Journal of Marine Systems 241 (2024) 103920

Contents lists available at ScienceDirect

Journal of Marine Systems

journal homepage: www.elsevier.com/locate/jmarsys

Environmental and behavioural drivers of Antarctic krill distribution at the South Orkney Islands: A regional perspective

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ARTICLE INFO

Keywords:
Antarctic krill
Regional ocean model
Individual based model
Ocean circulation
Sea ice
Transport processes
Southwest Atlantic Ocean
South Orkney Islands

ABSTRACT

Antarctic krill (*Euphausia superba*) is a key species in the marine ecosystem of the Southern Ocean, but is also the target of a commercial fishery, with an important fishing ground in the South Orkney Islands region. The potential for competition for krill between predators and the fishery requires risk management strategies for the fishery, underpinned by an understanding of the key physical and behavioural drivers of krill movement and retention in target areas. Here, we present the results of a regional modelling study, combining a high-resolution ocean-sea ice model and an individual-based model parameterised for krill, to elucidate the roles of oceanographic variability and krill behaviour on patterns of transport and retention on and around the South Orkney Plateau. Simulations suggest that oceanic transport from sources around the Antarctic Peninsula is restricted by the northward flowing Antarctic Slope Current. Around the South Orkney Plateau, anticyclonic flows associated with the Weddell Front and the shelf edge transport krill rapidly towards the main fishing grounds to the northwest of the plateau. Transport onto the shelf and subsequent retention are influenced by the strength and direction of regional winds; weaker on-shelf transport and shorter retention times are associated with stronger westerly and northerly winds. The incorporation of sea-ice associated behaviour, whereby krill are moved with sea ice when sea ice is present, significantly modifies the patterns from purely oceanic transport; it reduces the influence of strong regional oceanic flows and increases transport of krill to the South Orkneys region from the Antarctic Peninsula. The inclusion of diel vertical migration also modifies predicted patterns from oceanic transport, but to a lesser extent, and moderates the impact of including sea-ice associated behaviour. We highlight the importance of understanding the behaviour of krill, including age-dependent behavioural changes in response to sea ice conditions, for modelling and management of Antarctic krill populations.

1. Introduction

The South Orkney Islands region, in the southwest Atlantic sector of the Southern Ocean (Fig. 1), provides breeding and foraging habitat for numerous marine predators, including large colonies of seabirds and seals (Dunn et al., 2016; Lowther et al., 2020). These colonies are, in large part, maintained by the availability of Antarctic krill (*Euphausia superba*), a species that dominates the pelagic ecosystem and is a key prey item. However, the high abundance of krill in this region also sustains a predictable krill fishery that operates predominantly on the northern side of the South Orkney Plateau, along the shelf break and in submarine canyons (Krafft et al., 2018; Santa Cruz et al., 2022). Over recent years, concern has been growing that the increasing demand and spatial focus of the krill fishery in the southwest Atlantic could have a negative impact on local land-breeding krill predators (Hinke et al., 2017; Meyer et al., 2020). Results from recent UK-Norway fieldwork at the South Orkney Islands (Watkins, 2016), and analysis of chinstrap penguin foraging areas (Warwick-Evans et al., 2018), suggest that there is the potential for temporal and spatial overlap between the krill fishery and land-breeding predators in this region.

The Antarctic krill fishery is managed by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). Since the establishment of CCAMLR in 1982, there has been an ongoing priority to set catch limits for krill such that the risks to dependent predator populations of being inadvertently, or disproportionately affected by the fishery are minimised, whilst enabling the fishery to access the krill resource (Godø and Trathan, 2022). Although initial catch limits were refined to consider subareas within the southwest Atlantic, there is

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https://doi.org/10.1016/j.jmarsys.2023.103920
Received 24 March 2023; Received in revised form 14 July 2023; Accepted 28 July 2023

growing appreciation of the need to manage the krill fishery over smaller scales (e.g., Hinke et al., 2017; Trathan et al., 2018), such as through small scale management units (SSMUs; Hewitt et al., 2004). However, setting catch limits at smaller scales relevant to predator foraging, or fishing effort, requires a better understanding of krill biology, distribution, flux and retention, and the underlying physical and behavioural drivers of variability (Trathan et al., 2022).

The South Orkney Islands lie within the Weddell-Scotia Confluence (WSC), an oceanographically complex region located between the Antarctic Circumpolar Current to the north, and the Weddell Gyre to the south. Waters within the WSC are modified by injections of cold, dense waters from the continental shelf of the western Weddell Sea that flow eastwards into the South Orkney region from the tip of the Antarctic Peninsula (Meredith et al., 2011). Hydrographic and surface drifter data have revealed a complex system of fronts and associated currents in the northwest Weddell Sea. Closest to the Antarctic Peninsula lies the Antarctic Coastal Current, which flows westward around the tip of the peninsula into the Bransfield Strait (Moffat and Meredith, 2018). The Antarctic Slope Front (ASF) and associated Antarctic Slope Current (ASC) are located at the shelf break, broadly associated with the 1000 m isobath, with a dominant transport path northward through the South Scotia Ridge and into the Scotia Sea (Thompson et al., 2009). The strong topographic steering and hydrographic properties of the ASF suggest that it could act as a barrier to cross-slope exchange whilst promoting transport of Antarctic krill to the Scotia Sea, and thence to the South Georgia region (Murphy et al., 2004; Thompson and Heywood, 2008; Thorpe et al., 2007). Further offshore, the Weddell Front is located above isobaths between 2500 and 3000 m (Thompson and Heywood, 2008). Northward currents associated with the Weddell Front flow cyclonically around Powell Basin before continuing towards the South Orkney Plateau (Heywood et al., 2004; Thompson et al., 2009). On approaching the southwestern edge of the South Orkney Plateau the flows bifurcate; flows associated with the Weddell Front continue eastward while bathymetrically-steered flows associated with shallower isobaths turn northward (Azaneu et al., 2017).

Whilst the paths of Lagrangian drifters in the northwest Weddell Sea are strongly dictated by the largely topographically-constrained ocean fronts, they exhibit additional variability due to transient dynamics such as eddies or wind events (Thompson et al., 2009). Changes in wind forcing due to climate variability associated with the Southern Annular Mode (SAM) also impact the structure and dynamics of the fronts (Thompson and Youngs, 2013) and thus have an impact on transport pathways. In particular, enhanced cyclonic wind stress during positive phases of SAM drives an acceleration of the Weddell Gyre, with an associated increase in the strength of the ASC, and an increase in export to the Scotia Sea (Meijers et al., 2016; Renner et al., 2012; Youngs et al., 2015). A further source of variability arises from the strong seasonal cycle in sea-ice extent, which modifies water mass properties and the circulation of the Weddell Gyre through variability in the surface exchange of momentum, heat and freshwater (Vernet et al., 2019). Interannual variability in the timing and extent of sea-ice cover in the northwest Weddell Sea has been linked to modes of climate variability, with increased sea-ice extent related to stronger southerly winds in association with negative SAM (Simpkins et al., 2012; Stammerjohn et al., 2008). At the South Orkney Islands, which lie within the seasonal sea-ice zone (Fig. 1), observed interannual variability in the timing of fast-ice formation and breakout has been related to variability in regional sea surface temperatures, with a later fast-ice breakout also associated with a reduced SAM index, and weaker westerly winds, in spring (Murphy et al., 2014). Such variability impacts the physical oceanography of the South Orkney region and also the availability of suitable habitat for larval krill (Meyer et al., 2017).

Studies of krill transport in the southwest Atlantic have shown large-scale transport links between krill populations, with connections between the Antarctic Peninsula, the northwest Weddell Sea, and across the Scotia Sea to South Georgia and the South Sandwich Islands (Fach and Klinck, 2006; Murphy et al., 2004; Thorpe et al., 2004; Thorpe and Murphy, 2022). Such studies have elucidated the roles of key oceanographic fronts, such as the ASC and the Southern ACC Front, in mediating export of krill from the northwest Weddell Sea and the subsequent transport of krill across the Scotia Sea to populations downstream. At the regional scale, modelling studies have revealed key oceanographic drivers of krill transport onto and along the West Antarctic Peninsula, highlighting the role of shelf edge canyons as conduits for on-shelf transport, and the increased retention of krill in circulations associated with deep bathymetric features (Hudson et al., 2022; Piñones et al., 2011, 2013a). Studies of transport pathways in the South Georgia region have similarly illustrated the importance of small-scale processes in patterns of krill distribution (Young et al., 2014). However, cross-shelf transport and retention processes at the South Orkney Plateau are poorly understood.

