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RESEARCH ARTICLE OPEN ACCESS

Variability in Overwinter Antarctic Krill Transport Pathways and Connectivity in the South-West Atlantic Sector of the Southern Ocean

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Received: 19 April 2026 | **Revised:** 7 August 2026 | **Accepted:** 11 August 2026

Keywords: Antarctic krill | diel vertical migration | ecological connectivity | interannual variability | Lagrangian particle tracking | ocean currents | sea ice

ABSTRACT

Antarctic krill are central to the Southern Ocean ecosystem and support a commercial fishery. Late larval stages of Antarctic krill depend on sea ice for food and shelter during winter. As climate change alters sea ice habitats and polar ecosystems, understanding krill transport and retention is essential for ecosystem-based fishery management. These late-stage larvae have been observed to perform reverse diel vertical migration (DVM), moving from beneath the sea ice during the day to the upper water column at night. Variability in ocean currents and sea ice drift, together with behaviours such as DVM, can strongly influence krill transport and retention. To investigate the impact of this behaviour, we conducted Lagrangian particle tracking experiments using 32 years of daily sea ice and ocean velocities from a 0.1° global ocean–sea ice model (ACCESS-OM2-01). Virtual particles were released in the south-west Atlantic sector of the Southern Ocean and tracked over winter (April–October), a key period prior to spring recruitment. To assess sensitivity to DVM, we applied five scenarios in which particles spent different proportions of each day influenced by ocean currents and sea ice drift under sea ice. Transport driven solely by ocean velocities resulted in the highest proportion of particles on the Antarctic Peninsula shelf by winter's end, with low interannual variability (55.5% ± 7% of released particles). Increasing exposure to sea ice drift reduced shelf retention and increased variability (33.6% ± 10.9%). Our results show that including sea ice interactions enhances overwinter connectivity from the Antarctic Peninsula to South Georgia and between management areas, highlighting sea ice-driven northward transport of young krill. As krill depend on declining sea ice habitats, connectivity across the Antarctic Peninsula and Scotia Sea may shift in the future. Understanding interannual transport variability between fishing regions improves stock assessment and supports sustainable management.

1 | Introduction

In the Southern Ocean, Antarctic krill (*Euphausia superba*; hereafter krill) are an integral part of the marine ecosystem, playing a crucial role in the food web (Murphy et al. 2016, 2007; Trathan and Hill 2016). They are the target of the Southern Ocean's largest fishery (Nicol and Foster 2016) and play an important role in nutrient cycling and sequestration of carbon (Cavan et al. 2019). Large fluctuations in krill biomass driven by environmental factors, including sea ice variability (Murphy et al. 2007), can exert bottom-up control on dependent predators (Trathan and Hill 2016). The primary driver of interannual krill abundance and population dynamics is krill recruitment, defined as the survival of krill to a year old

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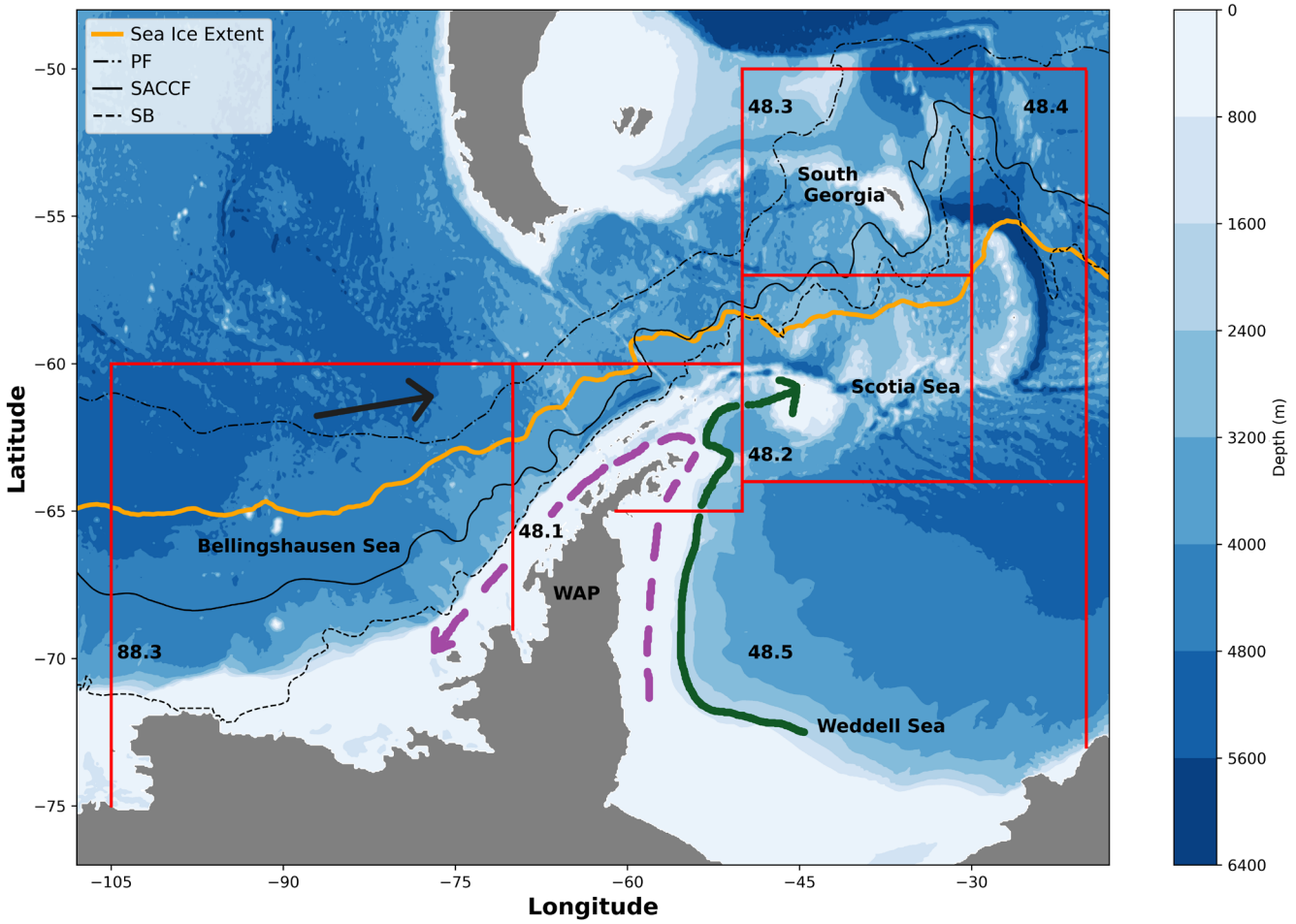

FIGURE 1 | Bathymetric map of the south-west Atlantic sector showing CCAMLR Subareas 48.1–48.5 and 88.3 (red outlines). The orange line represents the climatological August sea ice edge (15% concentration) averaged over 1987–2018 from the ocean–sea ice model. Major oceanographic fronts of the ACC are shown, including the Polar Front (PF), the Southern Antarctic Circumpolar Current Front (SACCF) and the Southern Boundary of the Antarctic Circumpolar Current (SB) (Orsi et al. 1995). The black arrow indicates the direction of the flows associated with the ACC fronts. The schematic incorporates additional key oceanographic features from previous studies, with the green line representing the Antarctic Slope Current (ASC; Dawson et al. 2023; Thompson et al. 2018; Young et al. 2024) and the dashed magenta line depicting the Antarctic Coastal Current (ACoC; Dawson et al. 2023). The Bellingshausen Sea, Scotia Sea, South Georgia, Weddell Sea and WAP are indicated. Model bathymetry is shaded in metres.

(Quetin and Ross 2003). Determining drivers of krill recruitment is essential for unravelling the environmental mechanisms that govern krill populations (Meyer et al. 2020; Veytia et al. 2021).

