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Subsurface Eddy Facilitates Retention of Simulated Diel Vertical Migrators in a Biological Hotspot

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Key Points:

- Simulated diel vertical migrating zooplankton have increased residence time compared to nonmigrators near a biological hotspot
- Shallow surface layers and long days lead to longer residence times of simulated diel vertical migrating zooplankton
- Field acoustic measurements show the presence of zooplankton diel vertical migration consistent with simulated migration

Supporting Information:

Supporting Information may be found in the online version of this article.

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Abstract Diel vertical migration (DVM) is common in zooplankton populations worldwide. Every day, zooplankton leave the productive surface ocean and migrate to deepwater to avoid visual predators and return to the surface at night to feed. This behavior may also help retain migrating zooplankton in biological hotspots. Compared to fast and variable surface currents, deep ocean currents are sluggish, and can be more consistent. The time spent in the subsurface layer is driven by day length and the depth of the surface mixed layer. A subsurface, recirculating eddy has recently been described in Palmer Deep Canyon (PDC), a submarine canyon in a biological hotspot located adjacent to the West Antarctic Peninsula. Circulation model simulations have shown that residence times of neutrally buoyant particles increase with depth within this feature. We hypothesize that DVM into the subsurface eddy increases local retention of migrating zooplankton in this feature and that shallow mixed layers and longer days increase residence times. We demonstrate that simulated vertically migrating zooplankton can have residence times on the order of 30 days over the canyon, which is five times greater than residence times of near-surface, nonmigrating zooplankton within PDC and other adjacent coastal regions. The potential interaction of zooplankton with this subsurface feature may be important to the establishment of the biological hotspot around PDC by retaining food resources in the region. Acoustic field observations confirm the presence of vertical migrators in this region, suggesting that zooplankton retention due to the subsurface eddy is feasible.

Plain Language Summary Diel vertical migration (DVM) is considered the world's largest migration by biomass. Zooplankton migrate into the sea's surface waters to feed at night when risk of predation by visual predators is low. During the day, zooplankton migrate to deeper waters when risk of predation by predators like seabirds and fish is highest. This behavior may also retain zooplankton in areas of high biological activity, or hotspots. Migration between a rapidly moving surface layer and a sluggish subsurface layer may reduce the net horizontal movement of organisms. Since this behavior is modulated by light intensity, more daylight hours may increase the time spent in the slower subsurface layer and help retain zooplankton in these hotspots. We used simulated zooplankton in a numerical model over Palmer Deep Canyon to test how DVM behavior, and the factors that control the time spent in the subsurface layer, affects zooplankton retention within biological hotspots. Retention was highest for zooplankton when migrations were deepest, days were long, and surface mixed layer was shallow. Performing migrations also increased retention relative to near-surface nonmigrating zooplankton. Acoustic observations within our study site suggest that the magnitudes of DVM simulated are feasible in this system.

1. Introduction

Diel vertical migration (DVM) occurs in zooplankton and fish species across the world (Brierley, 2004). Many zooplankton perform this behavior daily, migrating from great depths to surface waters at night and returning to these depths during the day (Brierley, 2004; Hays, 2008). This migration is likely a trade-off between predator avoidance and feeding (Brierley, 2004; Hays, 2008). Migrators feed at night in surface waters when visual predation is low. During daylight hours, they migrate to depth, limiting visual predation (Brierley, 2004; Hays, 2008).

There are many cues that trigger DVM and control the depth of migration. These include, but are not limited to, day length (DL; Benoit et al., 2010; Cohen & Forward, 2005; Hobbs et al., 2018, 2021), circadian rhythms (Cohen & Forward, 2005), food availability (Cresswell et al., 2009; Sha et al., 2020), ontogeny (Hays, 1995), and predation pressures (Cresswell et al., 2009; Hays, 1995; Sha et al., 2020). These cues can vary widely across species and latitudes, and within populations (Benoit et al., 2010; Conroy et al., 2020; Cresswell et al., 2009; Hays, 2008; Sha et al., 2020; Thibodeau, 2015).

DVM may also increase retention of migrators in biologically productive regions or hotspots (Batchelder et al., 2002; Carr, 2003, 2006; Emsley et al., 2005; Lavoie et al., 2000; Marta-Almeida et al., 2006; Peterson, 1998). For example, in areas where along-shore winds create Ekman induced upwelling, organisms are pushed offshore in surface waters. When organisms migrate down out of this surface layer, they can be advected back inshore by the subsurface return flow, thus retaining them within the system (Batchelder et al., 2002; Peterson, 1998). This mechanism retains crab larvae in upwelling systems off the Coast of Portugal (Marta-Almeida et al., 2006) and several copepod species in upwelling systems associated with eastern boundary currents worldwide (Peterson, 1998).

Other subsurface circulation features have been shown to increase retention of migrators (Carr, 2003, 2006; Emsley et al., 2005; Lavoie et al., 2000). In the Gulf of St. Laurence, euphausiids perform DVM between two different flow fields in the Laurentian Channel, which results in their accumulation inshore (Lavoie et al., 2000). Simulated particles in a two-layer system within Monterey Bay suggest that performing DVM increases the retention of juvenile euphausiids and other zooplankton (Carr, 2003, 2006). In the Irish Sea, the presence of DVM in simulated *Calanus* spp. copepods increased the probability of retention from 4.87% to 17.46% after 90 days due to the presence of a subsurface eddy (Emsley et al., 2005). Recent modeling work in the same region, however, suggests that DVM can reduce residence times by half in the West Irish Sea (McGeady et al., 2019). McGeady et al. (2019) hypothesized that DVM decreased retention times by reducing the amount of time spent at depths where eddy circulation is strongest.

Time spent within retentive features is dependent on both DL (how long the sun is above the horizon) and mixed layer depth (MLD). DL has a significant impact on DVM in high latitudes where its seasonal variability is greatest (Benoit et al., 2010; Cohen & Forward, 2005; Conroy et al., 2020; Hobbs et al., 2018, 2021). Long days can decrease the migration depth of DVM, or stop it completely at high latitudes (Cisewski et al., 2010; Conroy et al., 2020). When stratification is high, the surface mixed layer is distinct from the rest of the water column, and driven by different forcing mechanisms than the waters below (Johnston & Rudnick, 2009). Flow within the mixed layer may be more driven by wind or freshwater inputs, while flow below the MLD may be driven by bathymetry, and can differ significantly from the surface (Kohut et al., 2018). MLD is often used as a proxy depth for the boundary between these layers. Given the possibility for significant differences in current velocity between the two layers, there could be benefits to migrating out of the more dynamic surface mixed layer and into a slower-moving, more consistent, subsurface layer. Shallower mixed layers may increase retention of migrating zooplankton by reducing the vertical distance required to reach the quiescent or recirculating subsurface, and increasing the time spent at these depths. While previous studies have suggested that both MLD and DL affect zooplankton DVM migration depth (Conroy et al., 2020), their effects on retention are relatively unknown.

