). These percent differences were greatest when migrations occurred to 300 m, with simulated krill delivery rates 370% (154–618%) and 665% (178–2200%) greater when PDC was present in model simulations in the Adélie and gentoo penguin foraging regions, respectively (Fig. 7a).

Percent differences in delivery rates from the eddy were also highly variable in both penguin foraging regions when simulated krill migrated to 50 m (Fig. 7b). As migrations deepened to 150 m, delivery rates from the eddy region continued to be highly periodic until early February in the Adélie penguin foraging region, while delivery from the eddy region remained periodic through the austral summer in the gentoo penguin foraging region (Fig. 7c). In the Adélie penguin foraging region, delivery of simulated krill from the eddy region was consistently 100% greater when PDC was present in model simulations, with the exception of 2 short events at the end of the austral summer, when simulated krill migrated to 300 m (Fig. 7d). Delivery from the eddy region to the gentoo foraging region at this migration depth was similar, except there were more extreme events where simulated krill delivery from the eddy region was nearly 100% greater when PDC was absent from simulations or nearly 10^8% greater when PDC was present in simulations (Fig. 7d). The 2 instances when percent changes within the gentoo foraging region were on the order of 10^8% greater in the presence of PDC (Fig. 7d) occurred when no simulated krill entered the foraging region on the corresponding day when PDC was absent from simulations.

4. DISCUSSION

Along the WAP, and throughout the Southern Ocean, many penguin colonies are associated with nearby submarine canyons, which has led to the hypothesis that the presence of these canyons is mechanistically responsible for the physical and biological processes that result in high biological activity in these regions (Fraser & Trivelpiece 1996, San-

tora et al. 2020). The mechanisms that drive the increased biological activity in submarine canyon systems along the WAP are an area of active research. Recent modeling studies, coupled with *in situ* observations from PDC, have described a subsurface, retentive eddy that forms over the canyon during the austral summer, and this feature is capable of retaining both non-migrating (Hudson et al. 2021) and vertically migrating simulated zooplankton (Hudson et al. 2022).

The concentration of macrozooplankton such as krill, which have intermediate (10^2–10^3) Reynolds numbers (Oliver et al. 2019), is possible within this feature because their distributions can be influenced by both their behavior and advection by currents. The subsurface retentive eddy over PDC has the potential to influence krill distribution by virtue of their DVM behavior. Therefore, the DVM of krill can ecologically link the influence of the subsurface eddy to the surface, where most penguin foraging takes place. Here, we used simulations to test this hypothesis. To test the effects of the canyon, we removed PDC from model simulations, and compared residence times, simulated krill concentrations, and krill delivery metrics with and without the presence of PDC. We hypothesized that the presence of PDC would increase simulated krill (1) residence times over PDC and in regional foraging areas; (2) concentrations in foraging regions; (3) delivery to; and (4) delivery from the subsurface eddy region to the foraging areas.

While the presence of PDC significantly increased residence times of simulated krill over PDC, our overall results indicated that the effect of PDC and the resulting subsurface eddy on nearby penguin foraging areas is highly dependent on the depth of DVM behavior of simulated krill. Apart from when migrations occurred to 50 m in the gentoo foraging region, median percent increases of all krill distribution metrics (counts and delivery rates) indicated that metrics were greater in the presence of PDC and differences were greatest when migrations were deepest, suggesting that the subsurface retentive eddy had the largest impact when DVM was deep.

4.1. Effect of a highly retentive eddy on krill concentrations and delivery rates

When the canyon was present in the model, residence times of non-migrating particles released at 300 m within PDC are on the order of 175 d (Hudson et al. 2021). When DVM behavior was added to simulate zooplankton behavior, residence times over PDC were over 30 d when simulated krill migrated to 300 m (Hudson et al. 2022). Residence times over the same region in the absence of PDC were less than 9 d regardless of migration depth. These increases in retention when PDC was present were due to the subsurface eddy present over PDC. The northeast current present in the region in the absence of PDC likely drove this decrease in residence times, quickly moving simulated krill out of the region through the Bismarck Strait. This supports our first hypothesis that residence times over PDC would be higher due to the presence of the subsurface eddy.

Residence times within the penguin foraging regions, however, did not differ between the simulations. There were some instances when retention was greater when PDC was absent. These short residence times within the foraging regions are likely due to the way the subsurface eddy acts as a sink for simulated krill and the minimal (<25%) overlap between the eddy region and subsurface eddy. As a result, simulated krill released within the foraging regions were likely quickly pulled into the subsurface eddy, reducing their residence times within the foraging region. This would also explain how residence times increased slightly within the foraging regions in the absence of PDC. The absence of this sink, and corresponding low current velocities within the foraging regions, would keep simulated krill within these regions longer.