The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) and the Scientific Committee on Antarctic Research Krill Expert Group (SKEG) have highlighted the need for a krill stock hypothesis to guide management of the Antarctic krill fishery (Meyer et al. 2025). This conceptual model describes krill population dynamics, including spawning, recruitment, dispersal and movement. Our study addresses key knowledge gaps by examining how krill are distributed by ocean and sea ice velocities and how connectivity (movement between regions and transit time) responds to environmental factors using particle tracking experiments. The commercial krill fishery is currently limited to the south-west Atlantic sector of the Southern Ocean (Meyer et al. 2025), within CCAMLR Area 48, which is divided into five management areas (Figure 1). Previous studies have explored krill transport pathways and interannual variability in this region (Gallagher et al. 2023; Mori et al. 2019; Murphy et al. 2004; Piñones et al. 2013; Sylvester et al. 2026; Thorpe et al. 2004, 2007; Veytia et al. 2021; Young et al. 2014, 2024). This study builds on previous work by incorporating ocean and sea ice velocity fields to examine the effect of diel vertical migration (DVM) behaviour on transport pathways, and to evaluate the resulting implications for krill fishery management in the south-west Atlantic.

To manage a fishery, it is important to understand the distribution of new recruits, as well as the processes that influence their survival and successful development (Meyer et al. 2020). Krill spawn during late austral spring and summer. The embryos sink before hatching at depth (Siegel 2005). On hatching, the larvae ascend towards the surface and develop through multiple stages before overwintering, eventually transitioning into juveniles that join the adult population (Kawaguchi 2016; Siegel 2005). Successful recruitment is therefore defined as the proportion of individuals that survive these early life stages and are

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incorporated into the population in the following spring (Meyer et al. 2017; Siegel 2005). The success of recruitment, and the resulting seasonal and interannual variability in krill distribution and abundance, is influenced by a range of factors, including the magnitude and timing of krill inputs, local environmental conditions and oceanographic features (Hofmann et al. 1998; Murphy et al. 2004; Thorpe et al. 2007). Because local current speeds often exceed the swimming capacity of late-stage larval krill, their movement and distribution are largely governed by prevailing ocean currents, and they are therefore commonly represented as passive particles in modelling studies (Murphy et al. 2004, 2007; Thorpe et al. 2007).

The tip of the Antarctic Peninsula has been identified as the main recruitment hotspot for krill in the south-west Atlantic region (Atkinson et al. 2017, 2019). Understanding transport within and from this area is therefore critical. Larvae need to find suitable overwintering regions (Meyer et al. 2020), and regional circulation along with key oceanographic features strongly influence their dispersal. Along the Antarctic Peninsula, the Antarctic Coastal Current (ACoC), a shallow and fast-flowing westward current (Heywood et al. 2004), flows along the tip of the Antarctic Peninsula into the Bransfield Strait (Moffat and Meredith 2018) and continues across the western Antarctic Peninsula (WAP) region (Schubert et al. 2021). In the adjacent Weddell Sea, the Antarctic Slope Current (ASC) also flows westward and then northward along the continental slope (Azaneu et al. 2017), transporting water into the Scotia Sea (Thompson et al. 2009) and subsequently towards South Georgia. However, the ASC is absent around the WAP and the Bellingshausen Sea. In these regions, circulation near the continental shelf is instead influenced by the eastward-flowing Antarctic Circumpolar Current (ACC; Smith et al. 1999). The ACC is characterised by several fronts, among which the Southern ACC Front (SACCF) and the Southern Boundary (SB) are particularly important for transport from the Antarctic Peninsula towards South Georgia (Orsi et al. 1995). Despite this strong influence, ocean circulation is not the only physical driver affecting krill distribution.

Krill larvae are closely associated with sea ice at winter onset, which strongly shapes their distribution, recruitment and population dynamics (Quetin and Ross 2001, 2003; Thorpe et al. 2019). Sea ice can be crucial for larvae, providing refuge from predators (Meyer et al. 2017) and serving as a vital winter food source in the algae that grow on its underside for krill who lack lipid reserves (Arrigo 2014; Kohlbach et al. 2017; Meyer et al. 2017; Schmidt et al. 2014). While krill are thought to rely on ice algae to meet overwinter energy demands under favourable sea ice conditions (Bernard et al. 2019), this dependency remains debated, with some studies suggesting that krill may persist through winter without direct reliance on ice algae (Walsh et al. 2020). The motion of sea ice is influenced by a combination of ocean currents and winds, resulting in a pattern of movement that is distinct from the ocean velocities underneath (Steele et al. 1997). Large-scale climate patterns influence sea-ice distribution near the Antarctic Peninsula, which exhibits significant interannual variability. Ocean–ice–atmosphere interactions further amplify warming, contributing to additional variability in the region (Murphy et al. 1995, 2014; Stammerjohn et al. 2008; White et al. 1996). The close association of late larval krill with sea ice means that both ocean currents and sea ice movement can play an important role in their transport (Murphy et al. 2004; Thorpe et al. 2007; Young et al. 2024).

Understanding krill distribution and connectivity in the CCAMLR management areas is crucial not only for developing a stock hypothesis, but also for supporting the long-term survival of the species under rapid climate change. The sensitivity of sea ice to global warming, particularly the recent reduction in its extent (Gilbert and Holmes 2024; Purich and Doddridge 2023), could have profound implications for polar ecosystems (Abram et al. 2025; Doddridge et al. 2025; Meredith et al. 2019). While the krill stock hypothesis provides a framework for management of the krill fishery, the hypothesis must also account for climate-driven changes in sea ice, ocean circulation and productivity that are reshaping the Southern Ocean. To support this, we focus on key aspects of connectivity during the winter period, including: (i) on-shelf and off-shelf transport processes, and (ii) krill flux dynamics within CCAMLR Area 48 and the neighbouring subarea to the west, Subarea 88.3, which may serve as a source region for krill populations along the Antarctic Peninsula (Bahlburg et al. 2023; Piñones et al. 2013).

2 | Methods

2.1 | Model Description

To investigate transport of larval Antarctic krill, we use a Lagrangian particle tracking scheme (see Section 2.2). The daily velocity fields used for this particle tracking were obtained from the 0.1-degree configuration of the Australian Community Climate and Earth System Simulator Ocean Model (ACCESS-OM2-01; Kiss et al. 2020). ACCESS-OM2-01 is a global ocean–sea ice coupled model comprising version 5.1 of the Modular Ocean Model (MOM5; Griffies 2012) and version 5.1.2 of the Los Alamos sea-ice model (CICE; Hunke et al. 2015). We used a simulation forced by a prescribed atmosphere for the period 1958–2018, obtained from the 55-year Japanese Reanalysis for driving ocean–sea ice models (JRA55-do; Tsujino et al. 2018). Our study uses 32 years of daily sea ice and ocean velocities for the period 1987–2018. The model used an Arakawa B-grid configuration and has 75 vertical levels. Although ACCESS-OM2-01 lacks data assimilation and underestimates Antarctic summer sea ice extent (Kiss et al. 2020), the model performs well in simulating winter Antarctic Sea ice extent, the marginal ice zone and the timing of the seasonal cycle of the sea ice, capturing key features relevant for ecological assessment focused on winter processes (Fierro-Arcos et al. 2023).