Palmer Deep Canyon (PDC) is a nearshore, submarine canyon along the West Antarctic Peninsula (WAP; Carvalho et al., 2016; Fraser & Trivelpiece, 1996; Kavanaugh et al., 2015; Schofield et al., 2013). It is considered a biological hotspot due to its proximity to Adélie (*Pygoscelis adeliae*) and Gentoo (*P. papua*) penguin colonies and foraging regions, as well as high rates of whale foraging activity (Fraser & Trivelpiece, 1996; Schofield et al., 2013). These predators feed on zooplankton that perform DVM including euphausiids such as the Antarctic krill (*Euphausia superba*), several calanoid copepod species, and ostracods (Conroy et al., 2020; Demer & Hewitt, 1995; Goodrich, 2018; Thibodeau, 2015). These zooplankton perform DVM to a variety of depths. For example, the euphausiids *Thysanoessa macrura* and *Euphausia crystallorophias,* as well as several copepod species, have been shown to perform DVM during the austral summer near South Georgia and along the WAP from 10 m down to ~50 m (Atkinson et al., 1992a, 1992b; Conroy et al., 2020). In the sub-Antarctic Southern Ocean, populations of *Euphausia vallentini* have been documented performing DVM between ~10 and 150 m near the Prince Edward Island Archipelago (Perissinotto & McQuaid, 1992). Zooplankton in the Lazarev Sea also migrate from the upper 50 m to over 300 m, especially around the austral spring and summer equinoxes (Cisewski et al., 2010). DVM of the Antarctic krill, a keystone macrozooplankton species along the

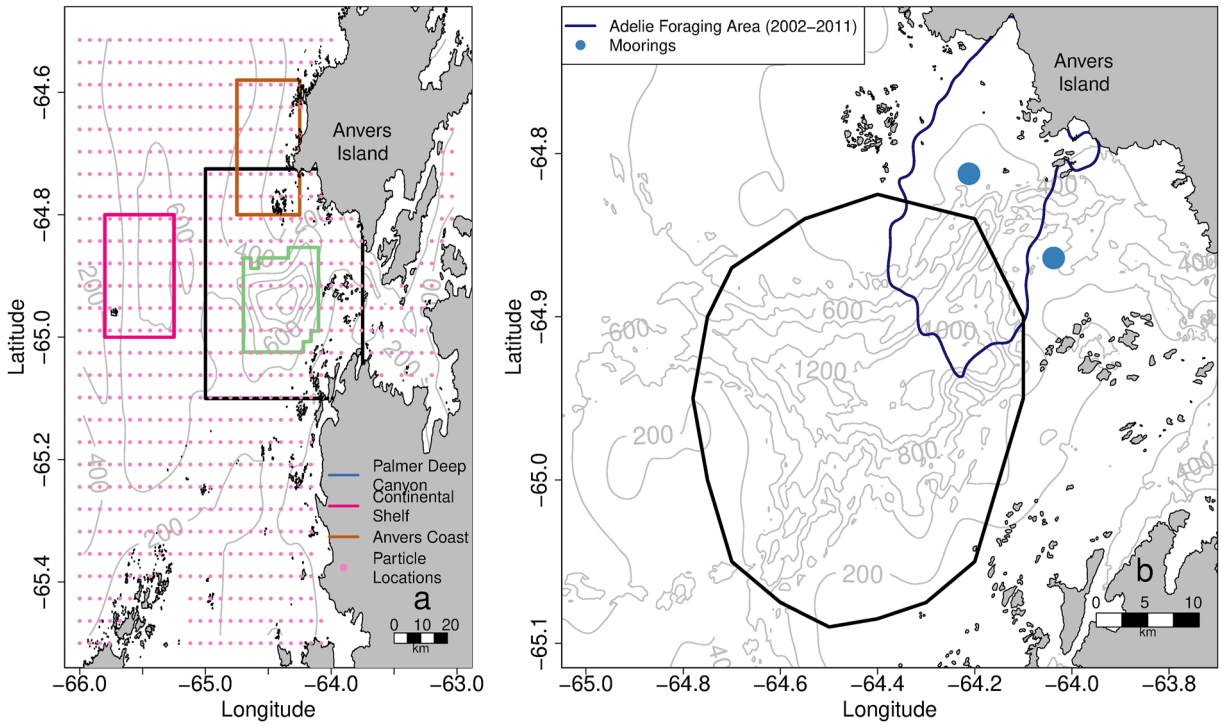

Figure 1. (a) Bathymetric map of Palmer Deep Canyon (PDC) and the surrounding shelf area. Pink points illustrate locations where neutrally buoyant and migrating zooplankton were seeded in Regional Ocean Modeling System (ROMS) experiments. The colored boxes indicate regions used for residence time calculations. The black box outlines the area in panel (b) Bathymetry is from ROMS. (b) Bathymetric map of PDC and 2020 mooring locations used in this analysis. The black circle outlines the approximate location of the subsurface eddy. The navy line represents the 99.5% contour for Adélie penguin foraging locations for penguins tagged between 2002 and 2011. Bathymetry is from GRMT (Ryan et al., 2009).

WAP and in the Southern Ocean, is highly variable, with some studies showing krill DVM from the near-surface down to ~350 m, while others show a complete lack of krill DVM or even reverse DVM, where krill spend the days in the surface to feed and migrate to depth at night (Demer & Hewitt, 1995; Espinasse et al., 2012; Tarling et al., 2018; Tarling & Thorpe, 2017). In addition, the extent of zooplankton migrations throughout the WAP is highly variable by season and latitude during the summer for certain zooplankton species (Cleary et al., 2016; Conroy et al., 2020; Thibodeau, 2015). For example, the abundant calanoid copepod *Metridia gerlachei* is a strong vertical migrator (50–350 m) in the south WAP (Conroy et al., 2020). In the north WAP, a small fraction of the population migrates between ~50 and 300 m (Conroy et al., 2020).

DL and MLD both influence DVM along the WAP for migrators moving between the upper mesopelagic (>200 m) and epipelagic (<200 m) zones. Analysis of zooplankton tows within the Palmer Long Term Ecological Research program sampling grid from 1993 to 2017 show that ostracods and some copepods decrease the distance of migration by up to 60 m when DLs increase from 17 to 22 hr (Conroy et al., 2020). In addition, the night:day ratio of *T. macrura* abundances integrated over the top 50 m decrease from ~60 to nearly zero as MLD deepens from 10 to 80 m (Conroy et al., 2020). The decline in night:day ratio suggests that this euphausiid is more abundant in the top 50 m at night when MLDs are shallow, suggesting increasing DVM with shallower MLD (Conroy et al., 2020).