In addition to physical transport processes, krill transport and retention can be influenced by age- and environment-dependent krill behaviour. Field studies have provided observations of aspects of krill behaviour, such as off-shore spawning migrations (Siegel, 2005), behaviour of larval krill under sea ice (Meyer et al., 2017), swarming (Cox et al., 2010), and diel vertical migration (DVM; Zhou and Dorland, 2004). Life-stage dependent movements have also been inferred from age-specific krill distributions (e.g. Perry et al., 2019). Such studies are, however, limited both spatially and temporally. Numerical models

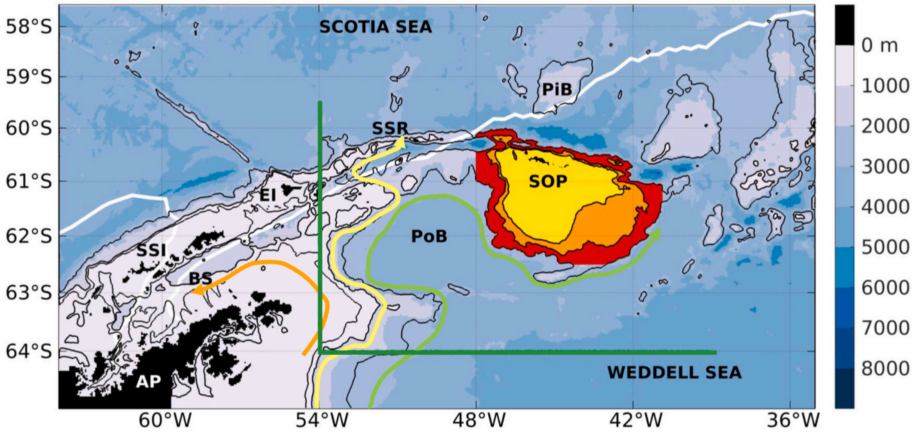

Fig. 1. Map of the South Orkney Islands region. Model bathymetry (blue shading) is derived from the Gebco_2014 grid, version 20150318 (www.gebco.net) with contours at 500, 1000, and 2500 m. Particle release locations used for the krill transport simulations are shown; lines upstream (dark green) of the South Orkney Plateau, on the shelf (yellow shading), on the shelf edge (orange shading) and slope (red shading). Climatological locations of the major fronts and associated currents in the northwest Weddell Sea are illustrated; Weddell Front (light green line), Antarctic Slope Current (yellow line), Antarctic Coastal Current (orange line). White line shows the median (1981–2010) September sea-ice extent from the National Snow and Ice Data Center (Fetterer et al., 2017). AP: Antarctic Peninsula; SOP: South Orkney Plateau; SSI: South Shetland Islands; BS: Bransfield Strait; EI: Elephant Island; SSR: South Scotia Ridge; PoB: Powell Basin; PiB: Pirie Bank. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

focussing on specific aspects of krill behaviour have furthered our understanding of the impacts of certain behaviours on krill distribution. Models incorporating the early life cycle stages of krill have detailed the likely distribution of successful spawning areas on both circumpolar (Hofmann and Hüsrevoğlu, 2003; Thorpe et al., 2019) and regional scales (Piñones et al., 2013b). Similarly, high-quality spawning habitat at the circumpolar scale has been predicted using mechanistic modelling incorporating thermal and food requirements for krill egg production (Green et al., 2021). Transport patterns along the West Antarctic Peninsula were found to be relatively insensitive to the introduction of DVM behaviour (Piñones et al., 2013a), whilst sea ice has been found to have an important, spatially-varying influence on regional and large-scale transport and distribution patterns (Mori et al., 2019; Thorpe et al., 2007).

Numerical modelling provides a valuable tool with which to investigate in detail the interaction and relative importance of relevant physical and biological processes, and to provide further understanding of the drivers of variability in krill transport and distribution. Here, we describe a numerical modelling study of krill transport and retention on and around the South Orkney Plateau. We focus on regional-scale patterns of transport, cross-shelf exchange and retention, the key drivers of variability in these patterns, and consider the results in the context of the management of the krill fishery.

2. Methodology

An individual-based modelling (IBM) approach was used to investigate the physical and behavioural processes contributing to krill movement on and around the South Orkney Plateau. The underlying ocean flows and sea ice fields were provided by a high-resolution regional ocean-sea ice model. Full details of the ocean-sea ice model are provided in Appendix A; a summary is presented here.

2.1. Ocean-sea ice model

The South Orkney Islands ocean-sea ice model is a regional application of NEMO (Nucleus for European Modelling of the Ocean; https://www.nemo-ocean.eu/). NEMO is a highly versatile modelling system and includes a range of options for model parameterisation that enables good representation of regions characterised by complex bathymetry, precipitous shelf edges, and sea ice. The South Orkney Islands model grid extends from 65°S, 64°W to 57.5°S, 35°W with a horizontal resolution of 1/20° longitude by 1/40° latitude (~2.5–3 km, varying with latitude). The vertical dimension is represented by 75 levels arranged as partial-cell z-levels, and with variable cell depth such that vertical resolution is enhanced over the shallower shelf regions. The simulation of sea ice is included by coupling with the LIM3 sea-ice module (Rousset et al., 2015). The model is forced at the open boundaries with tides from a global tidal model (TPXO7.2; Egbert and Erofeeva, 2002), and with barotropic flows, sea surface height, temperature, salinity and sea ice from a global application of NEMO at 1/12° horizontal resolution. Atmospheric forcing is derived from reanalysis (DFS5.2; Dussin et al., 2016). Climatological spatially-varying terrestrial freshwater input is derived from a combination of precipitation data from the DFS5.2 reanalysis, and Antarctic Peninsula glacier basin discharge data from the Regional Atmospheric Climate Model (RACMO; van Wessem et al., 2017). The ocean-sea ice model has been validated by comparison with a combination of in-situ (temperature and salinity profiles) and satellite-derived (sea surface temperature and sea-ice fraction) data for the period July 1997 to June 1998 (Appendix A). The results of the validation demonstrate that the model achieves a good representation of observed water mass properties and seasonally-varying sea-ice distribution. However, there is a tendency for sea ice to extend too far north and west in winter, and to retreat too far south in summer; the implications of this for the present study are considered in the discussion.

For this study, we focussed on a 5-year period, 2006/2007–2010/2011, which encompassed a range of Southern Annular Mode (SAM) conditions, a key climate variability indicator for the region (Marshall et al., 2006). Model fields were stored as 5-day means, including 3-dimensional ocean velocities, and sea-ice concentration and velocity. These model outputs were used to drive an individual-based model, described below.

2.2. Individual-based model

This study used an established individual-based model, the Hydrodynamics-based Algorithm for Lagrangian simulations (HAL). This model has been applied previously to studies of zooplankton, including krill, on and around the South Georgia shelf and West Antarctic Peninsula (Trathan et al., 2022; Ward et al., 2007; Young et al., 2014), and for the simulation of fish egg and larval transport over local (Young et al., 2012) and basin scales (Young et al., 2015; Young et al., 2018). In summary, particles are advected at each model time step (5 min, chosen to ensure stability in the particle tracking scheme so that particles fully sample the model flow fields) according to the imposed three-dimensional velocity field, using a second-order Runge-Kutta method. Additional horizontal and vertical diffusions are included using a random-walk approach (Dyke, 2001), and there is an option for diel vertical migration (DVM) behaviour. HAL was further developed for this study to incorporate additional behavioural traits relevant to krill, specifically the option to change behaviour in response to local sea-ice conditions.

The key objectives of the model study were to identify the dominant transport pathways around the plateau and the key areas for cross-shelf exchange, both on- and off-shelf, and to determine areas of retention and residence times on the shelf. Four release configurations were used to address these (Table 1). Model krill were released between December and May for *shelf*, *shelf edge* and *slope* releases to capture the key overlap period between the krill fishery and penguin foraging during the more constrained brood and creche periods (Lowther et al., 2020; Phillips et al., 2021; Warwick-Evans et al., 2018). For *line* simulations, model krill were released year-round to resolve seasonal variability in transport to the South Orkney Islands region. Particles were released every 5 days and tracked for 9 months in all experiments. Regularly spaced particle releases at high resolution were imposed to ensure the capture of the full range of transport pathways. Interactions between variable flow and heterogeneous krill distribution are likely to be important. However, there are insufficient observations at present to define a spatially

Table 1
Details of the particle release configurations used for the individual-based model simulations. Model grid cells refers to the underlying ocean model grid.

Release location (cf. Fig. 1)	Definition	Release period	Release interval	Release depth (m)	No. particles released per model grid cell
Line	West-East line at 64°S, 54°W–39°W; North-South line at 54°W, 59.5°S–64°S	Year round	5 days	50	5
Shelf	Model grid cells with depth < 500 m	December–May	5 days	50	1
Shelf edge	Model grid cells with depth 500–1000 m	December–May	5 days	50	1
Slope	Model grid cells with depth 1000–2500 m	December–May	5 days	50	1

variable particle release.