2.2 | Lagrangian Simulations

Lagrangian simulations allow for virtual particles to be tracked within the flow fields of hydrodynamic models and thus provide insight into pathways and connectivity patterns in marine environments (e.g., Lange and Van Sebille 2017). We conducted Lagrangian particle experiments using the Parcels Lagrangian simulation framework version 3.1.2 (Delandmeter and Van Sebille 2019). Parcels employs a fourth order Runge–Kutta iteration scheme to advect virtual particles, in this study representing late-stage larval krill, using velocity fields from ocean

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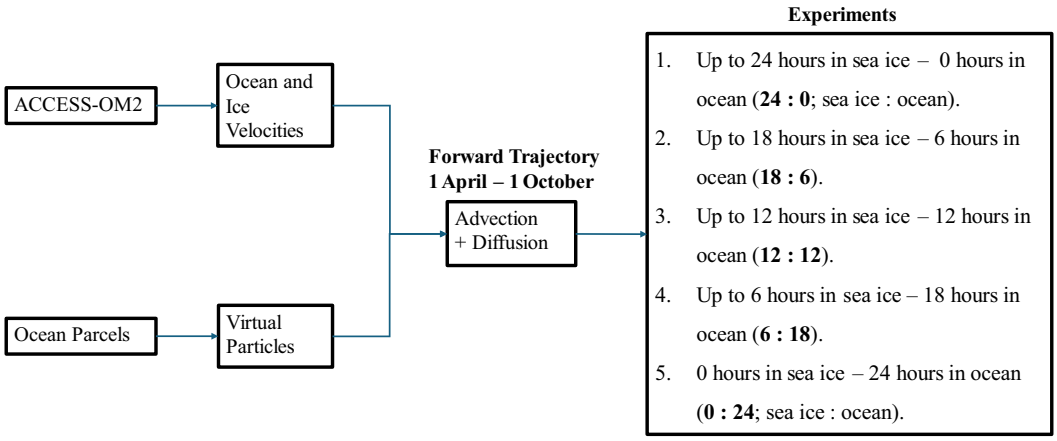

FIGURE 2 | Schematic outlining the experimental design for simulating virtual particle trajectories to represent the transport of larval Antarctic krill. Ocean and sea ice velocities were obtained from the ACCESS-OM2 model, and trajectories were computed using virtual particles in the Parcels Lagrangian simulation framework with an advection–diffusion scheme. Particles were first released on 1 April and tracked until 1 October. In subsequent simulations, releases occurred daily between April and May, with all trajectories integrated until 1 October. Five experiments were performed that varied the daily time spent in sea ice versus the ocean, ranging from 24:0 to 0:24 h. Note that in all scenarios, particles will move with the sea ice while it is present (defined as sea ice concentration > 15%) but will revert to moving with the ocean if there is no sea ice at that time.

general circulation models. Horizontal diffusion was included in all simulations using a random-walk approach (Dyke 2001), with a diffusion coefficient of 10 $m^2 s^{-1}$ (Young et al. 2014), consistent with Southern Ocean observations (Sheen et al. 2013; Watson et al. 2013).

To assess krill transport and connectivity, particle trajectories were calculated with different DVM behaviours (Figure 2) within CCAMLR Area 48. Firstly, particle movement was simulated using ocean-only (referred to as 0:24 simulation; see below) velocity fields to represent transport at a fixed depth of 50 m. While the nearest model depth layer was centred on 48.9 m, we refer to it as 50 m for simplicity. Late-stage larval krill have been observed to migrate vertically through the upper 50–100 m of the water column in winter (Lascara et al. 1999). To test sensitivity to potential variability in krill behaviour and environmental conditions, pathways of particles were also assessed at depths of 100, 150 and 200 m. Across these depths, particle transport exhibited consistent spatial patterns, with only limited changes in particle distribution and pathway extent relative to 50 m. Consequently, the primary analysis focuses on the 50 m depth, which provides a conservative representation of near-surface transport, given that larvae generally remain within the upper ~20 m of the water column (Meyer et al. 2017). In our second approach, particles were transported with sea ice velocities (referred to as 24:0) whenever the modelled sea ice concentration was > 15% and with the ocean velocity fields at 50 m when sea ice concentration was at or below this threshold.

We conducted three additional DVM experiments whereby the particles spent varying durations of time in the ocean (at 50 m depth) and sea ice over a 24-h period to approximate different DVM scenarios (Figure 2). In our simulations, we assume a fixed DVM pattern, with krill ascending to the sea-ice layer near the surface during the day and descending at night to 50 m depth, regardless of daylight conditions. While light availability, which is the primary cue for DVM (Piccolin et al. 2020), varies across the release region and throughout the simulation period, our approach does not dynamically link migration timing to solar cues. The DVM experiments are referred to by the ratio of the hours spent moving with sea ice velocities to those spent moving with ocean velocities for 1 day (hence 0:24 is where the particles move only with ocean velocities and 6:18 means 6 h spent moving with sea ice velocities if sea ice is present and 18 h moving with ocean velocities).

2.3 | Particle Release Configurations

The key objectives of this study were to determine the dominant transport pathways around the WAP, both on and off the shelf, and connectivity in the vicinity of the Antarctic Peninsula and Scotia Sea over the winter period. Two sets of release configurations were used to address these objectives, as described below.

2.3.1 | On- and Off-Shelf Connectivity

To analyse on-shelf transport in the Antarctic Peninsula region, 10,000 particles were released within the 1000 m isobath in CCAMLR Subarea 48.1 (Figure 3a). Particles were released on 1 April, at the onset of austral winter, for each year from 1987 to 2018. The Lagrangian particle tracking, conducted with a time-step of 1 h, was integrated forward for 6 months until 1 October, coinciding with the retreat of sea ice and a critical period for krill recruitment (Meyer 2011). Particle locations were saved every 10 days during the simulation.

On-shelf retention was defined as the percentage of particles that were located on the shelf at the end of the simulations (i.e., on the 1st of October). This includes particles that exited and re-entered the shelf region (defined by the 1000 m contour) during the simulation. For each year, retention was calculated as the fraction of particles remaining within the 1000 m isobath on 1 October, and the annual values were then

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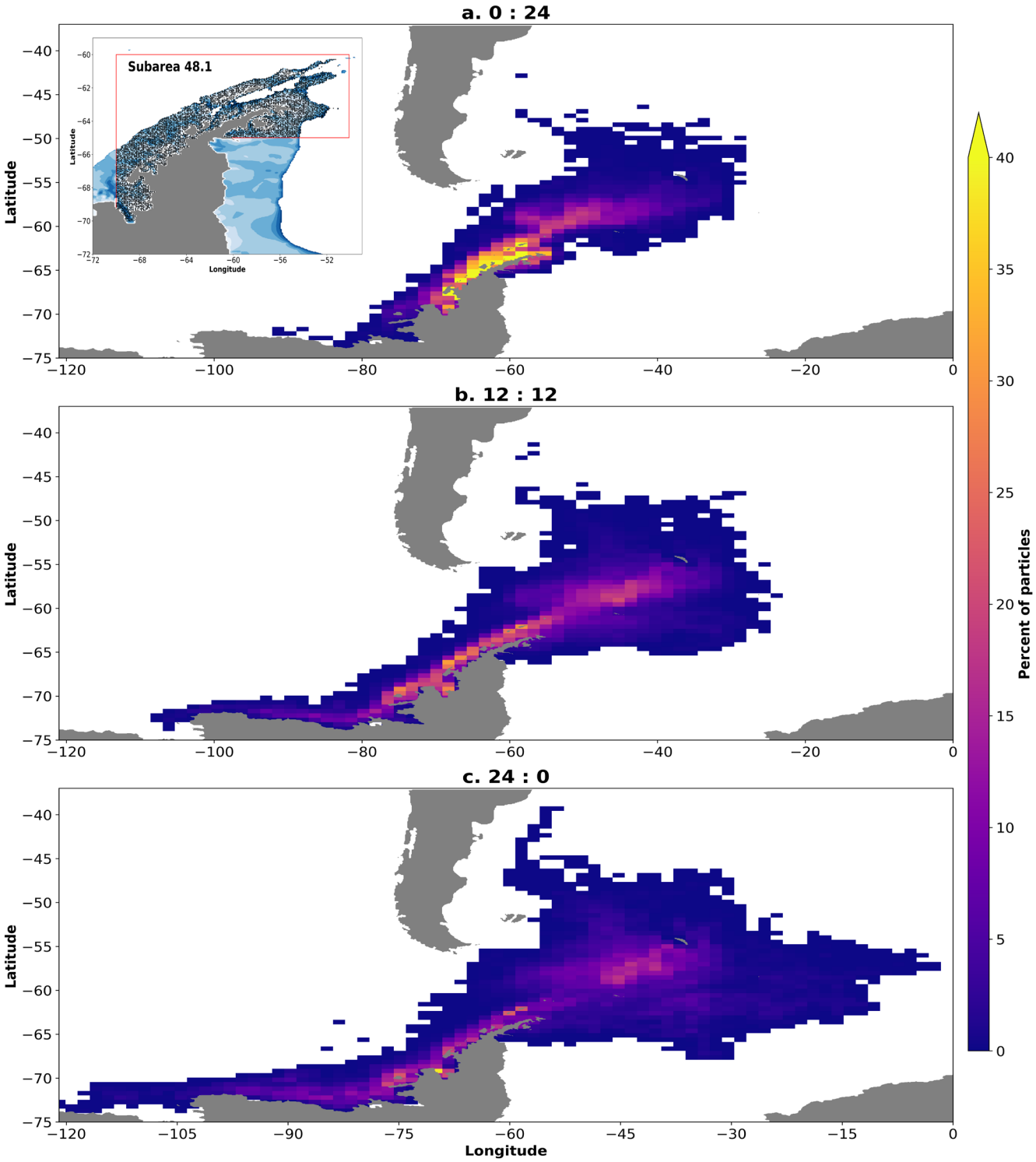