Our residence time estimates suggest that simulated krill are retained within the foraging regions for at least 1 d. Gentoo penguins tend to complete foraging trips along the WAP within a single day during the austral summer (Kokubun et al. 2010). Adélies have been observed making multi-day trips during the austral summer (Riaz et al. 2021, Oosthuizen et al. 2022). Around PDC, however, foraging trips of both species are nearly always less than a day (M. Cimino, M. Oliver, G. Voirol unpubl. data). Therefore, while residence times in the foraging regions are much lower than over PDC itself, residence times within the foraging regions may still be long enough to concentrate resources within them with mechanisms such as Lagrangian Coherent Structures in the surface mixed layer (Oliver et al. 2019). The short foraging trips may also suggest that accumulation and delivery of resources to the foraging regions from the nearby subsurface eddy provides ample resources within the foraging regions to provide foraging penguins.

Simulated krill counts within our study area may illustrate why penguins might forage in certain

areas. Both Adélie and gentoo penguins are capable of foraging far from their colonies, with breeding Adélies having an estimated foraging range of 10–130 km and nonbreeding individuals foraging as far as 200 km from their colonies during the breeding season (Oosthuizen et al. 2022). Gentoos have been observed foraging as far as 30–70 km during the breeding season (Kokubun et al. 2010, Camprasse et al. 2017). These ranges would give these predators access to our entire study region. However, on the coast of Anvers Island, the penguins at the colonies studied here foraged much closer to their colonies (~10 km; Oliver et al. 2013, Cimino et al. 2016, Pickett et al. 2018, Nardelli et al. 2021). In addition, penguins foraged in regions where simulated krill was, for the most part, greater in the presence of PDC. While foraging range has been linked to colony size, and the colonies studied here are relatively small (Santora et al. 2020), it is possible that these penguins are selecting for their respective foraging regions due to the increased simulated krill counts provided by PDC and the associated subsurface eddy.

The retention and concentration of resources locally by this subsurface eddy may have a greater ecological impact on local Adélie and gentoo penguins than the number of krill in or delivered directly to the penguin foraging regions. For example, energetic modeling studies have suggested that Adélie penguins near Anvers Island require a large amount of low-quality (low lipid content) krill to be successful in this area, especially when Antarctic silverfish are absent from their diets (Chapman et al. 2010, 2011). The subsurface eddy could therefore be retaining these krill in the region, thus allowing these colonies to persist in the absence of Antarctic silverfish.

4.2. Assumptions about DVM, krill, and penguin behavior

While these simulations have suggested that PDC and the associated subsurface eddy can increase krill counts and delivery rates to nearby penguin foraging regions, several key assumptions that were made in this study need to be addressed. The first is that krill are readily available within our study site. Multiple studies have discussed the heterogeneous distribution of krill near PDC and elsewhere along the WAP (Atkinson et al. 2008, 2019, Bernard & Steinberg 2013, Steinberg et al. 2015, Cimino et al. 2016, Bernard et al. 2017, Tarling et al. 2018, Nardelli et al. 2021). Future simulations could take into account the heterogeneous distribution of krill to determine the impacts that concentrating mechanisms such as the subsurface eddy within PDC have on prey and predator distributions.

The second assumption is that DVM is prevalent in krill populations around PDC. The extent of DVM in the region has been difficult to quantify. Recent studies in the region have observed zooplankton DVM as deep as 300 m in PDC (Hudson et al. 2022), where residence times of non-vertically migrating particles are approximately 175 d (Hudson et al. 2021). These studies, however, focused on acoustic scatterers in general and did not identify individual targets. Quantifying DVM in krill within PDC has been difficult, as observations of this behavior in krill are limited. However, other studies in the area surrounding PDC, such as nearby Wilhelmina Bay, have observed krill DVM down to at least 300 m in May (Nowacek et al. 2011, Espinasse et al. 2012, Kane et al. 2018). While these observations of krill DVM occurred in the early austral spring or late austral fall, earlier and later than our simulations, they illustrate that the migration behaviors to the depths simulated here are possible for krill and other zooplankton populations. Observations elsewhere in the Southern Ocean, however, are highly variable and illustrate that DVM can stop during the austral summer (Tarling & Thorpe 2017, Tarling et al. 2018). More *in situ* observations of DVM are necessary over PDC, especially over the austral summer, to quantify the extent and depths to which this behavior occurs. Our study suggests that a better understanding of local krill DVM is crucial to determining the importance of the presence of PDC and the resulting retentive eddy to the formation of this biological hotspot.