To determine the transport and retention of krill in the South Orkney Islands region and the sensitivity to krill behavioural traits, specifically association with sea ice and DVM, the following model experiments were run:

(i) *Ocean*: For the baseline simulations, no behaviour is included; model krill are advected by the 3-dimensional ocean velocity fields, constrained to the upper 100 m.

(ii) *Ice*: when sea ice is present (sea-ice concentration $>$ 15%), model krill are moved with the sea ice; away from sea ice, krill move with the ocean currents as in the baseline simulations.

(iii) *Ocean* + *DVM*: model krill perform DVM over the upper 100 m, based on observations of krill swarm behaviour in the open ocean (Tarling et al., 2018), triggered by local sunrise and sunset, with krill coming to the surface at dusk and descending at dawn.

(iv) *Ice* + *DVM*: model krill exhibit reversed DVM behaviour, based on observed larval krill behaviour under sea ice (Meyer et al., 2017). Thus, krill move with the sea ice during the day (as in option (ii)) and migrate away from the sea ice at night to a maximum depth of 30 m. In the absence of sea ice, the maximum depth at night reverts to 100 m.

As the imposed DVM patterns are different for experiments (iii) and (iv), with reverse DVM in *Ice* + *DVM*, the addition of DVM has contrasting effects. Thus, for *Ocean* + *DVM* simulations particles are at the surface at night, so spend a larger proportion of time at the surface during winter when daylight hours reach a minimum of ~5.5 h per day. Conversely, for *Ice* + *DVM* simulations particles are at the surface during daylight, so spend more time at the surface during spring and early summer when days are longer, peaking at ~19 h of daylight in December. The model representations are necessarily a simplification of the complex behaviour of krill, which varies with age, location, and environmental conditions. The *Ocean* and *Ocean* + *DVM* simulations may be considered of relevance to all krill life stages, whilst those incorporating ice-associated behaviour are of more relevance to larval krill. The potential implications of the simplified model representations are considered in the discussion.

The model experiments were repeated for each of the 5 study years to capture interannual variability in the predicted transport and retention patterns, with >2.1 million particles released for each set of simulations per year. Simulated particle tracks were analysed to identify persistent features and levels of variability in predicted krill transport and retention. Dominant transport pathways for model krill were determined by calculating the number of unique model krill that passed through each model grid cell. *Shelf edge*, *slope*, and *line* releases were analysed for key aspects of shelf recruitment, specifically the proportion of krill recruiting to the plateau, the origin of these model krill, and the location at which they entered the plateau. Here, we define recruitment as the transport of particles onto the South Orkney Plateau, with the plateau defined as the region shallower than 500 m or 1000 m for the analyses of

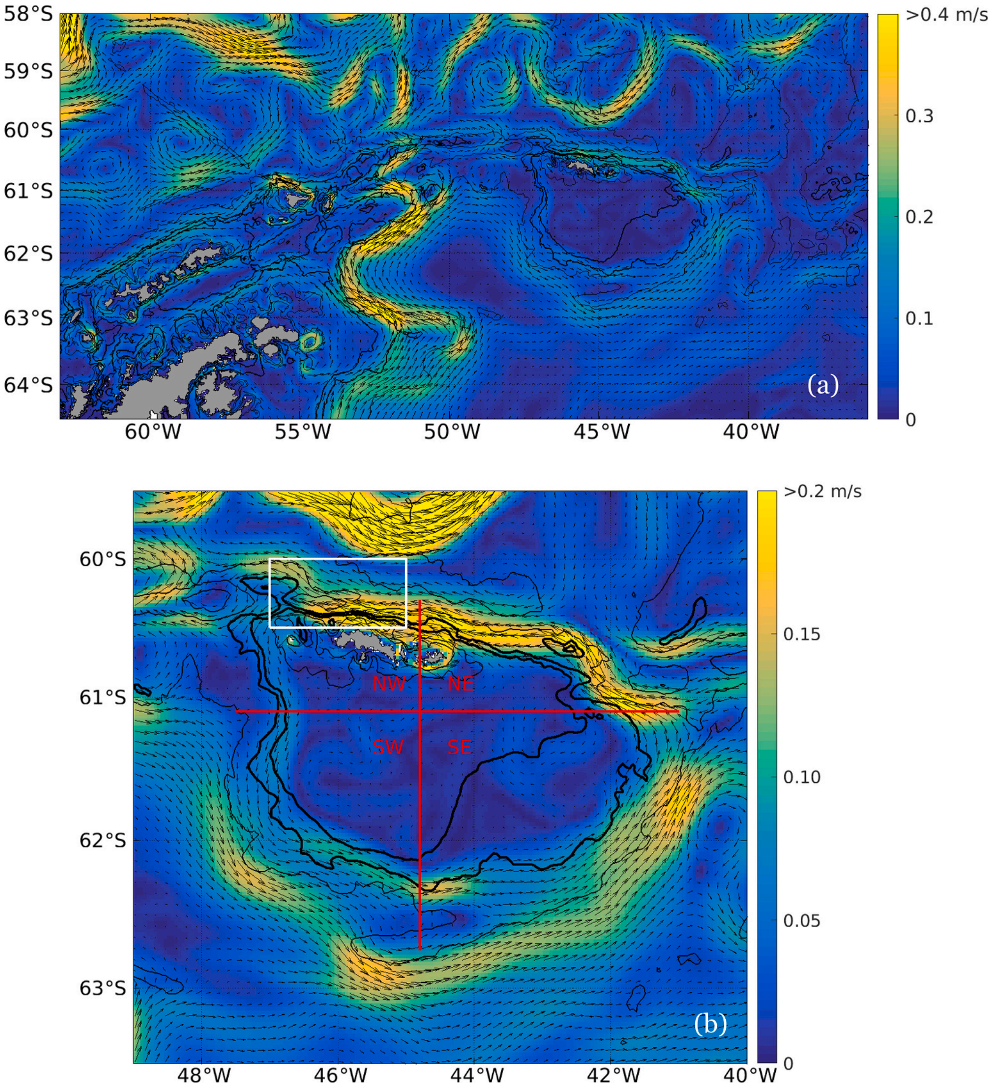

Fig. 2. Mean velocity field for the upper 100 m for January 2010 from the regional South Orkneys sea ice-ocean model. Shading is current speed ($m\ s^{-1}$) and velocity vectors are plotted every (a) 5th, and (b) 3rd model grid cell. Geographical quadrants (red lines) used in analyses and the location of the key fishery area (white box; Warwick-Evans et al., 2018) are shown in (b). Isobaths are at 100, 200, 500, 1000 and 2500 m, with bold contours at 500 and 1000 m. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

shelf edge and *slope* releases, respectively. The geographical distribution of entry points to the wider plateau region (shallower than 2500 m) was considered for the *line* releases. *Shelf* releases were used to identify geographical and temporal patterns in retention, and the locations at which model krill exited the plateau. Flushing rates were illustrated by considering the mean length of time model krill occupied each model grid cell ('mean particle occupancy') and by calculation of the e-folding time (the time taken for the number of model krill on the shelf to reduce to 1/e of the number released). The geographical distributions of entry and exit points to/from the South Orkney Plateau were also divided into quadrants (Fig. 2b) to facilitate interpretation of the impacts of inter-annual variability and krill behaviour.

Analyses of the results of the *Ocean* simulations and of those with behaviour included were compared to reveal the impacts of different behaviour strategies on transport and retention patterns. The role of environmental variability on krill transport in the South Orkney region was determined by comparing variability in simulated recruitment and retention with the seasonal sea ice cover from the regional ocean-sea ice model, and with regional winds extracted from the DFS5.2 reanalysis. For the latter analyses, the zonal and meridional components of the wind were spatially averaged over an area encompassing the South Orkney Plateau (48°–41°W and 62.5°–60°S) for comparisons with local recruitment and retention, and over the northwest Weddell Sea (55°–39°W and 65°–59.5°S) for comparisons with regional-scale recruitment. The area-averaged components of wind were then averaged over time periods from 1 to 120 days (*shelf*, *shelf edge*, and *slope* releases) or 1 to 180 days (*line* releases) following particle release to find the averaging period that maximised the correlation with recruitment and retention for the 5-year release period. The maximum averaging period was chosen to encompass the predicted range of retention and transport timescales.