FIGURE 3 | Mean distribution of particles at the end of the winter simulations under different transport scenarios for particles released from the Antarctic Peninsula shelf in Subarea 48.1. Panel (a) shows the particle release locations and the 0:24 scenario, where particles spent 24 h in the ocean; (b) 12:12 indicates particles spent up to 12 h in sea ice and 12 h in the ocean; and (c) 24:0 indicates particles spent up to 24 h in sea ice. The plot shows the mean density of the end locations of particles on 1 October over the full 32-year study period (1987–2018). The colourbar indicates the percentage of total particles within each grid cell. Figure S1a–c presents the annual particle distribution from 1987 to 2018 for the three different scenarios which highlight interannual variability in the particle end locations.

averaged. Particles that were located outside the 1000 m contour on the 1 October were counted as off shelf (Figure 4). To quantify the predominant direction of particle movement, we analysed the final longitude of all particles at the end of the simulation period. Particles that were located west of 70° W were classified as westward transport into the Bellingshausen Sea, whereas those located east of 50° W were classified as eastward transport into the Scotia Sea and Weddell Seas,

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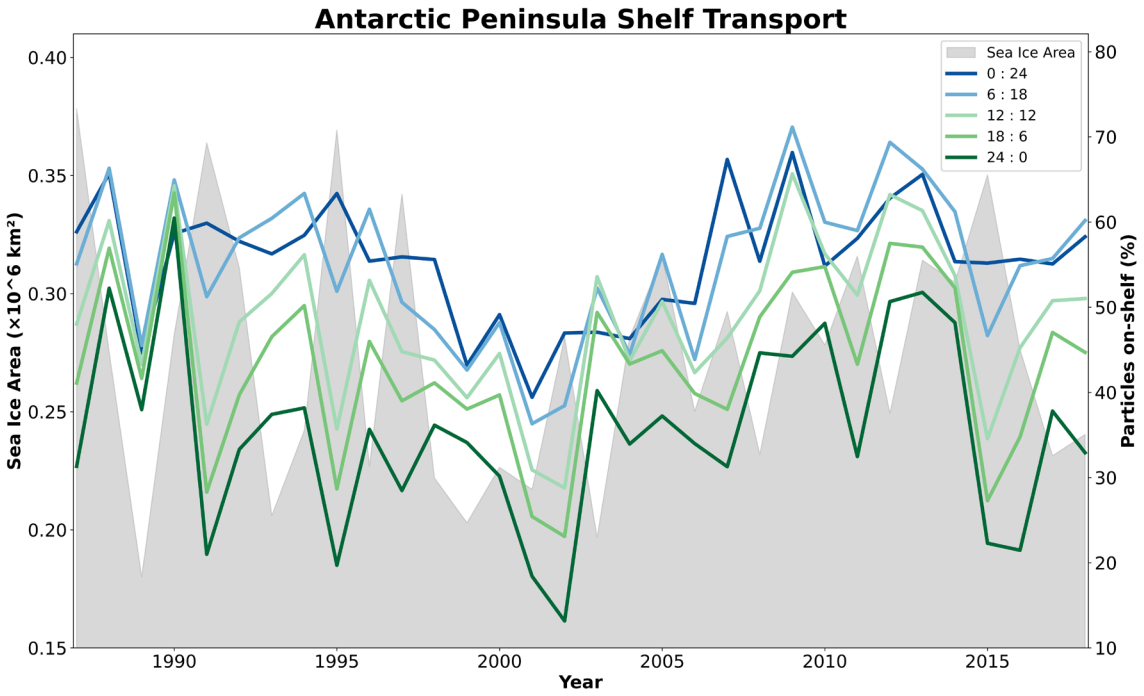

FIGURE 4 | On-shelf retention of simulated particles at the end of the winter period. Time series (1987–2018) showing the percentage of particles located on the Antarctic Peninsula shelf under different DVM scenarios (coloured lines). The shaded area shows total sea ice area in August of each year for Subarea 48.1 (red box in Figure 3a). Particle release locations are indicated in Figure 3a. Experiments represent the five DVM scenarios, with varying time spent moving with the sea ice versus the open ocean (0:24, 6:18, 12:12, 18:6, 24:0; hours per day moving with sea ice:ocean).

corresponding to the western and eastern boundaries of Subarea 48.1 (Figure 1). We also examined the end locations to determine how many particles reached South Georgia, as defined by a designated box surrounding the island. These analyses were conducted under three different advection scenarios (24:0, 12:12, 0:24) to quantify how varying DVM patterns influence large-scale dispersal and connectivity.

2.3.2 | CCAMLR Area 48 Connectivity

Our second aim was to understand the connectivity between different subareas in CCAMLR Area 48 and Subarea 88.3. To estimate the spatial and temporal dynamics of connectivity, particles were released daily over a 2-month period from 1 April to 31 May for the years 1987 to 2018. All particle trajectories were tracked until 1 October. Particles were uniformly distributed throughout each subarea to ensure comprehensive spatial coverage, with release locations chosen to evenly represent the full extent of each region other than for Subarea 48.5 where particles were released only in the northern half and Subarea 88.3 where particles were released in the eastern section. This decision reflects the observed krill density distribution reported by Atkinson et al. (2004), noting that the apparent absence of krill in the southern portion of Subarea 48.5 likely results from limited sampling rather than true absence. The primary focus of this study was Area 48; however, we also included the eastern region of Subarea 88.3, which includes the Bellingshausen Sea, an area that has been identified as a potential key location for krill spawning (Siegel and Watkins 2016). Particle trajectories were integrated forward in time using a Lagrangian timestep of 1 h, with positions recorded every 10 days. The particle locations on 1 October were analysed to quantify overwinter connectivity between subareas. In both release configurations, no mortality was applied and all particles survived throughout the simulations.

2.4 | Sea Ice Area

We analysed sea ice area data from the ACCESS-OM2 model for the years 1987–2018. For each year, we used the peak sea ice area, which in the model occurs in August, 1 month earlier than observed (Fetterer et al. 2017; Fierro-Arcos et al. 2023). Total sea ice area was calculated as the sum of sea ice concentration multiplied by grid cell area for the study region, and the mean sea ice edge was determined by applying a 15% concentration threshold. To calculate sea ice area specifically for Subarea 48.1, we extracted the portion of the ACCESS-OM2 sea ice data falling within the subarea boundaries. For each year from 1987 to 2018, we calculated the average sea ice area from 1 April to 1 October, capturing the seasonal ice conditions within the region.

3 | Results

3.1 | Wider Off-Shelf Dispersal of Sea Ice-Associated Particles

3.1.1 | Particle Hotspots

We begin by exploring the cumulative distribution of the final location of particles released from the Antarctic Peninsula shelf under three different behavioural scenarios from all 32 years of

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model simulations (Figure 3). In all scenarios, particles were found on the shelf at the end of the simulation, while others were transported into offshore regions during the winter period. However, as only final positions were analysed, this does not necessarily imply continuous retention on the shelf, and final distributions varied across the three scenarios. When particles were transported only with ocean currents (0:24), their final positions were largely concentrated along SB and on the shelf, with minimal dispersal into offshore areas. Particles originating in the Weddell Sea, near the eastern side of the Antarctic Peninsula, were transported westward by the ACoC into the Bransfield Strait or north-eastwards by the ASC, eventually becoming entrained along the SB.