Recent *in-situ* and modeled observations of PDC show that a closed, subsurface eddy is present over PDC during the austral summer (Movie S1 in Supporting Information S1; Hudson et al., 2021). The eddy has a diameter of approximately 50 km (Figure 1b; Movie S1 in Supporting Information S1; Hudson et al., 2021). Models suggest that the flow dominates below the surface mixed layer and is mostly barotropic (depth-driven), with a small baroclinic (density-driven) component (Hudson et al., 2021). *In-situ* observations of isopycnal doming over the canyon are consistent with the presence of a subsurface eddy below the MLD (Hudson et al., 2021). At 150 m depth in the subsurface eddy, residence times of neutrally buoyant, nonmigrating are up to 175 days, which is much longer

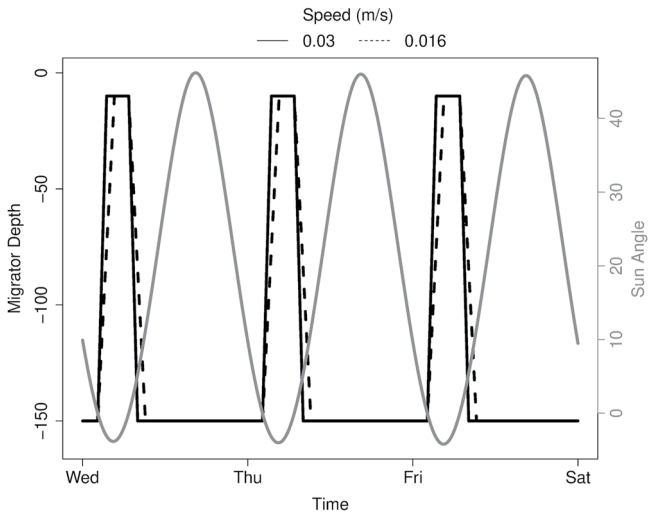

Figure 2. Idealized diel vertical migration (black lines) of simulated particles within Palmer Deep Canyon (PDC) over a four-day period in early January 2020 as cued by sun angle (light gray, right *y*-axis) at the two different swimming speeds used in this study. Time is local to PDC. *Note.* this figure illustrates an idealized example of Palmer Deep Canyon and does not include the vertical advective velocity or random walk that is parameterized in ROMS.

than the 2–4 days residence time in the surface mixed layer found in modeling (Hudson et al., 2021) and observations (Kohut et al., 2018).

Surface mesoscale eddies have been shown to have significant impacts on zooplankton distributions and community structure through the enhancement of local productivity and/or retention of discrete communities (Bernard et al., 2007; Eden et al., 2009; Piontkovski et al., 1995). When mesoscale eddies result in the upwelling of nutrient rich deep waters, they can result in phytoplankton blooms (Falkowski et al., 1991), which in turn can impact local zooplankton biomass and communities. Eddies, and their resulting impacts on biogeochemistry, have also been shown to impact zooplankton behavior, including DVM (Eden et al., 2009; Piontkovski et al., 1995). The subsurface eddy over PDC, however, differs from these open ocean surface mesoscale eddies in that it is bathymetrically driven and contained by PDC (Hudson et al., 2021) and does not appear to drive upwelling (Hudson et al., 2019). This feature, however, still has the potential to impact zooplankton distributions through localized retention. If zooplankton perform DVM in and out of this subsurface feature, their residence time could be increased in the region, thereby providing a reliable food resource for the local biological hotspot (Hudson et al., 2021).

Here, we examine how DVM, and the factors that control it, may impact zooplankton residence times using the Regional Ocean Modeling System (ROMS). Using simulated zooplankton with DVM behavior, we test the following hypotheses: (a) the presence of a subsurface eddy over PDC increases the residence time of vertically migrating zooplankton relative to near-surface residence times; and (b) the depth of the boundary between the surface mixed layer and subsurface eddy, approximated by MLD, and DL significantly impact these residence times, with shallower MLDs and longer days increasing local retention. In addition, we use field observations from 2020 to examine the extent of DVM within PDC. If DVM both facilitates the retention of zooplankton and is present within the canyon system, the subsurface eddy could facilitate the formation of the biological hotspot near and in PDC by providing a reliable food resource for higher trophic levels.

2. Materials and Methods

2.1. DVM and Residence Time Calculations in ROMS

ROMS (Haidvogel et al., 2008) based simulations were used to test the impacts of DVM on zooplankton residence times within PDC. The updated (Hudson et al., 2021) WAP version of ROMS (Graham et al., 2016) has a 1.5 km horizontal resolution with 24 terrain-following vertical layers. It includes modeling of dynamic sea ice (Budgell, 2005) and the interactions between floating ice shelves and the water beneath them (Dinniman et al., 2011; Holland & Jenkins, 1999). Atmospheric forcing is from the Antarctic Mesoscale Prediction System (Powers et al., 2012) and tidal forcing is from the CATS2008 regional Antarctic tidal model (Padman et al., 2002). Simulations were run from November 2008 to May 2009.

Simulated particles, which served as a proxy for zooplankton and are henceforth referred to as simulated zooplankton, were released on an approximately 4 km grid around PDC (Figure 1a), for a total of 720 simulated zooplankton released at each release event. Zooplankton release events occurred every 2 days from 1 November 2008 through the end of March 2009, and followed for at least 30 days. 90 releases occurred, for a total of 64,800 simulated zooplankton released per depth and migration. Simulated zooplankton were advected at every model time step (50 s) and included a vertical random walk (Hunter et al., 1993; Visser, 1997) to mimic the transport effect of vertical turbulence (which is parameterized in ROMS). Zooplankton positions were saved every hour. DVM was added to zooplankton based on local solar angle (Figure 2). When the sun rose above the horizon at the position of the zooplankter, a downward velocity was added to the advective and random vertical velocities as long as the zooplankter was above the prescribed migration target depth. When the sun set at the position of the zooplankter, an upward velocity was added as long as the simulated zooplankter was below 10 m depth.

Migration depths were based on previously published *in situ* observations of zooplankton near PDC, along the WAP, and in the Southern Ocean (Atkinson et al., 1992a, 1992b; Cisewski et al., 2010; Conroy et al., 2020; Espinasse et al., 2012; Kane et al., 2018; Komoda & Mizunuma, 2019; Nowacek et al., 2011; Perissinotto & McQuaid, 1992), as well as observations of DVM from subsurface moorings (see Section 2.2). Zooplankton in this region and in the open ocean have previously been observed migrating from the near surface (~10 m) to 50, 150, and 300 m (Atkinson et al., 1992a, 1992b; Cisewski et al., 2010; Conroy et al., 2020; Espinasse et al., 2012; Kane et al., 2018; Komoda & Mizunuma, 2019; Nowacek et al., 2011; Perissinotto & McQuaid, 1992), with observations between the near surface, and depths at, or around 300 m (280–350 m) being the most common. This was also true in mooring observations (see Section 3.1). Therefore, we chose to simulate vertical migration from 10 to 50 and 300 m. The final migration depth (150 m) was chosen as an approximate intermediate between 50 and 300 m.

Migration speeds were based on previously published vertical swimming speeds of zooplankton (Cisewski et al., 2010; Kane et al., 2018; Kils, 1981). Mean vertical swimming speeds of krill in the late spring were estimated as 0.23 body lengths per second (Kane et al., 2018). We used a mean body length estimate of 5 cm to calculate a swimming speed of 0.016 m s^{-1}, which was similar to previously published vertical swimming speeds from acoustic backscatter data (Cisewski et al., 2010). We also used a speed of 0.03 m s^{-1} from Kils (1981).

In addition to simulating zooplankton migration from 10 m, down to 50, 150, and 300 m at 0.016 m s^{-1} and 0.03 m s^{-1}, neutrally buoyant, nonmigrating zooplankton were also released without DVM at 10, 50, 150, and 300 m. For all simulations, zooplankton were considered passive drifters with the current other than DVM and modeled vertical diffusion. Active swimming against or with currents was not considered.