3. Results

3.1. Oceanographic environment

The ocean-sea ice model resolves key features of the regional oceanography, including the northward flowing Antarctic Slope Current (ASC), the Antarctic Coastal Current, and flows associated with the Weddell Front (WF) (Fig. 2). In agreement with observations, the ASC splits as it nears the South Scotia Ridge and the eastward branch, together with flows associated with the WF, flows cyclonically around the Powell Basin towards the South Orkney Plateau. On reaching the vicinity of the Plateau, flows are steered anticyclonically around the

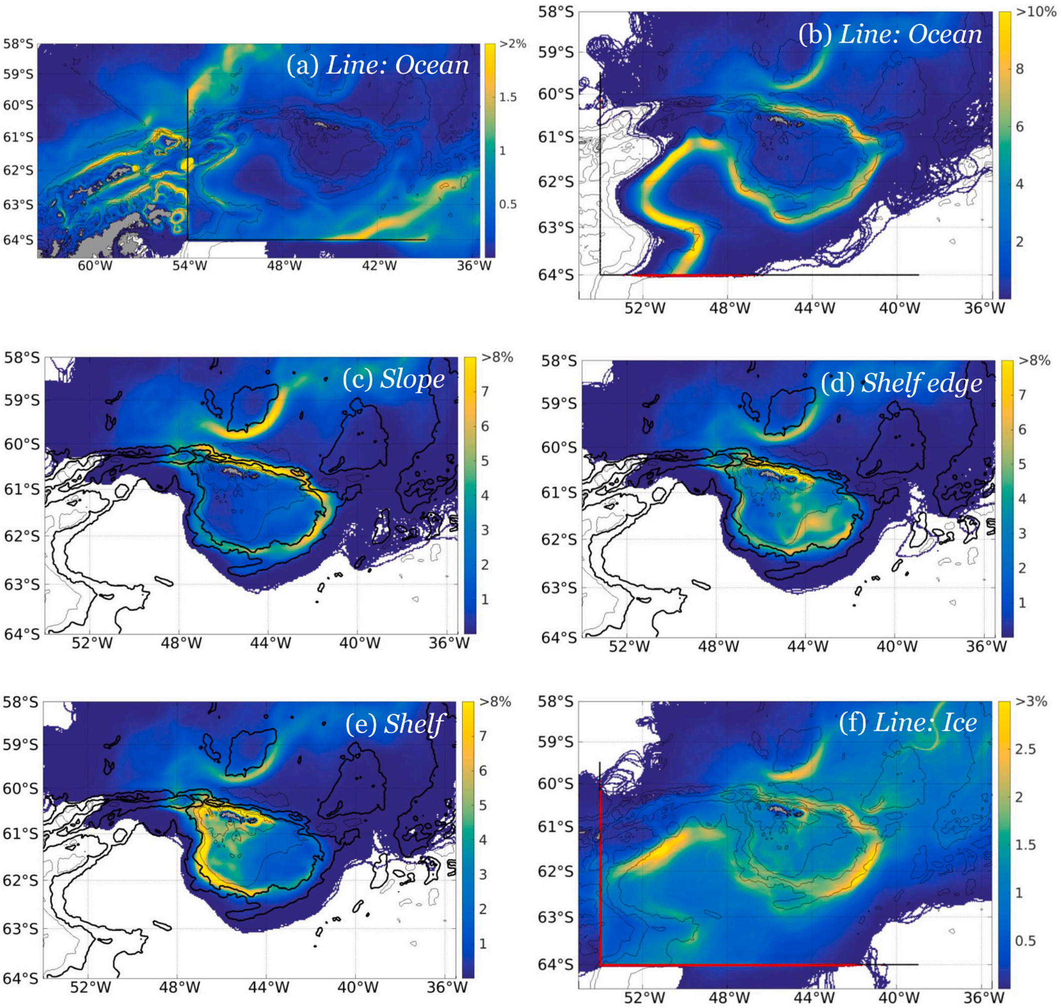

Fig. 3. Dominant transport pathways for particles released (a, b, f) along lines upstream of the South Orkney Plateau, (c) in the slope region, (d) in the shelf edge region, (e) in the shelf region; (a) to (e) *Ocean* simulation, (f) *Ice* simulation. Shading is the percentage of particles released during the 5-year simulation period that pass through each model grid cell. Panels (b) and (f) show pathways for the subset of particles that reach the South Orkney Plateau, with shading the percentage of these particles that pass through each model grid cell, and red dots marking the origins of successful particles. Isobaths are at 250, 500, 1000, 2500 and 5000 m. Bold contours in panels c-e are at 1000 and 2500 m. Release regions are shown in Fig. 1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

shelf edge, continuing to the northwest of the South Orkney Islands. Here, the flows split with the stronger branch continuing westward before retroflecting eastward and passing to the southeast of Pirie Bank. The weaker branch continues southward along the shelf edge, thus generating a complete anticyclonic transport path around the plateau. The anticyclonic shelf edge flows over the top 100 m generally exceed mean speeds of 0.15 m s^{-1}. However, the southward flows along the western edge of the plateau are weaker, with mean speeds below 0.1 m s^{-1}. Over the shallow bathymetry of the plateau, flows are more variable in direction and much weaker, with mean speeds generally below 0.05 m s^{-1}. In agreement with observations (Holland and Kwok, 2012), sea-ice drift in the model is broadly northeastward in the Weddell Sea, driven by surface winds. This exerts a drag on the ocean surface such that, in the presence of sea ice, near-surface ocean currents gain a northeastward component.

3.2. *Dominant transport pathways*

The baseline *Ocean* simulations for particles released along lines upstream of the South Orkney Plateau reveal the influence of the strong, persistent oceanic flows in the northwest Weddell Sea region (Fig. 3a). Particles released on the shelf edge east of the Antarctic Peninsula on the east-west line tend to be transported northward in the ASC and exit the Weddell Sea over the South Scotia Ridge to the west of the South Orkney Plateau. Particles released on the Antarctic Peninsula shelf follow convoluted paths; some continue north and exit the Weddell Sea to the east of Elephant Island, whilst many are transported by the Coastal Current into the Bransfield Strait. Of the latter particles, some are entrained in the cyclonic circulation in the Strait and continue their paths around the South Shetland Islands and Elephant Island, whilst others are transported close to the peninsula in small-scale flows associated with the complex bathymetry, as highlighted previously by Trathan et. (2022). Particles released east of ~47°W remain south of the South Orkney Plateau and are transported east/northeastward in the Weddell Gyre.

Particles that successfully reach the South Orkney region are released in a relatively small longitude band, between ~52.5°W and ~47°W, with most released between ~51°W and ~49.5°W (Fig. 3b). The majority of these particles follow a path approximately along the 2500 m isobath, in flows associated with the WF, travelling cyclonically around the Powell Basin and then anticyclonically around the South Orkney Plateau. Whilst a minority of particles then continue on an anticyclonic path around the plateau, the majority retroflect eastward to the north of the plateau before continuing northeastward around the southeast edge of Pirie Bank in the southern Scotia Sea. The location of retroflection shows considerable temporal variability; most frequently, it occurs at ~48°W, but periodically it extends westward to ~51°W, and can vary by several degrees of longitude over a 6-month period.

The dominant transport pathways for particles released on the slope suggest that the majority of these particles are confined to a narrow path around the plateau, close to the 1000 m isobath (Fig. 3c), in accordance with the dominant anticyclonic shelf edge flows (Fig. 2b). The eastward retroflection to the north of the plateau, revealed in the line release simulations, is again evident, and there is also a circulation around the small basin of deeper bathymetry centred at 60.25°S, 48°W, arising from persistent cyclonic flows at this location. A somewhat weak transport pathway onto the plateau in the east is evident along the 500 m isobath, associated with a weak and variable southwestward flow (Fig. 2b), with subsequent dispersal of particles onto the shallower South Orkney Plateau.

Transport pathways onto regions of the plateau shallower than 500 m are further revealed by the movement of particles released along the shelf edge (Fig. 3d), with a clear preferred route onto the shelf in the south and southeast (Appendix A, Fig. A.5c). Particles are then transported northwards, the majority passing to the east of the South Orkney Islands before continuing westwards in the anticylonic shelf edge flows. There is a second pathway to the south of the South Orkney Islands, which is weaker and shows more interannual variability, with particles transported westwards and then southwards in the anticyclonic shelf edge flows. The general northward movement of particles from the southeastern plateau is also evident in pathways for particles released on the shelf (Fig. 3e), with a subsequent concentration of pathways along the shelf edge to the north of the South Orkney Islands. Particles released on the western shelf tend to follow more varied pathways; whilst some are transported to the east of the South Orkney Islands, most have a westward trajectory, becoming entrained in the anticyclonic shelf edge flows. A proportion of the latter particles subsequently re-enter the shelf in the south. The pathways for both shelf edge and shelf releases suggest that the majority of particles leave the region to the northwest (cf. Appendix A, Fig. A.5d), with subsequent transport pathways as described earlier.