In contrast, particles spending equal time in the ocean and sea ice (12:12) displayed broader dispersal, while those moving exclusively with sea ice (24:0) when sea ice was present exhibited the widest spatial extent, with final locations covering much of the Scotia Sea. In both of these scenarios, hotspots along the Antarctic Peninsula shelf and in the Bellingshausen Sea indicate strong westward transport. This suggests that sea ice velocities, driven by underlying ocean currents and wind, facilitate offshore transport while also promoting westward transport along the Antarctic Peninsula shelf towards the Bellingshausen Sea. Interannual variability in the timing of sea ice advance and retreat further shapes these hotspots, influencing both the extent and location of particle dispersal. These results suggest that while most particles moving with sea ice are transported far offshore, promoting long-range transport, a portion is retained on, or returns to, the shelf.

3.1.2 | Off-Shelf Dispersal

Across the 32-year simulation period, particles released on the continental shelf had a mean on-shelf retention of $55\% \pm 7\%$ when transported solely by ocean currents (Figure 4). Retention decreased when particles were advected with sea ice, with only $36\% \pm 11\%$ located on the shelf at the end of the simulations when transport occurred exclusively with sea ice.

In years with larger sea ice extent, particles moving with the ice were more widely dispersed, resulting in fewer particles retained on the shelf (e.g., 1995, 1997, and 2011; Figure 4). Conversely, in years with lower sea ice extent, particle retention on the shelf increased (e.g., 1990 and to some extent in 2003). These patterns were supported by a negative correlation between sea ice extent and particle retention ($R = -0.21$, $p = 0.24$). Although the correlation is weak, it suggests that increased sea ice coverage was associated with reduced shelf retention.

Incorporating sea ice-associated DVM into the experiments significantly influenced particle retention on the shelf ($p < 0.05$, one-way ANOVA; Table S1). Over the 32-year period, particles associated with sea ice were more widely dispersed, suggesting that prolonged interaction with drifting sea ice increases their spread across the shelf and surrounding waters. The Tukey test results indicate significant differences between most experiments, except for the comparisons between 12:12 and 18:6, and between 6:18 and 0:24, where retention did not differ significantly.

3.1.3 | East–West Transport

We observed a clear trend across all experiments that the proportion of particles transported out of Subarea 48.1, either to the west or the east, increased as particles spent more time associated with sea ice (Figure 5a). In the 0:24 scenario, only 4% of particles moved westward and 17% eastward. However, as particles begin to spend time moving with sea ice, the proportion of particles transported in both directions increases progressively, reaching 21% westward and 48% eastward for the 24:0 behaviour scenario. This pattern suggests that sea ice-related behaviour significantly influences particle transport.

Notably, the increase in eastward transport consistently outpaced westward movement across all scenarios, further emphasising the asymmetry in connectivity potential between the Bellingshausen and Scotia Seas. This dominance of eastward movement reflects the influence of the fast-flowing ACC, the eastward circulation of the northern limb of the Weddell Gyre and transport beneath the sea ice, contrasting with the relatively weaker and more localised westward coastal currents. In addition, stronger winter coastal easterly winds may enhance westward sea ice drift, reinforcing the role of sea ice-mediated transport in shaping particle pathways. Moreover, the variability observed across all scenarios demonstrates a strong link to interannual changes in sea-ice extent and ocean circulation patterns.

3.2 | Regional Connectivity

3.2.1 | South Georgia

The percentage of particles transported from the Antarctic Peninsula to South Georgia was strongly dependent on the behaviour scenario with longer time associated with sea ice resulting in more particles located in the vicinity of the island at the end of the winter (Figure 6). The mean proportion of particles reaching South Georgia under this scenario was $2.80\% \pm 2.44\%$. In comparison, advection solely by ocean velocities resulted in only $0.60\% \pm 0.33\%$ of particles at South Georgia at the end of winter.

The annual maximum sea ice extent strongly influences the proportion of particles reaching the South Georgia region between years. In 1997, when the August sea ice edge advanced well beyond the climatological mean (black line in Figure 6a), particle transport peaked with the 24:0 scenario showing the highest percentage of particles reaching South Georgia. The northward-advanced sea ice allowed particles to remain beneath the sea ice for a longer distance, allowing them to travel farther under sea ice before entering into open water and increasing their delivery to South Georgia. In contrast, 2003 was one of the years with low transport, coinciding with a much smaller sea ice extent and therefore limited sea ice-associated transport. Overall, the time series shows large year-to-year variability, with consistently higher particle transport in the 24:0 scenario ($R = 0.3$, $p = 0.1$), while the 0:24 scenario remained consistently low throughout the overwinter period, indicating that near-surface ocean circulation did not lead to high accumulation of particles at South Georgia at the end of the winter period of simulation.

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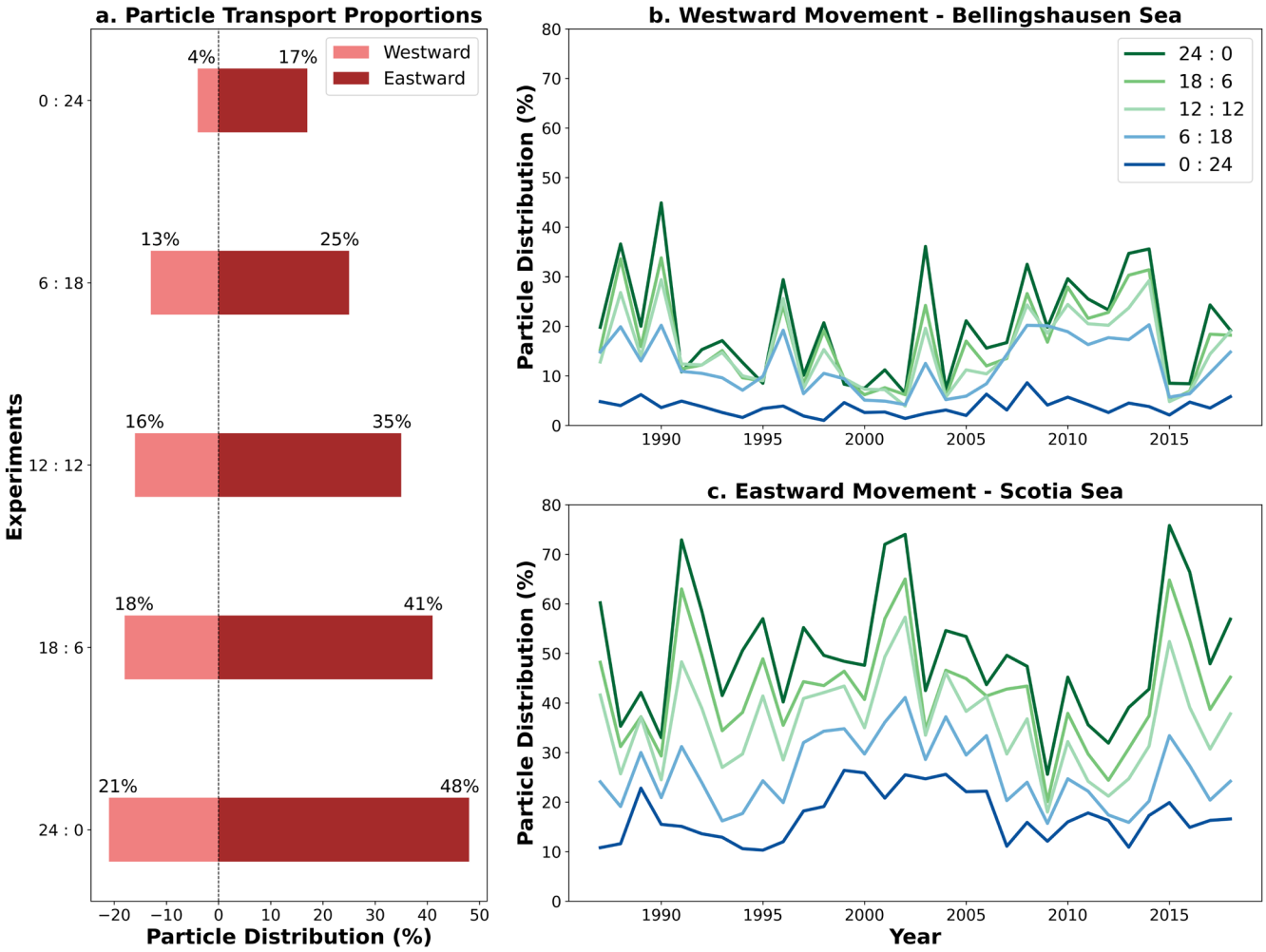

FIGURE 5 | (a) Mean percentage of particle transport westward and eastward over the 32-year period for particles released on the Antarctic Peninsula shelf (Figure 3a), summarising the directional transport under the different imposed behavioural scenarios. Time series of the percentage of particles transported (b) westward or (c) eastward from the Antarctic Peninsula shelf under different DVM behaviours, calculated from the distribution of particles at the end of each simulation. Experiments represent five DVM scenarios, varying the time particles spend moving with sea ice versus the open ocean (0:24, 6:18, 12:12, 18:6, 24:0; hours per day moving with sea ice:ocean).