Residence times were calculated using the e-folding method, defined as the time needed for the concentration of simulated zooplankton to drop to 1/e (~37%; Couto et al., 2017; Kohut et al., 2018; Piñones et al., 2013). Residence times were calculated for simulated zooplankton released over PDC, using the 400 m isobath to define PDC, as well as regions with less significant bathymetric variability along the Coast of Anvers Island and on the continental shelf adjacent to PDC (Figure 1a). Residence times were calculated for the period between 21 December 2008 and 21 February 2009 when the subsurface eddy was most coherent over PDC based on daily averaged currents (Movie S1 in Supporting Information S1). Median residence times and their associated 95% confidence intervals over this period were calculated by bootstrapping using the *boot* package in R (Canty & Ripley, 2021). Since these residence times are based on simulated zooplankton, statistically significant differences based on frequentist approaches to p-values could easily be manipulated by increasing the number of simulated zooplankton in the model, or the number of modeled runs. Therefore, our analysis to determine differences between different migrations and behaviors will instead focus on the difference in median residence times in different model conditions.

DL was calculated in hours from ROMS. MLD was calculated using the depth of maximum Brunt-Väisälä frequency (N^2; Carvalho et al., 2017). DL and MLD were averaged over the calculated residence time (from particle release to the time when particle concentration dropped to ~37%) for each release. The effect of MLD and DL on residence times of migrating simulated zooplankton was compared using Weighted Least Squares (WLS) multiple regressions without interaction. WLS was used, and the interaction was not considered, to control for homoscedasticity in the data and collinearity of MLD and DL, respectively. Homoscedasticity was tested using *ncvTest* in the *car* package in R (Fox & Weisberg, 2019). Variance Inflation Factors (VIF) were calculated using *vif* in the car package (Fox & Weisberg, 2019). Weights (w) were generated using the following equations:

$$mod1 = lm(RT \sim meanMLD + meanDL) \quad (1)$$

$$fitted.values = lm(|mod1\$residuals| \sim mod\$fitted.values)\$fitted.values \quad (2)$$

$$w = {}^{1}/_{fitted.values^2} \quad (3)$$

Three models were constructed considering the effects of MLD and DL on the three migration depths independently. Swimming speeds were pooled for each migration depth. Outliers were detected using the *outlier Test* function in the *car* package (Fox & Weisberg, 2019). Two outliers were removed from simulated zooplankton migrating down to 300 m, one from each migrating speed, to help meet model normality assumptions, which were tested using a Shapiro-Wilk test in the *stats* package (R Core Team, 2020). As with our analysis of residence

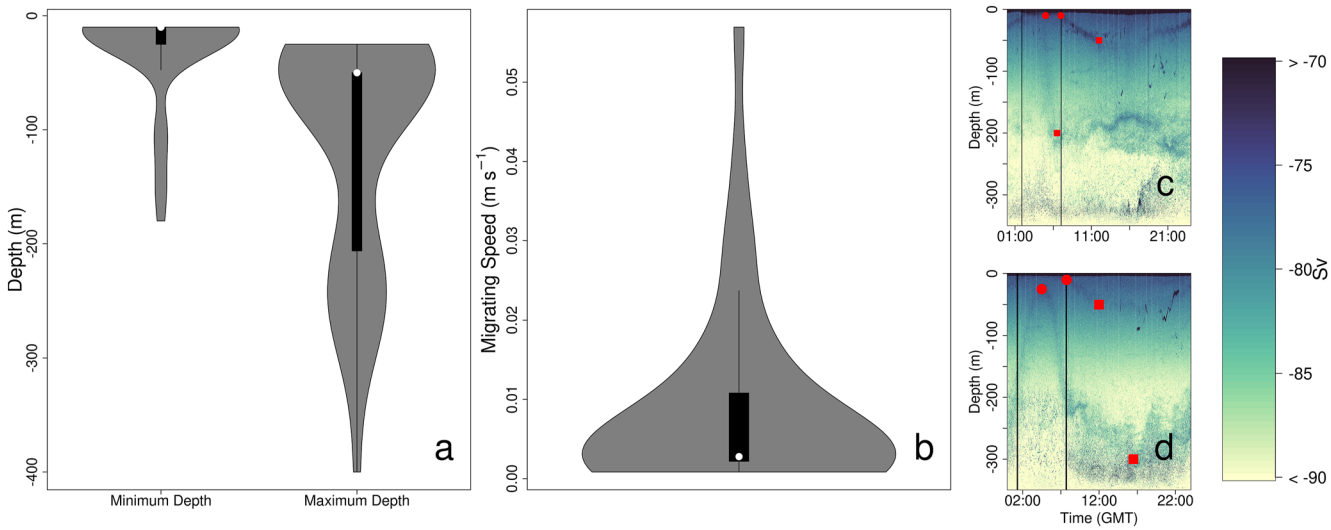

Figure 3. Violin plots illustrating the distribution of the minimum and maximum migration depths (a) and migrating speeds (b) observed by the two subsurface moorings used in this analysis. White dots illustrate the median, black bars illustrate the interquartile range, and lines denote 1.5× the interquartile range. The width of the shape illustrates the probability of migrations occurring to that depth. Panels c and d illustrate two examples of the observed diel vertical migration from the eastern mooring on 20 January and 31 January 2020, respectively, and the estimated minimum (circles) and maximum (square) migration depths. Vertical lines represent sunset and sunrise.

times, p-values could be manipulated by simply increasing the number of simulated particles and runs. Therefore our statistical analysis will be focused on the test statistic and the relative size of the effect of MLD and DL on residence times.

2.2. Mooring Observations of DVM in PDC

Two Nortek Signature100 echo sounders equipped with upward-facing transducers were deployed within PDC during the austral summer of 2020 to look for evidence of zooplankton DVM in the PDC region (Figure 1b). The western mooring was deployed on 6 January 2020 at 345 m and recovered on 3 February 2020 (28 days deployed). The eastern mooring was also deployed on 6 January 2020 at 400 m and recovered on 7 March 2020 (61 days deployed).

The echo sounders pinged at 6 s intervals and recorded echo amplitudes computed by their internal processors in 1,168 bins representing 0.375 m in range. While the echo sounders deployed here had a frequency sweep from 70 to 120 kHz, only the data from the narrowband 120 kHz frequency echo sounder were examined for this study following Tarling et al. (2018).

To look for evidence of DVM observed by the moorings, echograms representing S_v by time and depth of 6-s mean volume backscattering strength were analyzed visually. Sunrise and sunset were estimated by determining when solar angle at each of the moorings was zero using the *sunAngle* function in R package *oce* (Kelley & Richards, 2020). Minimum and maximum depths and speeds of DVM, if present, were visually estimated from daily time series and recorded for each full day of data collection at each of the moorings, excluding recovery and deployment days.