3.3. *Recruitment patterns*

Considering the baseline *Ocean* simulations, the geographic distribution of entry points to the South Orkney region (depth < 2500 m) for particles released along lines upstream of the plateau shows the majority of entries occurring in the west and southeast (Appendix A, Fig. A.5a). However, once in this region, entry points to the shallower plateau are more widely distributed. Entry points to the plateau for particles released in the slope region encircle the plateau, albeit with fewer entries in the north, and with patchy hotspots of preferred entry points (Appendix A, Fig. A.5b). Particles released in the shelf edge region also have fewer entries to the plateau in the north, with entry points concentrated in the south and southeast regions (Appendix A, Fig. A.5c). The entry points were divided into quadrants (Fig. 2b) to facilitate interpretation of the broad patterns of distribution and to identify interannual variability in the patterns. The results suggest that there is little variability in the annual mean distribution of entry points, or in the number of particles recruiting to the plateau, for *Ocean* simulations (Fig. 4, bars (i)).

Further understanding of recruitment patterns can be obtained by considering the locations of source points for particles successfully recruiting to the South Orkney Plateau. Integrated over the 5 simulation years, there are very few release locations in the shelf edge and slope regions from which no particles reach the plateau. However, the frequency of successful recruitment from each release point is generally lower in the north and decreases away from the plateau (Appendix A, Fig. A.6). This is most noticeable for the slope region where particle trajectories are influenced by the strong shelf edge flows that tend to transport particles around the edge of the plateau and limit on-shelf transport. Particles released along lines upstream of the plateau successfully reach the South Orkney region from a relatively small longitude band (Fig. 5), with the most successful release points coinciding with the northward flows associated with the Weddell Front (Fig. 2a). Over the 5-year simulation period, only 11 of the 324,850 particles released along the north-south line reach the plateau region. The mean time taken for particles to reach the South Orkney Plateau region varies along the east-west release line. For the highest concentration of particles between ~51°W and ~49.5°W, transit times increase eastward, with the minimum coincident with the peak in flows associated with the Weddell Front (Fig. 2a). Continuing eastward to ~49°W particles have decreasing transit times, due to a more direct eastward pathway at ~63°S suggested by the mean flow fields. Over the 5-year simulation period, mean transit times by release location range from a minimum of 46 days to a maximum of 268 days, with the majority (88%) between 50 and 120 days, and an overall mean transit time of 72 days.

Considering in more detail the temporal variability in recruitment to the South Orkney Plateau for the *Ocean* simulations, particles released along the lines upstream of the plateau have low recruitment throughout the 5-year simulation period (Fig. 6a). Recruitment ranges between 1.4 and 6.6% of the particles released every 5 days, with a mean of 3.7%, and with no clear trends in the low levels of interannual and seasonal

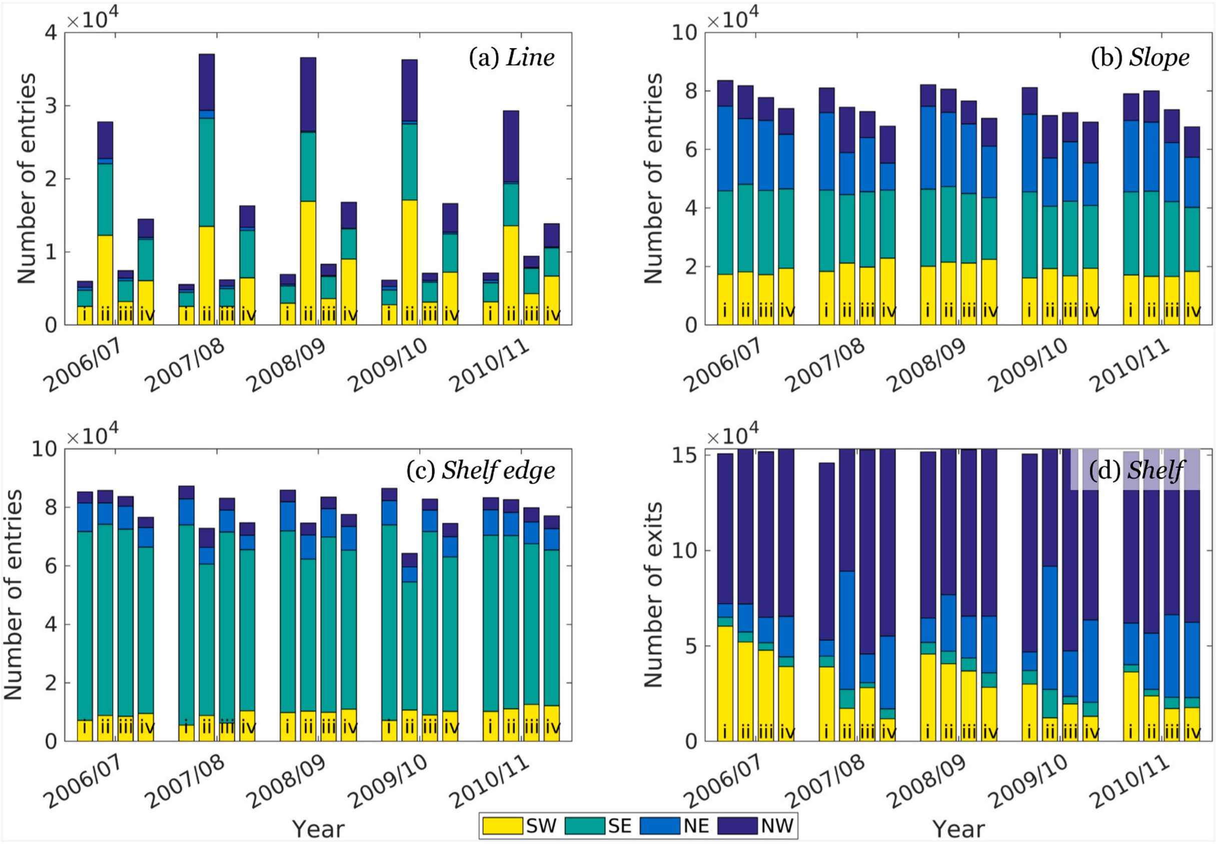

Fig. 4. Variability in the numbers of particles entering the South Orkney Plateau by quadrant (cf. Fig. 2b) for (a) particles released along lines upstream of the plateau, entering region <2500 m depth, (b) particles released in the slope region entering region <1000 m depth, (c) particles released in the shelf edge region entering region <500 m depth. (d) Variability in the numbers of particles exiting the South Orkney Plateau by quadrant. For each year, the 4 bars represent simulations with (i) *Ocean*, (ii) *Ice*, (iii) *Ocean* + *DVM*, (iv) *Ice* + *DVM* behaviour scenarios. Release regions are shown in Fig. 1.

variability. Contrary to the line releases, recruitment is consistently high for particles released in the shelf edge region, with a mean value of 89.7%. However, temporal variability in recruitment is similarly low, with a range over the 5-year simulation period of 10.8% and a mean range of 6.5% within the 6-month release periods (Fig. 6c). Recruitment is somewhat lower for particles released in the slope region, with a mean value for the 5-year simulation period of 75.4% (Fig. 6b). There is also more temporal variability, with a range of 17.7% over the 5-year simulation period and high levels of recruitment variability within each 6-month simulation period (mean range of 9.9%). In 4 of the 5 years, there is an underlying trend of increasing recruitment from December to April.

3.4. Retention and export patterns

The geographical variability in retention on the South Orkney Plateau is illustrated by plots of mean particle occupancy and the coefficient of variation of mean occupancy for the 5 years of the *Ocean* simulations (Fig. 7a,b). Most notable are the areas of persistent, slower flushing around the South Orkney Islands and in a region of the western plateau centred on 61.25°S, 46°W. Conversely, there is a band of more rapid flushing along the 500 m contour in the south, extending northwestwards onto the plateau and with low interannual variability. This feature is associated with the on-shelf transport pathway identified in Section 3.2.

Considering further the temporal variability in retention on the shelf, the e-folding time reveals both interannual and seasonal variability (Fig. 6d). The mean across all *Ocean* simulations is 66 days with a range of 37 to 99 days, however the large range of e-folding times for each 6-month period (mean range of 31 days) dominates the pattern, suggesting a strong influence of processes acting over seasonal timescales. In particular, ice cover at the start and end of the 6-month simulation periods tends to increase e-folding times and is a strong driver of the variability.

The mean geographical distribution of shelf exit points for particles released on-shelf for the 5 years of *Ocean* simulations suggests that particles preferentially leave the shelf to the north and west (Appendix A, Fig. A.5d), as suggested by the dominant transport pathways described in Section 3.2. However, more detailed analyses of particle exits by quadrant reveal some interannual variability in the distribution (Fig. 4d, bars (i)), with 40% of particles exiting from the southwest quadrant in 2006/7 (compared to a mean across the 5 years of 28%) and 14% exiting from the northeast in 2010/11 (compared to a mean of 8%). Overall, there is little variability in the total number of particles leaving the shelf as by the end of the 9-month simulations very few particles remain on the plateau.