3.2.2 | CCAMLR Management Areas

Understanding how krill are transported between the operational areas of the fishery is crucial for sustainable management (Meyer et al. 2025). Here, we show the average particle distribution across all five experiments (Figure 7), where particles were released uniformly distributed throughout each subarea (Figure 7a; Table S2), with variability across individual experiments shown in Figure S2. Overall, the results show that particles tend to spread widely from their release region, primarily moving eastward across the study area.

Subarea 48.1 emerged as an important source region, showing overwinter connectivity with all other subareas of Area 48 as well as with Subarea 88.3 (Figure 7). This indicates that particles released in Subarea 48.1 can be widely advected and contribute to connectivity across the broader region. In contrast, influx into Subarea 48.1 was limited, with particles arriving predominantly from Subareas 88.3 and 48.5. Thus, while Subarea 48.1 can export particles broadly across the regions, its own inputs are restricted to only two neighbouring source areas during the winter period.

The results indicate that particles originating in the Bellingshausen Sea (Subarea 88.3) and those released in the Weddell Sea (Subarea 48.5) do not exhibit connectivity with each other at the end of the simulated period. While it may be possible for particles from either region to be transported between the two subareas, such exchange did not occur within the 6-month time frame considered in this study. Particles released from Subareas 48.1–48.4 are predominantly transported eastward by the ACC. This eastward flow connects multiple subareas, allowing particles to travel long distances and linking different parts of the Scotia Sea.

The SB serves as a key conduit for particle transport from the Bellingshausen Sea (Subarea 88.3) into Subarea 48.1, as well as into Subarea 48.2 from where particles are advected northeastward with the ACC into Subarea 48.3 and 48.4. The high number of particles found in Subarea 48.5 at the end of the simulation period is driven by the Weddell Gyre. Some particles from this subarea are either moved west by the ACoC into Subarea 48.1 or follow the 1000 m isobath within the ASC into the Scotia Sea, from where they are further transported by the SACCF and the SB into Subareas 48.2–48.4.

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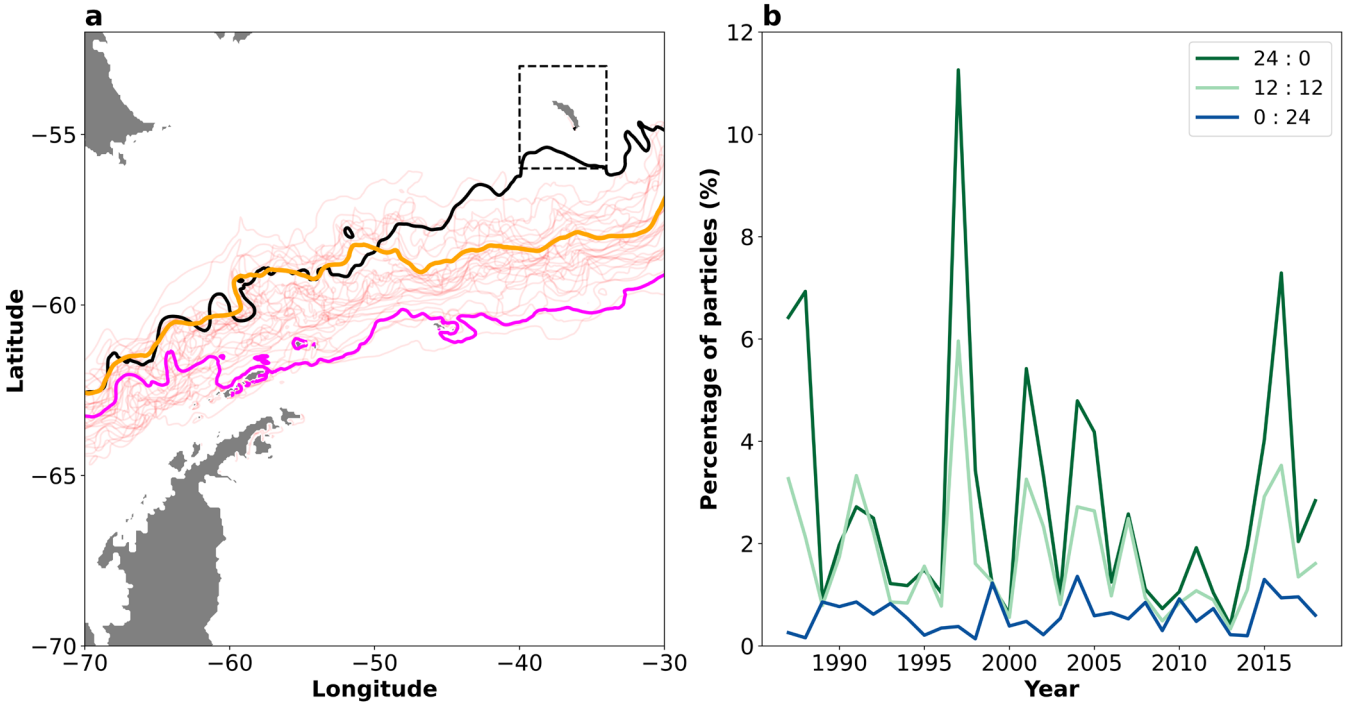

FIGURE 6 | (a) August sea ice extent in the Scotia Sea. The orange line represents the 32-year mean sea ice extent for August (15% threshold). Annual August sea ice extents are shown as lines in the background, with the 1997 extent highlighted in black and the 2003 extent highlighted in magenta. Dashed box indicates the South Georgia region, used to determine transport to South Georgia. (b) Time series of the percentage of particles located in the South Georgia region from 1987 to 2018 under different behaviour scenarios, calculated from the final location of particles at the end of each simulation. Experiments represent three DVM scenarios, varying the time particles spend moving with sea ice versus the open ocean (24:0, 12:12, 0:24; hours per day moving with sea ice:ocean).

4 | Discussion

Our results demonstrate that interactions with sea ice increase the complexity of connectivity, influencing linkages between krill populations and different regions. Using 32 years of Lagrangian particle tracking experiments, our study investigated interannual variability in simulated krill overwinter transport pathways. Previous modelling studies have explored the transport of larval krill across different locations, such as the WAP and the south Atlantic (e.g., Gallagher et al. 2023; Hofmann and Hüsrevoğlu 2003; Meyer et al. 2002; Piñones et al. 2013; Thorpe et al. 2007; Veytia et al. 2020; Young et al. 2014, 2024), and more recent work has begun to incorporate the developmental descent-ascent cycle into transport modelling (e.g., Sylvester et al. 2026). Our work builds on this foundation by incorporating ice-ocean DVM behaviour spanning more than three decades of simulated variability.

4.1 | Ocean Versus Sea Ice Transport

Particles released from the WAP shelf were advected in both directions, travelling eastwards via the ACC and westwards with the ACoC across all behaviour scenarios. The combination of these currents and sea ice motion results in distinct hotspots of accumulation by the end of the winter period including along the WAP to the Bellingshausen and Scotia Seas. The eastward transport from the WAP is more pronounced across all experiments, with a higher number of particles moving eastward compared to those moving westward.