3. Results

3.1. Observations of DVM in PDC

The subsurface mooring observed DVM in zooplankton populations in PDC (Figure 3). The median minimum depth of migration was 10 m and the median maximum depth was 50 m (Figure 3a). The minimum and maximum depths of the migrations were significantly different from each other as determined by a Mann-Whitney U test ($p < 0.01$). Zooplankton in the top 50 m occasionally migrated to 300 m, where layers of organisms were greater than 50 m thick during the day (Figure 3d). Of the 45 migrations observed, 9 of these occurred to approximately

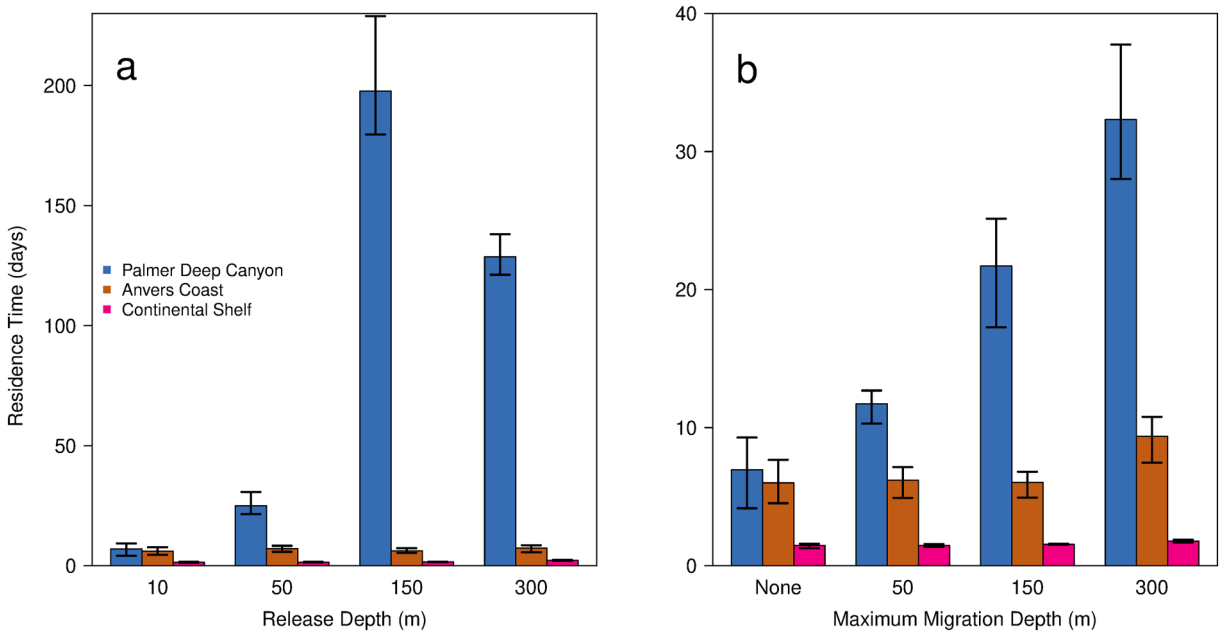

Figure 4. Median residence times (±95% confidence interval) in days of simulated zooplankton released without Diel vertical migration (DVM) (a) and with DVM at three different migration depths (b) over Palmer Deep Canyon (blue), along the Coast of Anvers Island (brown), and on the continental shelf (pink). Swimming speeds were pooled because there was no difference between the two migration speeds.

300 m while 24 occurred to approximately 50 m. There were also instances where multiple layers of migrators were present in a single day (Figures 3c and 3d). The median vertical swimming speed of zooplankton performing DVM was 0.003 m s^{-1} and migration speeds ranged from <0.001 to 0.06 m s^{-1} (Figure 3b). DVM was observed in 31 of the 61 sampling days across both moorings. Most of these observations occurred between mid-January and mid-February. When zooplankton did not migrate, zooplankton were present both in the surface and at depth within mooring observations. The purpose of these data is only to confirm that the range of simulated zooplankton DVM were reflected in observations of DVM in our study region.

3.2. Residence Times of Simulated Zooplankton

The residence time of neutrally buoyant simulated zooplankton generally increased with depth over PDC (Figure 4a). Nonmigrating, neutrally buoyant simulated zooplankton released at 10 m over PDC had a median residence time of nearly 7 days, which increased to 25 days for simulated zooplankton released at 50 m. Nonmigrating simulated zooplankton released at 150 and 300 m had residence times of approximately 200 and 125 days, nearly 28 and 18 times greater than residence times of simulated zooplankton released at 10 m, respectively (Figure 4a). Along the Anvers Coast, residence times of nonmigrating, neutrally buoyant simulated zooplankton increased slightly with depth, ranging from ~6 to 10 days (Figure 4a). Residence times in this region were shorter than those over PDC except when zooplankton were released at 10 m (Figure 4a). On the continental shelf, residence times of nonmigrating simulated zooplankton remained low (~1–2 days) regardless of depth and were always lower than those over PDC (Figure 4a).

As simulated zooplankton migrated deeper, residence times over PDC increased in comparison to nonmigrating particles released at 10 m (Figure 4b). There were little to no differences in residence times over PDC between the two swimming speeds simulated (0.03 and 0.016 m s^{-1}) so speeds were pooled (Figures 5b and 5c). Simulated zooplankton migrating to 50 m over PDC had median residence times of approximately 11 days (Figure 4b). In contrast, simulated zooplankton migrating to 150 and 300 m over PDC had residence times of approximately 22 and 33 days, respectively (Figure 4b). Residence times at depth were ~3 and 5 times greater than residence times of near-surface, nonmigrating simulated zooplankton, respectively (Figure 4b).

Residence times of migrating zooplankton in the Anvers Island and continental shelf regions were all lower than those over PDC (Figure 4b). Similar to the residence times nonmigrating, neutrally buoyant simulated

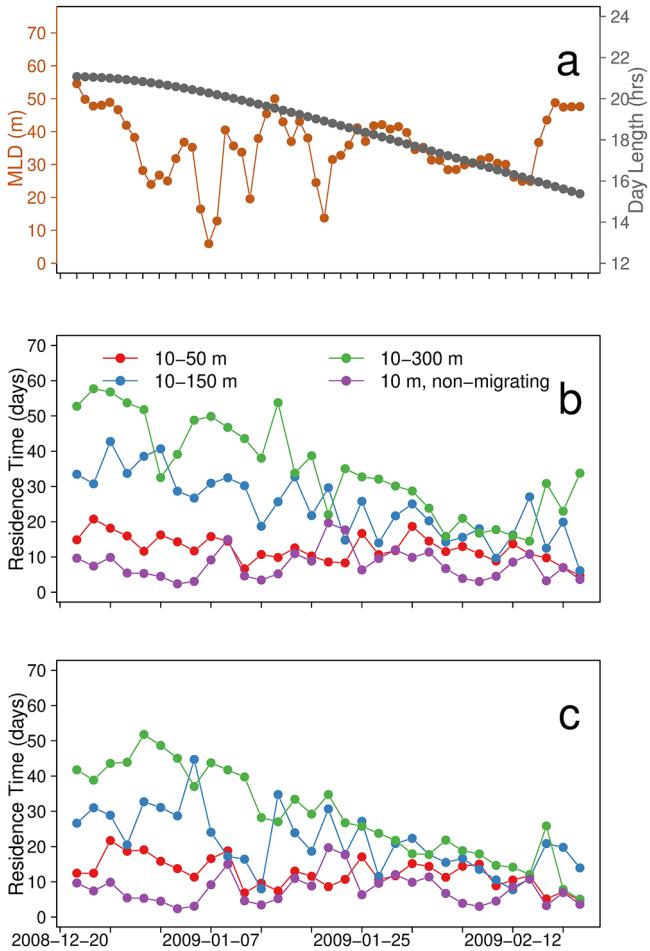

Figure 5. Time series of mixer layer depth (orange) and day length (gray) (a); and residence times of simulated migrating particles at 0.016 m s^{-1} (b) and 0.03 m s^{-1} (c) compared to residence times of simulated nonmigrating particles released at 10 m when the subsurface eddy is most coherent in the austral summer.

zooplankton, the differences in residence times of simulated migrating zooplankton between the three regions increased with migration depth (Figure 4b). In these regions, residence times were ~10 days on the Coast of Anvers Island, and less than 5 days on the continental shelf (Figure 4b).