3.5. Impacts of sea-ice presence and sea-ice associated behaviour

The addition of sea-ice associated behaviour (*Ice*) affects the dominant pathways of particles at both the regional and local scale. Particles released along lines upstream of the South Orkney Plateau follow more diffuse pathways, dominated less by strong underlying ocean currents including those associated with the Antarctic Slope Front and Weddell Front (Fig. 3f). Similarly, particles released on and around the plateau are influenced less by the anticyclonic shelf edge currents and follow a more diffuse northeastward pathway with the sea ice drift, when sea ice is present. Such changes to the transport pathways impact the origins of particles reaching the South Orkneys region, the time taken for particles to reach the region, the numbers of particles both recruiting to and being

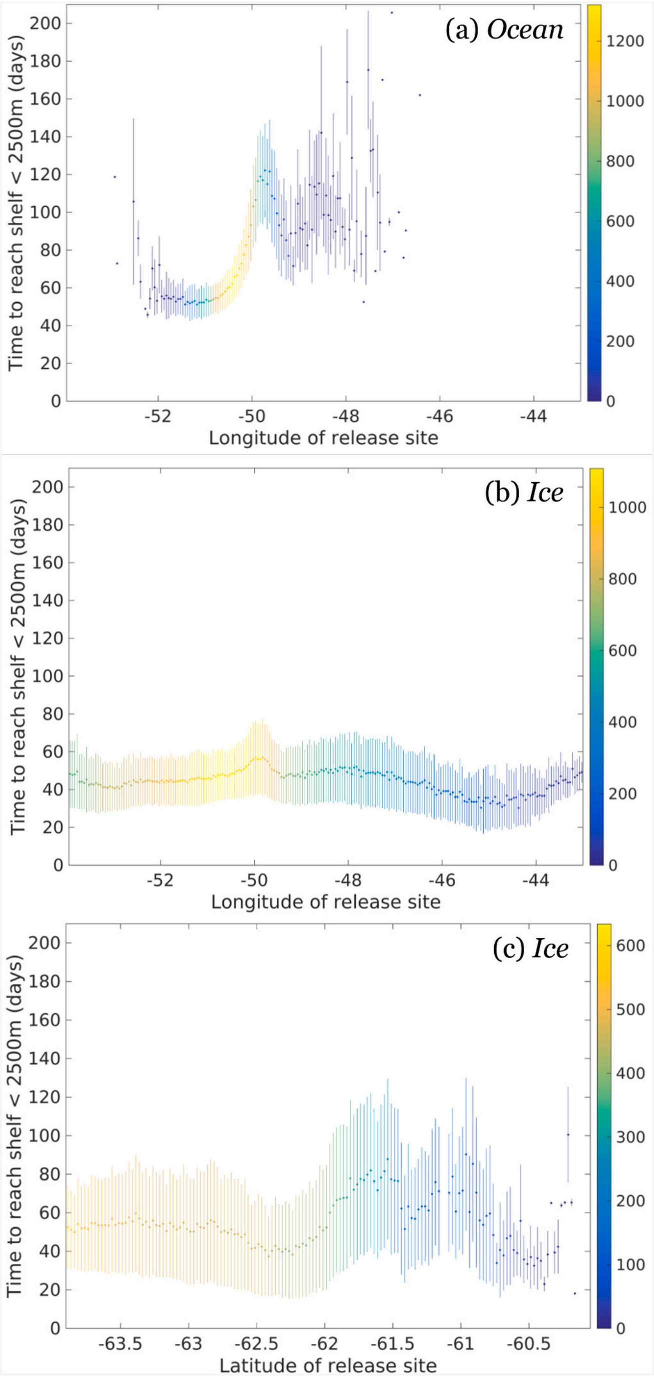

Fig. 5. Mean and standard deviation in time taken for particles released along the (a, b) east-west line and (c) north-south line upstream of the South Orkney Plateau (Fig. 1) to reach the plateau region <2500 m depth; (a) *Ocean* simulation, (b, c) *Ice* simulation. Coloured shading indicates the number of particles from each release point along the line that reached the plateau during the 5 study years. Release lines are shown in Fig. 1.

retained on the shelf, and the distribution of dominant shelf entry and exit locations.

Considering first the regional-scale particle transport, the addition of sea-ice associated behaviour results in particles reaching the South Orkney Plateau from the majority of release sites along both the east-west and north-south lines (Fig. 3f). Thus, there is a much wider geographical distribution of potential origins for krill to reach the South Orkney region than for purely oceanic transport. Most notably, the successful transport of particles released along the north-south line suggests that with the additional behaviour, krill could reach the South Orkney region from shelf areas around the Antarctic Peninsula, and potentially from source areas along the West Antarctic Peninsula. There is also a reduction in the transit time for particles to reach the South Orkney region, relative to the *Ocean* simulations (Fig. 5). Over the 5-year simulation period, mean transit times by release location range from a minimum of 18 days to a maximum of 228 days, with the majority (92%) between 30 and 70 days, and an overall mean transit time of 49 days, which is ~2/3 the mean transit time from the baseline *Ocean* simulation. However, there is more variability in the transit times for a given release location when sea-ice associated behaviour is included, due to the seasonal variability in sea-ice extent and concentration.

The change in transport pathways and increase in potential source regions for particles with sea-ice associated behaviour generates an increase in the flux of particles to the South Orkney region from the upstream line releases relative to the *Ocean* simulations (Fig. 6a). Recruitment to the South Orkney region ranges between 1.3 and 52.3% of the number of particles released every 5 days, with a mean of 20.0%, more than five times the mean recruitment for the *Ocean* simulations, and with peaks in recruitment during periods of maximum sea ice concentration (approximately May to September). There is, however, considerable interannual variability in recruitment due to variability in the timing and geographical distribution of the sea ice (Fig. 6a). For example, sea ice remains close to the South Orkney Plateau in austral summer 2007/08, leading to relatively high particle flux during the period of minimum sea ice.

If sea ice is still present when particles reach the South Orkney region, the continuing northeastward transport carries particles with sea-ice associated behaviour away from the region, reducing recruitment to the plateau. Thus, local recruitment of particles to the plateau tends to be lower for both shelf edge and slope releases when sea ice is present and sea-ice associated behaviour is included (Fig. 6b,c). Similarly, there is a reduction in retention of particles released on the plateau when sea ice is present (Fig. 6d). Also notable is the much greater variability in recruitment from off-shelf particle releases, and in retention of particles released on the plateau, relative to the baseline *Ocean* simulations, due to the seasonality and interannual variability of sea ice extent and distribution.

While the combination of sea ice and sea-ice associated behaviour allows more particles to reach the South Orkney region, model results suggest that the positive effect is counteracted by the reduction in recruitment and retention to/on the shallow plateau (Fig. 6). Strong recruitment to the South Orkney Plateau in summer for particles with sea-ice associated behaviour therefore requires enhanced inputs through the presence of sea ice in spring but with the timing of sea-ice retreat such that it reduces losses from the region in early summer. The temporal duration of successful local recruitment and retention is affected by the timing of sea-ice advance, with reduced recruitment and retention of particles in autumn in years with earlier sea-ice growth. However, for particles in the baseline *Ocean* simulations, the presence of sea ice in December and May increases retention. The presence of sea ice reduces the direct effect of winds on the ocean surface and the subsequent potential for off-shelf transport of particles in wind-driven flows. The lag between loss of sea ice and decrease in retention times (Fig. 6d) suggests that there is also some shielding from wind forcing immediately after the ice melts due to the shallow freshwater layer at the surface.

The changes in transport patterns due to sea-ice associated behaviour are also reflected in the distribution of shelf entry and exit locations. Although sea-ice associated behaviour only occurs when sea ice is present, so only a proportion of the releases are affected, the impact of including this behaviour is sufficiently large that the effect can be seen in the overall quadrant analyses. For all release locations, there is a tendency for the proportion of particles entering on the western side of the region to increase with the inclusion of sea-ice associated behaviour, with a decrease in the proportion entering on the eastern side (Fig. 4a–c). This pattern is reflected in changes to exit pathways from the