Although our analysis is based on particle end positions rather than full trajectories, their spatial distribution provides insight into dominant transport pathways. The observed patterns suggest that particles generally move from the northern Weddell Sea towards the Antarctic Peninsula, entering the Bransfield Strait, while particles on the WAP shelf also follow the coastline towards the Bellingshausen Sea. These inferred pathways are consistent with previous studies (Dawson et al. 2023; Heywood et al. 2004; Moffat et al. 2008; Schubert et al. 2021). While most particles follow the coastline, some are retroflected northwards and exported from the shelf, consistent with Dawson et al. (2023). Overall, our inferred transport patterns align with earlier work suggesting that the ASC directs particles either along the slope into the ACC or retains them within the Weddell Gyre, leading to higher particle retention in this region. Thorpe et al. (2007), using the OCCAM (Ocean Circulation and Climate Advanced Modelling) global ocean circulation model, and Young et al. (2024), using the NEMO (Nucleus for European Modelling of the Ocean) framework, both identified similar transport pathways. Our model-based patterns are further supported by observational studies, which report similar krill hotspot distributions near the Antarctic Peninsula, South Georgia, and in the Scotia Sea during October–November (Perry et al. 2019).

Our results demonstrate that sea ice exerts a dominant control on particle distribution, resulting in enhanced dispersal across the study region by the end of the simulation. This influence is consistent with the wind-driven nature of sea ice transport, where sea ice motion is primarily driven by surface winds, while ocean currents provide a secondary contribution to mean

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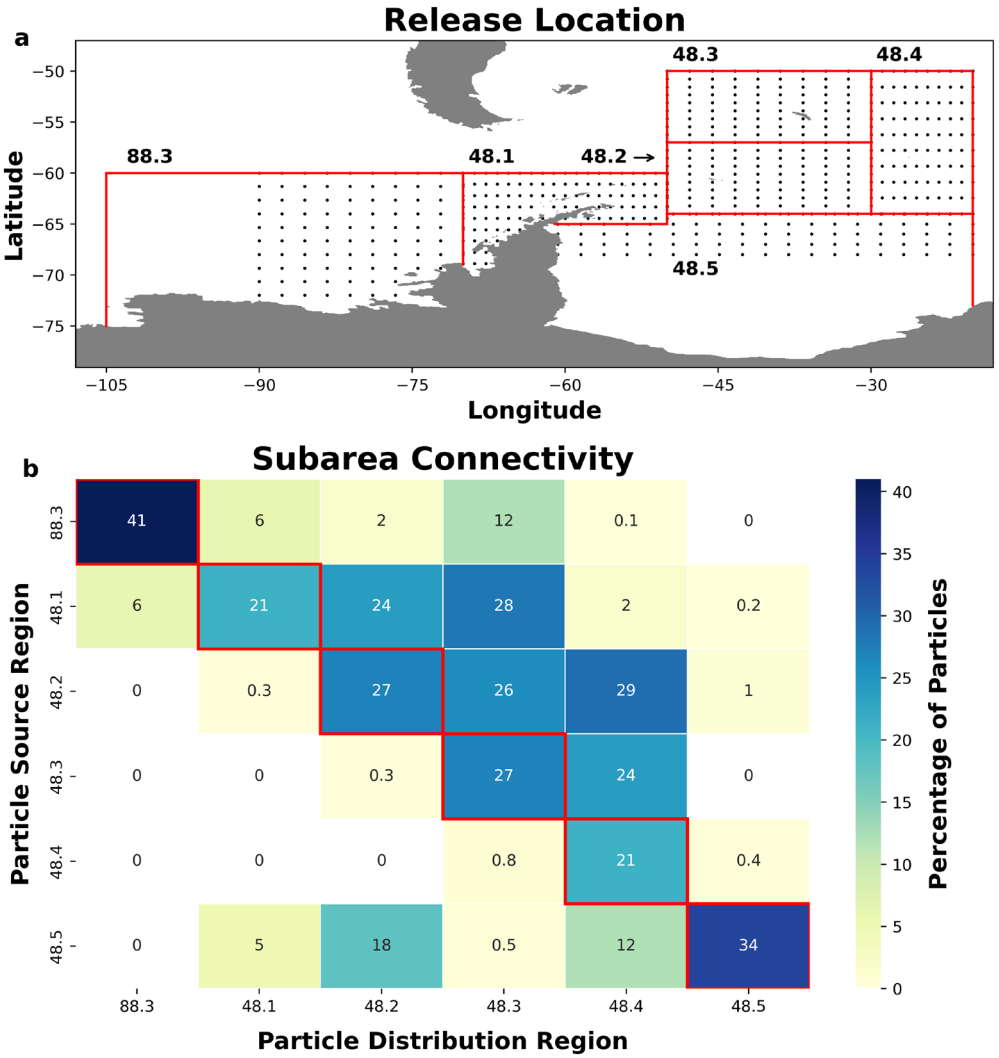

FIGURE 7 | (a) Map of the CCAMLR subareas, with particle release locations indicated by black dots. (b) Mean percentage connectivity across all five behaviour scenarios, showing the distribution of particles at the end of the overwinter simulation period within the subareas (red boxes) defined in panel (a). The *y*-axis represents the particle source region, and the *x*-axis represents the destination subarea. Cells on the diagonal (outlined in red) show self-connectivity within subarea. Percentages do not sum to 100% because some particles have final locations outside of the subareas.

drift, allowing sea ice to move differently from the underlying ocean circulation (Kimura 2004; Holland and Kwok 2012; Falco et al. 2024). Consequently, sea ice transport variability is not solely governed by ocean currents but is also shaped by atmospheric forcing (Kusahara et al. 2017; Purich et al. 2016). While ocean circulation shows interannual variability, the presence of sea ice adds an additional layer of complexity, leading to even greater year-to-year changes. Including sea ice-associated behaviour in the simulations enhances variability in krill transport pathways by creating and relocating high-density hotspots across years, compared to the more consistent patterns driven by ocean currents alone. Although our results do not explicitly isolate the impact of winds, the particle transport pathways we observe suggest that wind-driven sea ice motion likely contributes to the strong connection between the Bellingshausen Sea and the Antarctic Peninsula, as well as the transport from the Weddell Sea into the Scotia Sea. These pathways are consistent with Thorpe et al. (2007), who identified similar transport patterns using a global circulation model. The agreement between results derived from different modelling frameworks strengthens confidence in the robustness of these transport pathways.

4.2 | Diel Vertical Migration

Our results show that particles spending 12 h at a depth of 50 m and 12 h beneath the sea ice exhibited greater displacement from their starting locations and a wider spatial distribution compared with those that remained at depth. This finding highlights the enhanced dispersal potential of vertically migrating particles, with sea ice drift facilitating their broader transport across the marine environment.

Previous studies have highlighted variability in krill depth distribution, with DVM typically occurring within the upper water column. Meyer et al. (2017) observed that krill larvae feed on sparse ice-associated resources during the day and migrate into the upper 20 m beneath the sea ice after sunset. Observations from the Scotia Sea also indicate that krill swarms can occupy

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relatively shallow depth ranges (Tarling et al. 2018). Similar patterns have been reported around South Georgia and the Antarctic Peninsula (Cresswell et al. 2009; Everson 1982; Kalinowski and Witek 1980), suggesting that near-surface distributions are common in the Southern Ocean. While many of these studies include post-larval and adult krill, which can form swarms and exhibit broader depth ranges, observations of late-stage larval krill at greater depths remain limited. Adult Antarctic krill have been recorded at depths of 400–3500 m (Kawaguchi et al. 2011; Smith et al. 2025), well beyond the typical range of larval stages. Given the available evidence for predominantly shallow depth distributions in larval krill, our simplified use of sea ice velocities and ocean velocities at 50 m is consistent with observed larval habitat within the upper ocean. However, the vertical extent of late-stage larval migrations remains uncertain and warrants further investigation, particularly in shelf regions where vertical positioning may strongly influence transport dynamics (Young et al. 2024).