In ROMS, MLD over PDC was ~36 m on average during the study period, but was highly variable, especially in late December and late February (Figure 5a). DL decreased from 21 to 15 hr over the course of the modeled study period (Figure 5a). Residence times for simulated zooplankton migrating to 150 and 300 m declined gradually at both swimming speeds over the study period (Figures 5b and 5c). For late December releases, residence times ranged between 38 and 57 days for zooplankton migrating to 300 m and 20–42 days for particles migrating to 150 m (Figures 5b and 5c). This gradually declined to 7–30 days for releases at both swimming speeds and migration depths in the second week of February (Figures 5b and 5c). The declines in residence times correspond to the gradual decline in DL over the study period (Figure 5).

Residence times for simulated zooplankton migrating to 50 m were relatively stable at ~15 days but also eventually declined to just under 5 days (Figures 5b and 5c). Residence times of nonmigrating zooplankton released at 10 m were highly variable, ranging between 2 and 19 days (Figures 5b and 5c). There were periods in late December to early January and early February where these residence times were much lower than those of zooplankton migrating to 50 m at both swimming speeds. There were also releases in which these residence times were similar throughout January (Figures 5b and 5c).

3.3. Effect of MLD and DL on Residence Times of Simulated Zooplankton

Across all models, MLD had a negative relationship and DL had a positive relationship with residence times (Figure 6; Table 1). When simulated zooplankton migrated to 50 m, the residence times decreased by approximately 0.5 (±0.1) days (Table 1) for each meter the mixed layer deepened. Residence times increased by a similar magnitude, 0.5 (±0.28) days, for every additional hour of daylight when migrations were shallow (Table 1). When simulated zooplankton migrated to 150 m, residence times decreased by 0.7 (±0.4) days for every meter MLD deepened (Table 1). Residence times for simulated zooplankton migrating to 150 m increased by 2.4 (±0.8) days for every additional hour of daylight (Table 1). When simulated zooplankton migrated to 300 m, residence times decreased by 0.6 (±0.1) days for every meter MLD deepened and increased by 8.3 (±0.6) days for every hour DL increased (Table 1; Figure 6). Together, these variables explained nearly all variance present for the deepest migrations (Table 1).

4. Discussion

Biological hotspots can be functionally important regions in the life history of species, particularly for central place foragers who depend on the availability of food resources within range of their colonies while raising their offspring (Hazen et al., 2013 and sources therein). Understanding the mechanisms that sustain these critical areas will not only inform management decisions about these regions and the organisms they support, but also improve predictions about how they will shift under future climate change scenarios (Hazen et al., 2013).

One such biological hotspot exists in and around PDC. This region is highly productive in the austral summer, attracting prey species such as euphausiids and fish, which provide a critical food source for higher trophic levels (Carvalho et al., 2016; Kavanaugh et al., 2015; Schofield et al., 2013). Glider and satellite observations from PDC and the surrounding area suggested that the upwelling of warm, nutrient-rich subsurface water due to the presence of PDC was responsible for driving the increased primary production in the area (Kavanaugh et al., 2015;

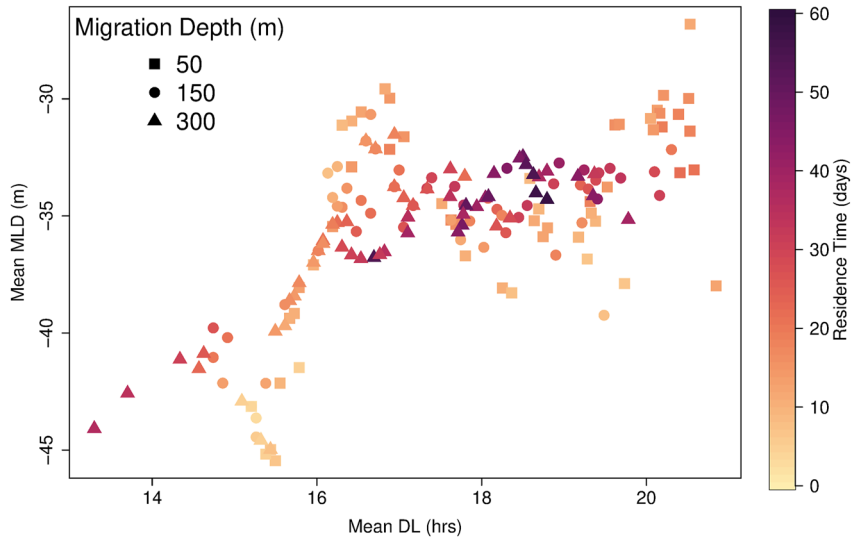

Figure 6. Residence time in days (color) as a function of mean mixer layer depth (m) and mean day length (hours) for particles migrating between 10 and 50 m (square), 10–150 m (circle), and 10–300 m (triangle) at both 0.03 m s^{-1} and 0.016 m s^{-1}.

Schofield et al., 2013). However, a lack of seasonal upwelling in long-term observations (Carvalho et al., 2016; Hudson et al., 2019), low surface residence times (Kohut et al., 2018), and a lack of physiological response in surface phytoplankton populations to this nutrient-rich water (Carvalho et al., 2020) suggest that upwelling is likely not driving this hotspot.

Observations of isopycnal doming within the canyon suggest that a subsurface eddy exists (Hudson et al., 2019). ROMS simulations also show a recirculating, subsurface eddy persisting over PDC in the austral summer (Movie S1 in Supporting Information S1; Hudson et al., 2021). Simulated nonmigrating zooplankton releases in this feature indicate that residence times increase significantly with depth, with median residence times as high as 175 days at 150 m during the austral summer (Hudson et al., 2021). Zooplankton have been observed at 300 m depth around PDC and these populations perform DVM between near-surface and these deep waters (Conroy et al., 2020; Espinasse et al., 2012; Komoda & Mizunuma, 2019). If zooplankton populations, which are a critical food source within PDC, are performing DVM, they are most likely interacting with the subsurface eddy, which could facilitate retention within and near the hotspot, thus potentially increasing zooplankton concentrations and availability to the food web in PDC. To examine this idea, we used ROMS to test how DVM impacts retention within PDC. We tested the hypotheses that (a) DVM increases simulated zooplankton residence times over PDC due to the presence of the subsurface eddy; and (b) the depth of the MLD above the subsurface eddy and DL have significant impacts on residence times of migrating zooplankton by modulating the amount of time spent within the subsurface eddy.