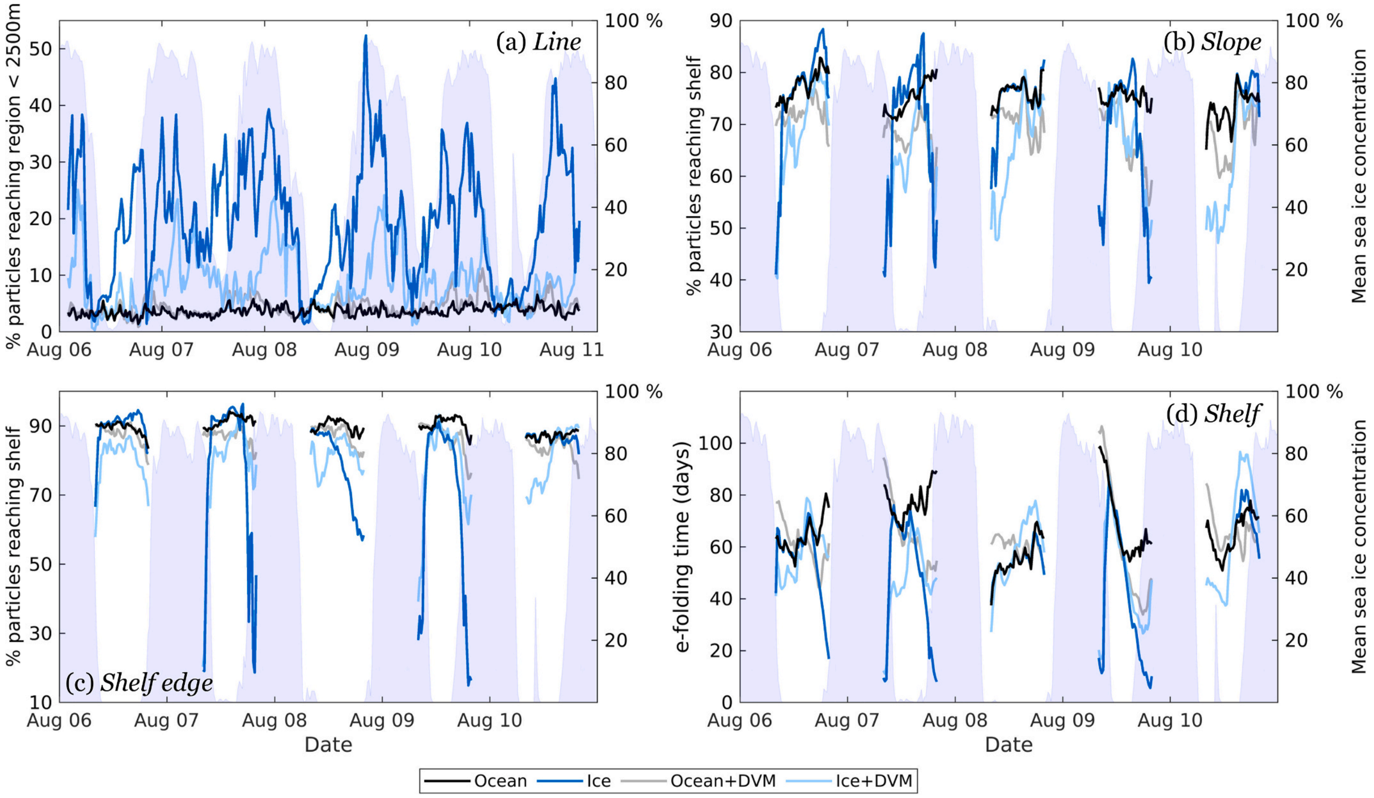

Fig. 6. Variability in the percentage of particles entering the South Orkney Plateau for particles released (a) along lines upstream of the plateau, entering region <2500 m depth, (b) in the slope region entering region <1000 m depth, (c) in the shelf edge region entering region <500 m depth. (d) Variability in the flushing (e-folding) time for particles released in the shelf region with bathymetry <500 m depth. Mean sea ice concentration for (a) the northwest Weddell region, (b) the plateau region with depth < 2500 m, (c) the plateau region with depth < 1000 m, and (d) the plateau region with depth < 500 m is shown. Release regions are shown in Fig. 1.

shelf, with a higher proportion of particles exiting on the eastern side of the shelf, and a smaller proportion exiting on the western side (Fig. 4d). However, there is interannual variability in the distribution of shelf entries and exits due to variability in both the extent and distribution of sea ice. For example, there were much larger increases in the proportion of particles exiting the shelf to the northeast in 2007/08 and 2009/10. Both these years had a longer period of sea ice cover in the South Orkney region (Fig. 6d), so particles released at the start and end of the 6-month release periods experienced more northeastward off-shelf transport through the combination of sea-ice presence, sea-ice drift, and sea-ice associated behaviour.

3.6. *Impact of diel vertical migration*

A further series of model simulations considered the impact of DVM on recruitment and retention in the *Ocean* and *Ice* simulations. Considering the impact on regional-scale recruitment, the addition of DVM to the *Ocean* simulations (*Ocean* + *DVM*) for line releases upstream of the plateau has little impact on the low levels, or the geographical distribution, of recruitment to the South Orkney region (Fig. 6a; Fig. 4a). However, there are predicted small increases in recruitment in winter, most notably in 2010. In winter, when nights are longer, particles spend longer at the surface where the flows have an enhanced northeastward component due to ice drag, which increases the number of particles transported towards the South Orkney region. By contrast, the addition of DVM to the *Ice* simulations (*Ice* + *DVM*) results in a decrease in recruitment, particularly in autumn and winter, with a smaller (larger) proportion entering the region in the northwest (southeast) quadrant relative to the *Ice* simulations (Fig. 6a; Fig. 4a). With shorter days, the particles spend less time moving with the ice, which reduces the influence of ice-associated transport on the quantity and distribution of recruitment to the South Orkney region. The *Ice* + *DVM* simulations tend to have a peak in recruitment for releases in September due to the combined influences of day length and the seasonal ice cycle; as day length increases towards the end of winter, recruitment increases as particles spend more time in the sea ice but, as sea ice retreats in spring, oceanic transport begins to dominate and recruitment decreases again.

On the local scale, the addition of DVM to the *Ocean* simulations tends to reduce recruitment for releases in the shelf edge and slope regions (Fig. 6b,c). However, this trend is temporally variable. Broadly, recruitment is similar to the *Ocean* simulations at the start of the 6-month simulation periods (December) when day length peaks and particles spend more time at depth. The largest reductions in recruitment are generally towards the end of the simulations (May) when days are shorter and *Ocean* + *DVM* particles spend a greater proportion of time in near-surface currents. Direct wind forcing and ice drag thus have a stronger influence on particle transport at this time, and together tend to reduce recruitment. The addition of DVM to the *Ice* simulations also tends to reduce recruitment for releases in the shelf edge and slope regions, although the picture is somewhat mixed. When sea ice is present at the start of the 6-month simulations, the addition of DVM behaviour has very little impact on predicted recruitment as, with the longer days in December, particles are spending most of the day in the sea ice. In the absence of sea ice (for example, 2008/09), the addition of DVM tends to decrease recruitment relative to the *Ice* simulations in this early period, with particles spending more time near the ocean surface. However, recruitment is similar to or greater than the *Ice* simulations during the latter part of the 6-month periods, most notably for the shelf edge releases, both with and without the presence of sea ice, as particles spend less time in the ice or near-surface and are influenced more by deeper