A key consideration is the amount of time krill spend in ocean versus sea ice habitats. We assume that krill not participating in DVM remain associated with either sea ice or oceanic habitats for 24 h/day, depending on their location. Overall, our findings suggest that when particles spend more time associated with sea ice, they are less likely to remain in the area where they were released. This underscores the potential influence of habitat preference on krill retention dynamics, suggesting that DVM behaviours may play a critical role in optimising habitat use between sea ice-covered and open ocean environments. Previous advection modelling studies conducted in Palmer Canyon on the Antarctic Peninsula (Hudson et al. 2021, 2022) revealed that DVM can significantly increase local retention, particularly within mesoscale subsurface eddies. We acknowledge that the DVM scenarios presented in this study are idealised and represent extreme, and potentially unrealistic, behaviours. While we acknowledge that these scenarios do not accurately replicate observations, they act as a sensitivity analysis, testing how strongly particle transport and distribution respond to different vertical migration patterns. By including extreme cases, where particles spend all their time either in sea ice or in the open ocean, we can assess the maximum possible influence of behaviour on transport pathways and distribution. We also include more realistic intermediate scenarios, where particles divide their time between these environments. Overall, this approach isolates the influence of vertical migration behaviour on transport, while interannual variability is captured by the 32-year simulation.

4.3 | Transport to South Georgia

Our model results reveal pronounced variability in particle transport to South Georgia from the Antarctic Peninsula shelf during the winter period. The transport of particles to South Georgia is primarily governed by the north-eastward flows of the ACC, with a critical influence exerted by the position and orientation of the SACCF (Ichii et al. 2023; Thorpe et al. 2002; Young et al. 2014).

During the simulated timeframe, the low number of particles reaching South Georgia under ocean-only velocities indicated limited connectivity in the absence of additional transport mechanisms. Nonetheless, interannual variability was still apparent, likely driven by shifts in the position of the SACCF (Boehme et al. 2008; Young et al. 2014). While sea ice scenarios introduce additional transport mechanisms, particles still spend time within the oceanic flow field, so changes in SACCF orientation could influence connectivity across all scenarios.

When sea ice-associated transport was included, more particles reached South Georgia on average within the winter period of transport, but the interannual variability increased, with some years showing very high transport and others extremely low. Previous studies have highlighted that interannual variability in sea ice across the Scotia Sea may influence transport to South Georgia (Murphy et al. 1995; Thorpe et al. 2007; Veytia et al. 2021). Our model results indicate that increased sea ice extent enhances particle transport to South Georgia. In particular, extreme sea ice conditions in the Scotia Sea strongly influence particle delivery to this region. Incorporating sea ice-associated transport leads to greater particle dispersal, allowing particles to reach South Georgia from both the Bellingshausen and Weddell Sea within the simulation timeframe.

4.4 | Future Directions

Recent years have seen a substantial decline in winter Antarctic sea ice extent (Gilbert and Holmes 2024; Purich and Doddridge 2023). Our results suggest that with continued reductions in sea ice extent, late-stage larval krill will remain confined to more southerly latitudes, consistent with Meyer et al. (2017). Understanding how future changes in sea ice conditions affect krill populations remains an important knowledge gap for the development of the krill stock hypothesis. Whether krill are transported with sea ice, remain in the surface ocean layer directly beneath it, or exhibit a combination of both behaviours appears to play a critical role in shaping dispersal patterns, highlighting the need for more detailed observational data to better constrain krill behaviour in these coupled environments. In this study, we used a 0.1° resolution sea ice–ocean model that captures essential ocean dynamics, however, transitioning to higher-resolution models would enable the resolution of finer-scale processes such as eddies, currents and turbulence, which may influence transport timescales and pathways (Drake et al. 2018; Tamsitt et al. 2017). Also, a more detailed comparison between modelled transport pathways and observed biomass distributions remains an important avenue for future research. Additionally, incorporating both horizontal and vertical migration into krill transport models, and evaluating the effects of climate variability and habitat conditions on krill population dynamics, will further strengthen the development of the krill stock hypothesis.

5 | Conclusion

Our modelling study reveals substantial interannual variability in the overwinter spatial connectivity of late-stage larval Antarctic krill in the south-west Atlantic sector of the Southern Ocean, largely driven by variability in sea-ice conditions. Simulated particle transport under different behaviour scenarios, including sea-ice association, ocean transport and diel

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vertical migration, indicates that sea ice can play a key role in shaping transport pathways. Variability in sea-ice extent and duration influences whether particles are retained locally or dispersed more widely, highlighting the importance of understanding the use of the sea ice habitat by larval krill. These results demonstrate that relying on mean current fields alone is insufficient to capture true connectivity patterns, as fine-scale processes and temporal variability can significantly alter transport pathways. Together, these findings provide important insights for developing krill stock hypotheses and improving management of the Antarctic krill fishery.

Author Contributions

Aditya Sharma: conceptualization, methodology, software, data curation, formal analysis, validation, visualization, investigation, writing – original draft, writing – review and editing. **Abigail J. R. Smith:** supervision, writing – review and editing, methodology, validation, software. **Sally E. Thorpe:** supervision, writing – review and editing, methodology. **Eugene J. Murphy:** supervision, writing – review and editing, methodology. **Hannah R. S. Dawson:** supervision, writing – review and editing, methodology, resources, software. **Stuart Corney:** supervision, writing – review and editing, funding acquisition, project administration, resources, methodology, validation, software.

Acknowledgements

This research was supported by the Australian Research Training Program and Australian Antarctic Program Partnership Scholarship. We acknowledge the Consortium for Ocean-Sea Ice modelling in Australia (COSIMA; www.coima.org.au) for creating and maintaining the ACCESS-OM2 model, and we also appreciate the Parcels development team for their ongoing work and support in advancing the Lagrangian particle tracking software. The simulations for this study were performed using high-performance computing resources provided by the National Computational Infrastructure (NCI), supported by the Australian Research Council Centre of Excellence for Climate Extremes. Sally E. Thorpe and Eugene J. Murphy were supported by the British Antarctic Survey National Capability Antarctic Logistics and Infrastructure program 'Research, Conservation and Leadership in Southern Ocean Ecosystems (CONSEC)', supported by the Natural Environment Research Council, a part of UK Research and Innovation. Open access publishing facilitated by University of Tasmania, as part of the Wiley - University of Tasmania agreement via the Council of Australasian University Librarians.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The model output from ACCESS-OM2-01 used in these simulations can be assessed through the COSIMA data repository at: https://doi.org/10.25914/608097cb3433f, specifically under the experiment labelled 01deg_jra55v150_iaf. The particle tracking was conducted using the OceanParcels framework, which is openly available at https://github.com/OceanParcels/parcels. The full set of particle trajectory data, along with the scripts used to run the tracking experiments, analyse the results and produce the figures in this study, is available on Zenodo upon request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1a:** Distribution of particles over 32 years with ocean velocity (0:24). Each panel represents the distribution of particles for an individual year. Density values are normalised (0–1) and represented using a colour scale from low (purple) to high (yellow). **Figure S1b:** Distribution of particles over 32 years with combined, 12 h in sea ice and 12 h in ocean velocity (12:12). Each panel represents the distribution of particles for an individual year. Density values are normalised (0–1) and represented using a colour scale from low (purple) to high (yellow). **Figure S1c:** Distribution of particles over 32 years with Sea ice velocity (24:0). Each panel represents the distribution of particles for an individual year. Density values are normalised (0–1) and represented using a colour scale from low (purple) to high (yellow). **Figure S2:** Particle distribution (%) across various CCAMLR subareas. Each panel represents a different subarea of particle release (48.1, 48.2, 48.3, 48.4, 48.5 and 88.3). The *x*-axis shows the subareas where particles are found, while the *y*-axis indicates the percentage of total particles. Coloured bars represent different DVM scenarios (ranging from 0:24 to 24:0 h), and error bars denote variability. **Table S1:** Results of the Tukey test showing pairwise comparisons of mean difference between groups. **Table S2:** Number of release sites in each subarea and total particles released per experiment. Particles were released daily from all sites within each subarea over a 61-day period each year, with this release schedule repeated across 32 years. The total particles per experiment for each subarea therefore reflects the cumulative releases over all years.

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