Table 1
Results From Weighted Least Squares Regressions on the Effect of Mixed Layer Depth and Day Length on the Residence Times (in Days) of Simulated Zooplankton Migrating to Three Depths Over Palmer Deep Canyon

Migration depth (m)	Model terms	Slope	Standard error	t-value	Model R^2
50	MLD (m)	−0.52	0.10	−4.95	0.48
	DL (hrs)	0.46	0.28	1.67	
150	MLD (m)	−0.74	0.40	−1.85	0.33
	DL (hrs)	2.43	0.77	3.17	
300	MLD (m)	−0.57	0.13	−4.50	0.94
	DL (hrs)	8.33	0.60	13.94	

Note. Migration speeds were pooled in these models.

4.1. Effect of DVM on Residence Time

Residence times of simulated zooplankton over PDC increased with deeper migrations, supporting our hypothesis that DVM increases residence times relative to near-surface zooplankton. While DVM also helped increase residence times of simulated zooplankton in other adjacent coastal regions, the increases with depth were greatest in PDC. This suggests that the presence of PDC, and the subsurface retentive eddy, is the major driver of the high retention of simulated zooplankton in this region.

The presence of DVM alters residence times relative to nonmigrating zooplankton because migrators experience strong vertical shear in current velocities in comparison to nonmigrators. Mean ROMS surface current velocities over PDC are faster and more variable than deeper waters (Figure S1 in

Supporting Information S1). Mean velocities at 300 m increased slightly in comparison to currents at 50 and 150 m (Figure S1 in Supporting Information S1). We hypothesize this is due to near-canyon rim effects at depth since the rim (upper limit of the canyon bathymetry) of the canyon is approximately 400 m deep. Previous studies of shelf-break canyons have illustrated strong flows above the rims of the canyons due to strong geostrophic and baroclinic flows (Allen et al., 2001). This can occur due to strong vorticity resulting from water column stretching. While not a shelf-break canyon like those modeled by Allen et al. (2001), PDC likely has similar effects on local subsurface currents.

Previous glider measurements suggest that near-surface (0–10 m) water properties are not dependent on proximity to PDC while mid-water properties (90–100 m), below the typical seasonal MLD, are dependent on the presence of PDC (Hudson et al., 2019). Hudson et al. (2019) hypothesized that PDC is a two-layer system consisting of a rapidly moving surface layer, and a more consistent subsurface layer shaped by the canyon. Previous estimates of residence times of nonmigrating, neutrally buoyant particles at different depths suggest that residence times shallower than 50 m do not differ significantly from each other, but are statistically different from residence times deeper than 50 m (Hudson et al., 2021). This suggests that the boundary between these layers may be at approximately 50 m (Hudson et al., 2021). This could explain why residence times of particles migrating to 50 m were not much different from those remaining near the surface. Higher residence times when migrations occurred down to 150 and 300 m suggest that migrating out of this layer and into the subsurface eddy increases the relative importance of this feature.

4.2. Effect of MLD and DL on Residence Time of Simulated Zooplankton

MLD and DL strongly predicted residence times of migrating simulated zooplankton over PDC. The influence of MLD suggests that migrating out of the surface mixed layer is important to increasing residence times of migrating zooplankton. Residence times were greatest in the presence of shallower MLD, supporting our hypothesis that a thinner surface layer, indicated by a shallower MLD, increases migrating zooplankton residence times. Importantly, ROMS predicts deeper MLD and less stratification during the summer in PDC (Hudson et al., 2021; Wang et al., 2022). A shallower, more stratified surface ocean means that it is more isolated from deeper water masses. If the surface layer is more isolated from depth, highly variable winds and other surface forcing mechanisms would introduce additional variability to the surface, increasing the ability of the subsurface eddy to retain migrating zooplankton in the region. Increased DL resulted in higher residence times, especially for deep migrators, supporting our hypothesis. Longer days meant simulated migrators spent more time at depth, where residence times are higher than in surface waters. Shorter days, and corresponding longer nights, resulted in less time spent in the subsurface retentive layer and more time spent within the rapidly moving surface mixed layer where residence times are low (Hudson et al., 2021; Kohut et al., 2018), thus decreasing residence times.

Decreasing DL over the study period likely is the major driver of the decreasing residence times observed in simulated zooplankton, especially when migrating to deeper depths. WLS regressions suggest that decreasing DLs by one hour would decrease residence times by 2.4 and 8.3 days for particles migrating to 150 and 300 m, respectively. Over the study period, DL decreases by approximately 6 hr, which suggests that residence times for organisms migrating to 150 and 300 m should decrease by approximately 15 and 50 days, respectively. Residence times decreased on the same order of magnitude as the model predicts for deeper migrations, suggesting that DL was the major driver of the residence times observed throughout the simulations.

4.3. Direct Observations of DVM

Echo sounder observations on two subsurface moorings showed the extent of DVM in zooplankton populations in and around PDC in the austral summer of 2020. The subsurface moorings documented DVM with maximum migration depths between 50 and 300 m (Figure 3a). This is similar to our simulated DVM depth ranges and also similar to other previously published results (Atkinson et al., 1992a, 1992b; Cisewski et al., 2010; Conroy et al., 2020; Demer & Hewitt, 1995; Espinasse et al., 2012; Perissinotto & McQuaid, 1992). While observed migrating speeds were smaller than modeled swimming speeds (Figure 3b), the range of migration speeds observed cover the speeds used in our simulations. This supports our hypothesis that DVM is present in local zooplankton populations in the PDC. Therefore, we believe that these observations show that the DVM behaviors modeled here are realistic.

Migration between 10 and 50 m was the most common migration observed in subsurface mooring data. Our simulations suggest, however, that this migration would only increase median residence times by approximately 4 days in comparison to near-surface residence times. This suggests that the zooplankton performing this shallower migration may not be retained over PDC in comparison to deeper migrators. However, because the MLD plays a role in determining residence time, differences between ROMS modeled MLD and actual MLD could play an important role in interpreting these results. If summer MLDs are shallower than the model predicts (Hudson et al., 2021; Wang et al., 2022), real migrating zooplankton over PDC may spend less time in the low residence time surface layer compared to our simulations. Therefore, the observed migrations to 50 m may still result in increased residence times, however, MLD predictions by ROMS need to be improved to test this hypothesis.

Migrations down to 300 m, which produced the highest residence times in our simulations, were present, but were not observed as frequently as migrations down to 50 m by the subsurface moorings. This suggests that at least a portion of the local migrating zooplankton is being retained for nearly 30 days over the PDC and could serve as a resource for local predator populations. Identifying these deep migrators, and increasing our understanding of DVM in this system, is critical to understanding if this interaction between DVM and the subsurface eddy may drive the biological hotspot adjacent to PDC.

4.4. Limitations of DVM Simulations

Our simulations suggest that zooplankton performing DVM may be retained within PDC, and that these residences times are driven by changes in MLD and DL. However, these simulations make two major assumptions about zooplankton behavior. First, they assume that zooplankton are passive drifters in the horizontal and only swim in the vertical. This is a common assumption in krill distribution modeling studies (Cleary et al., 2016) and horizontal advection has been suggested as one of the major drivers of zooplankton distributions (Bernard et al., 2017; Bernard & Steinberg, 2013; Schofield et al., 2013). While zooplankton are treated as passive drifters in the horizontal due to their low to moderate Reynolds numbers, this assumption ignores any predator avoidance or feeding behaviors that may affect distributions in the water column or migration distances (Cleary et al., 2016; Zhou & Dorland, 2004). For certain species, the depth of the chlorophyll maximum plays a role in the depth of DVM (Conroy et al., 2020). If, for example, zooplankton migrated to a minimum depth of 50 m to feed on a deeper chlorophyll maximum layer, rather than migrating to 10 m, we would predict that residence times of migrators would increase since residence times at 50 m are greater than those at 10 m.