The third assumption we made was that krill are net passive drifters in the horizontal and their only active swimming was DVM. Previous modeling studies have made similar assumptions about krill being passive drifters in the horizontal and have hypothesized that horizontal advection is a major driver of krill, and other zooplankton, distributions (Hofmann et al. 1998, Hofmann & Murphy 2004, Murphy et al. 2004, Thorpe et al. 2004, Piñones et al. 2011). Krill are macrozooplankton and have been observed swimming at speeds of 0.015–0.03 m s^{-1} (Kils 1981, Letessier et al. 2013, Kane et al. 2018). Depending on current velocities, krill would be capable of swimming against currents at least for a short time, whether to maintain their location or move to a different area. If the krill around PDC consistently show biased directional swimming (horizontal movement more akin to a correlated random walk), then it is unclear if our results would reflect how the PDC

affects krill distributions. In this scenario, PDC may still act as a local krill hotspot, by retaining food for krill, instead of krill themselves, and attracting them to the area. Smaller-scale behavioral models of Antarctic krill have suggested that krill move in the horizontal in response to food availability and predation risk near South Georgia, which in turn affects their local distributions (Cresswell et al. 2007, 2009). Therefore, parametrizing krill movement in the horizontal, as well as the vertical, around PDC would significantly increase our understanding of this system and how the subsurface eddy may impact this biological hotspot.

The fourth assumption is that the horizontal advection of simulated krill into the penguin foraging regions would make them accessible to foraging penguins. We only considered the 2D foraging regions here and did not consider vertical diving behavior of these predators. Adélie penguins have an average dive depth of approximately 17 m in and around PDC, while gentoos dive to an average of 41 m (Pickett et al. 2018). Vertical random walks were included in the model which could affect the depth of simulated krill within the foraging regions, but more simulations of DVM within the foraging depth ranges of these predators are needed to fully understand this mechanism and its impacts on local predators. The depth of simulated krill should also be considered when calculating concentration and delivery metrics in future studies.

In addition to these assumptions, it is important to note that we have simulated a single austral summer within ROMS. While the subsurface eddy is driven primarily by bathymetry in the model, it is important to note that there is possible interannual variability in the persistence of, and retention that results from, the subsurface eddy present over PDC during the austral summer that could impact our results. In addition, ROMS does not perfectly predict the coastal oceanography within and around PDC. Comparisons of *in situ* observations from the 2019–2020 austral summer and ROMS simulations from the same austral summer simulated here illustrate that the subsurface eddy over PDC is more baroclinic than simulations predict (Hudson et al. 2021). The model also predicts deeper mixed layers than observed by autonomous underwater gliders deployed within the region, suggesting that stratification is under-predicted in the model over PDC (Hudson et al. 2021, Wang et al. 2022). This has led to the hypothesis that surface waters are more isolated from the effects of the canyon than the model suggests and would explain why the eddy is often visible in the surface in the model (Hudson et al. 2021, this study) but is only observed in surface currents when stratification and winds are low (Hudson et al. 2021). ROMS also does not include all coastal buoyancy forces present along the WAP. This impacts the ability of the model to predict the Antarctic Coastal Current and is an area of active research. Changes in the Antarctic coastal current may impact accumulation and delivery of simulated krill to the penguin foraging regions used in this study.

4.3. Implications for understanding the PDC biological hotspot and beyond

Penguin foraging regions are relatively consistent around PDC (Pickett et al. 2018, Nardelli et al. 2021), suggesting that krill populations are relatively predictable despite a high amount of oceanographic and environmental variability. Our study suggests that PDC and the resulting retentive eddy may play a role in krill availability and delivery to nearby penguin foraging areas when krill perform DVM. This feature may be especially significant when prey resources are scarce. Antarctic krill recruitment and resulting population abundance are highly cyclical, with approximately 5 yr periodicities (Saba et al. 2014, Steinberg et al. 2015). As krill populations experience years of low recruitment and lower abundance, the retentive eddy could help concentrate these dilute resources and deliver them to the penguin foraging regions.

PDC is not the only submarine canyon along the WAP that is associated with a biological hotspot and increased upper trophic level predator activity (Schofield et al. 2013). Submarine canyons throughout the Southern Ocean have also been associated with high predator, specifically penguin, foraging activity (Santora et al. 2020). Therefore, these features may drive the surrounding biological hotspots by increasing local resource availability, similar to PDC. Further modeling studies are needed in these similar systems to examine how these features may structure the biological hotspots along the WAP. In addition, *in situ* observations from within these hotspots are necessary to determine if the upper trophic level predators that occupy these hotspots utilize these accumulated resources.

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