The second assumption is that zooplankton consistently migrate to fixed depths within PDC. While we showed that zooplankton perform DVM to the simulated depths around PDC, they may not consistently migrate to these depths. A variety of factors, including food availability (Berge et al., 2014), photoperiod (Cohen & Forward, 2005), ontogeny (Hays, 1995), and predation pressure (Cresswell et al., 2009; Tarling et al., 2002) may lead to inconsistent DVM. *In-situ* observations of euphausiids suggest that they can perform two migrations during the night – one early in the night and another closer to dawn (Tarling & Johnson, 2006; Tarling & Thorpe, 2017). Between these "twilight" migrations, euphausiids swim or sink downwards while they digest their meal, and then return to the surface just before dawn to feed again (Tarling & Johnson, 2006; Tarling & Thorpe, 2017). Migrations similar to "twilight" migrations were occasionally observed by the subsurface moorings, with a portion of zooplankton migrating down to their maximum depth, usually ~300 m, around solar midnight (Figure 3c), so this behavior could potentially increase retention within PDC by increasing the time spent away from the rapidly moving surface.

Calanoid copepod species along the WAP can perform reverse DVM – spending days in the surface and nights at depth when predation risk is highest near the surface at night rather than during the day (Conroy et al., 2020). If more zooplankton species performed this behavior, we would expect residence times to be lower than what we report here, since more time during the summer months would be spent in the rapidly moving surface layer. Reverse DVM by euphausiids, including larval krill, has been observed in the Scotia Sea (Tarling et al., 2018) but is rarely close to the shore so euphausiid residence times in PDC are less likely to be impacted (Klevjer et al., 2010). This behavior was not observed by the subsurface moorings, so it is unlikely that reverse DVM is present and impacting local zooplankton retention near PDC.

Observations along the WAP suggest that some zooplankton, including the euphausiids *T. macrura* and *E. crystallorophias*, decrease DVM at the peak of the austral summer (Conroy et al., 2020). Studies from the Scotia Sea

suggest that euphausiids stop performing DVM entirely, instead remaining closer to the surface during the peak of the austral summer to feed throughout the diel cycle, with DVM increasing in the austral spring and fall (Cisewski et al., 2010; Tarling et al., 2018). There were days in the sampling period where no DVM was observed by the subsurface moorings. Therefore, in the absence of DVM, retention would depend entirely on the depth where zooplankton reside. Zooplankton that remain in deeper waters would be retained longer than those that remain near the surface. While zooplankton DVM near and around PDC has been documented elsewhere, including near PDC (Espinasse et al., 2012; Kane et al., 2018; Komoda & Mizunuma, 2019; Nowacek et al., 2011), more thorough investigations of zooplankton DVM near biological hotspots are needed to understand how they could interact with subsurface retentive flows like that in PDC.

4.5. Implications for PDC and Other Similar Systems

Our study suggests that residence times of simulated zooplankton performing DVM would increase in comparison to nonmigrating zooplankton near the surface. While our simulations are of a simplified, idealized version of DVM, they suggest that if zooplankton perform DVM in PDC, they would be retained within the system for up to 30 days. Retention was variable through the austral summer. Our simulations suggest that retention of simulated zooplankton migrating below 150 m would be greatest in the austral summer (December–January) if surface mixed layers, where residence times are low (Kohut et al., 2018), were shallow, and days were long, with zooplankton spending more time at depth. At the end of the austral summer (February), decreasing DLs result in lower residence times, regardless of migration depth.

Mooring observations illustrate that zooplankton are present, and perform DVM to the depths simulated here. Therefore, we suggest that migrations into the subsurface eddy have the potential to be critical to local zooplankton retention. Furthermore, our study suggests that zooplankton DVM into the subsurface eddy present over PDC in the austral summer has the potential to link the subsurface eddy to the upper trophic levels that rely on the biological hotspot in and around PDC. We hypothesize that this increased retention of critical food resources over PDC could have positive impacts on the nearby biological hotspot by accumulating often sparse resources into a region that is within the foraging ranges of local predator species (Figure 1b; Cimino et al., 2016; Oliver et al., 2013; Pickett et al., 2018). Better definitions of DVM, especially in krill, in this system are necessary to understand if the interaction of the retentive subsurface eddy and zooplankton DVM is a driving feature of the biological hotspot near PDC.

Beyond potentially retaining critical resources near or within predator foraging grounds, the retention of zooplankton within PDC may be beneficial to the zooplankton themselves. PDC is considered a biological hotspot not only due to the high abundance of higher trophic level predators, but also due to high chlorophyll concentrations during the austral summer (Kavanaugh et al., 2015; Kohut et al., 2018; Schofield et al., 2018). Therefore, zooplankton would be retained in an area with abundant food resources. However, it is unclear if the benefits of being retained within this region with high phytoplankton biomass outweigh the risks associated with being retained within and adjacent to predator foraging grounds.

Retention of zooplankton within the subsurface eddy over PDC may also play a critical role in carbon cycling within the region. Mesoscale eddies have been hypothesized to be important carbon sinks, and that the role these features play in carbon cycling is highly dependent on the zooplankton communities they retain (Christiansen et al., 2018; Kwong et al., 2020). More work is necessary to determine if the subsurface eddy over PDC has any impact on the local carbon cycle and if it retains zooplankton communities that allow it to act as a carbon sink.

We used PDC to examine how subsurface circulation features can increase the residence times of organisms that perform DVM. However, it is unlikely that the processes described here are unique to PDC. Shallow surface mixed layers, as proxied by MLD, and long days may control retention in other systems. While we have used an example of a closed, recirculating subsurface eddy, the subsurface features that help increase retention of migrating zooplankton do not necessarily need to be closed, recirculating features. In coastal upwelling regions, these features can be a deep return flow that is opposite in direction to surface flows, thus reducing the net horizontal movement of migrators and retaining them within the system (Peterson, 1998). The thickness of the surface mixed layer and the subsurface layer also play a role, with shallower mixed layers increasing residence times of migrating particles by decreasing the migration distance necessary to move into the retentive subsurface layer. DL will alter DVM timing, and thus control the amount of time spent at depth. However, this phenomenon may be

unique to high latitudes where DLs are highly variable and have been shown to impact zooplankton DVM behavior (Conroy et al., 2020). Zooplankton interacting with both near-surface and subsurface circulation features via DVM has the potential to be the key to the establishment and persistence of biological hotspots worldwide, by increasing the residence times of zooplankton populations that serve as persistent food sources for higher trophic levels.

Data Availability Statement

Tracks from ROMS particle simulations (Dinniman et al., 2022) and mooring data (Kohut et al., 2022) are archived at BCO-DMO at http://www.bco-dmo.org/project/850844.

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