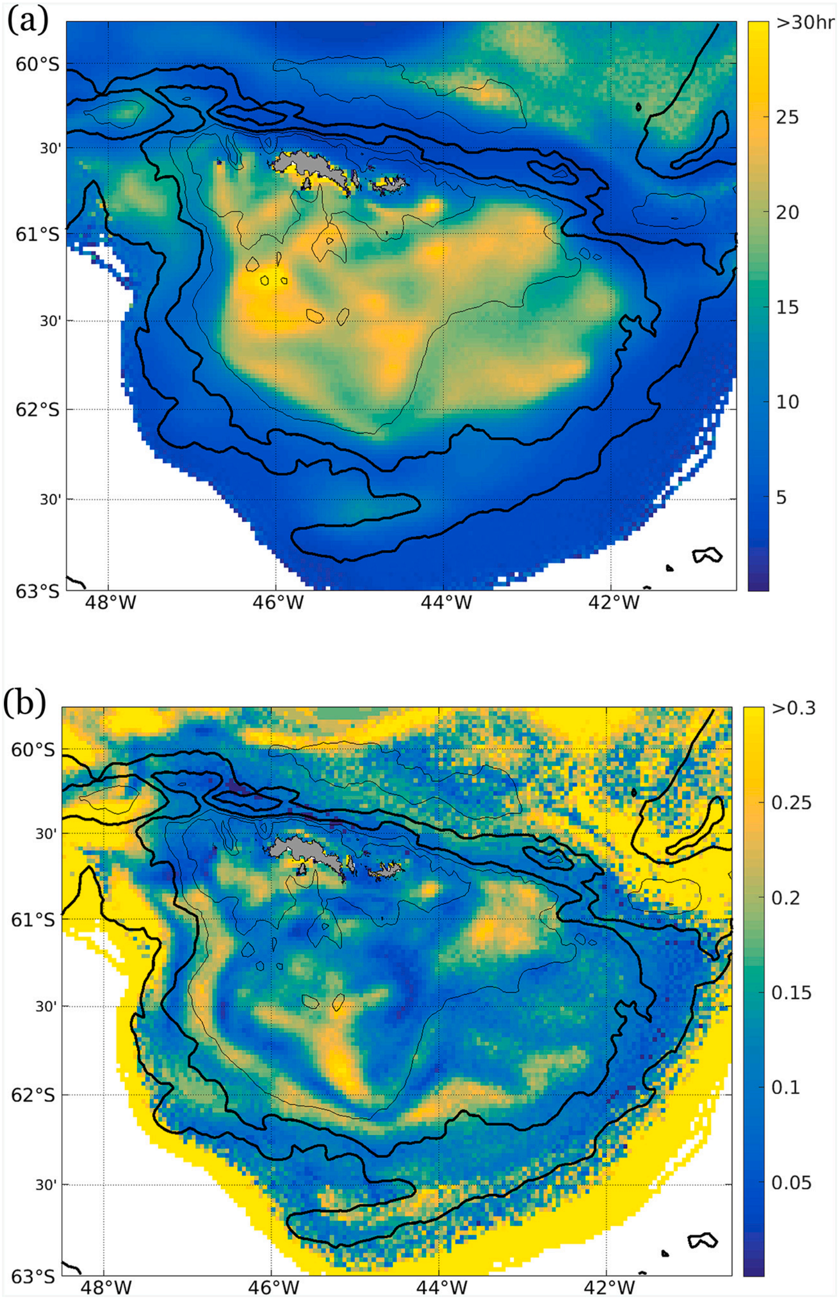

Fig. 7. Geographical distribution of the length of time particles released on the shelf spent in each model grid box for the *Ocean* simulation: (a) mean, (b) coefficient of variation. Isobaths are at 250, 500, 1000, 2500 and 5000 m, with bold contours at 1000 and 2500 m. Release region is shown in Fig. 1.

oceanic currents.

Considering particles released on the shelf, in early summer there is increased retention in the *Ocean + DVM* simulations (Fig. 6d); during the longer days, particles spend a greater proportion of time closer to the seabed where currents are weaker, thus decreasing flushing rates. Conversely in winter, there is decreased retention in the *Ocean + DVM* simulations as particles spend more time near the surface and are more strongly influenced by near-surface ocean currents, including the broadly northeastward drag of the sea ice on surface currents. The *Ice + DVM* simulations show an opposite effect on retention to the *Ocean + DVM* simulations. When sea ice is present in early summer, the addition of DVM to the *Ice* simulations has little impact on retention, as particles continue to spend the majority of time in the ice. However, DVM decreases retention when sea ice is not present as particles spend more time in the near-surface ocean flows. In winter, retention is increased in the *Ice + DVM* simulations as particles spend more time in the ocean at depth, and are less influenced by the northeastward drift of the sea ice.

The addition of DVM tends to have a smaller influence than sea-ice associated behaviour on the distribution of shelf entries and exits, although it becomes relatively more important in years with longer sea ice-free periods (2008/09 and 2010/11; Fig. 4b-d). For slope releases, in both *Ocean* and *Ice* simulations the addition of DVM increases the proportion of particles entering on the western side of the plateau and decreases the proportion entering on the eastern side (Fig. 4b). There is also a small increase in the proportion of recruitment to the southwest quadrant for shelf edge releases (Fig. 4c). These changes suggest that particles in the surface phase of the DVM cycles experience a stronger northeastward component in the near-surface ocean currents and sea-ice drift, which impacts recruitment patterns. Such effects can also be seen in the distribution of shelf exits; the addition of DVM to the *Ocean*

Table 2

Comparison of zonal and meridional components of wind forcing with particle retention (e-folding time) on the South Orkney Plateau, and recruitment for particles released in the shelf edge and slope regions, and along lines upstream of the South Orkney region from the *Ocean* simulations: averaging time scale for strongest correlation (*t, days*), correlation coefficient (*r*) and significance (*p*). Statistically significant correlations are shown in bold.

	Zonal wind			Meridional wind		
	t	*r*	*p*	*t*	*r*	*P*
E-folding time	**61**	**−0.40**	**<0.01**	**33**	**0.23**	**<0.01**
Shelf edge recruitment	120	0.15	0.04	**77**	**0.25**	**<0.01**
Slope recruitment	**82**	**−0.43**	**<0.01**	**39**	**0.58**	**<0.01**
Line recruitment	**93**	**0.24**	**<0.01**	**168**	**−0.29**	**<0.01**

simulations tends to increase the proportion of particles exiting to the northeast and decrease the proportion exiting to the southwest (Fig. 4d). However, the response of the *Ice* simulations to the addition of DVM is more complex and sensitive to the presence of sea ice. Broadly, the proportion of particles exiting to the southwest decreases, and there is an increase in exits to the northwest (Fig. 4d). The latter pattern is particularly evident in years with a longer duration of sea ice (2007/08 and 2009/10) when there is additionally a decrease in exits to the northeast. These trends suggest that for sea ice-associated particles the addition of DVM reduces the impact of northeastward sea-ice transport and increases the influence of the northwestward off-shelf oceanic transport pattern.

3.7. Impacts of atmospheric variability

The variability in recruitment and retention patterns during ice-free periods and in the *Ocean* simulations suggests the presence of important environmental drivers of variability, in addition to variability in sea ice. Here we consider the impact of atmospheric variability in a comparison of recruitment and retention from the *Ocean* simulations with local and regional wind forcing. For reference, the prevailing winds at the South Orkney Islands are westerly.

At the local scale, higher retention (e-folding time) and recruitment are associated with weaker westerly and stronger southerly wind components, with timescales for statistically significant correlations of between 33 and 82 days (Table 2, Appendix A, Fig. A.7). The shorter averaging periods for correlation with the meridional component of wind suggest that local recruitment and retention respond more rapidly to changes in the meridional winds. The correlations suggest that changes to near-surface flows due to weaker westerly and stronger southerly components of wind allow more particles to escape the strong anticyclonic shelf edge circulation to the south and east of the South Orkney Plateau, and subsequently enhance recruitment to the shallow shelf. Once on the shelf, weaker westerly and stronger southerly winds reduce particle losses to the east and south, and the South Orkney Islands restrict direct northward off-shelf transport, thus there is an overall increase in retention times.

Conversely, at the regional scale, increased recruitment to the South Orkney region from upstream sources is associated with stronger westerly and northerly wind components, with a more rapid response to the zonal wind component. The dominant oceanographic barrier for transport of particles towards the South Orkney Plateau from release points west of ~51°W is the northward Antarctic Slope Current (Fig. 2). The correlations suggest that changes to near-surface flows due to stronger westerlies and northerlies reduce the transport of particles over the South Scotia Ridge via the Antarctic Slope Current and increase the number of particles transported towards the South Orkney region in the flows associated with the Weddell Front, with a subsequent increase in recruitment.

4. Discussion

4.1. Recruitment and retention

When ocean flows dominate the transport of krill, the results of our study suggest that the majority of krill are transported towards the South Orkney Plateau from the northwest Weddell Sea in flows associated with the Weddell Front. Transport from the Antarctic Peninsula shelf region is restricted by the northward flows of the Antarctic Slope Current, which tend to transport krill northward through the South Scotia Ridge and into the Scotia Sea. This transport route, and its important role in supplying krill to the South Georgia region has been noted previously (Renner et al., 2012; Thorpe et al., 2007). Model krill tend to enter the South Orkney Islands region in the south and are subsequently steered anticyclonically around the shelf edge towards the main fishing area to the northwest of the South Orkney Islands. Krill that successfully recruit to the shallower plateau have dominant routes of entry in the southeast, and subsequent areas of higher retention on the western shelf and around the islands. Recruitment from the slope region tends to increase from December to April. This increase is related to the strength of the baroclinic component of the shelf edge flows. In early summer as sea-ice retreats, the associated melting leads to enhanced near-surface horizontal density gradients and stronger shelf edge flows, which increase the transport of particles around the shelf and reduce on-shelf recruitment. As the season progresses, turbulent mixing reduces the horizontal density gradients and corresponding baroclinic flows, with a resultant increase in on-shelf recruitment.

The addition of DVM to the *Ocean* and *Ice* simulations has a variable impact on predicted transport, recruitment and retention, related to the length of the near-surface phase of the DVM and subsequent impacts of atmospheric forcing and sea ice. The representation of DVM in the *Ocean + DVM* simulations is based on observations of krill swarms in the open ocean (Tarling et al., 2018), however, seasonal and spatial variability in behaviour has been observed, including an increase in depth range during austral autumn (Lascara et al., 1999; Taki et al., 2005). An increase in depth is likely to have a limited impact on transport pathways in the open ocean but could be expected to be more significant in shallower, shelf regions. As understanding of the complexities of krill behaviour improves, consideration of temporal and spatial variability would be a useful future development of this study.

Previous studies have demonstrated the potential role of sea ice in krill transport both at circumpolar scales, and within the Scotia Sea (Meyer et al., 2017; Murphy et al., 2004; Thorpe et al., 2007). The results of the present study suggest that patterns of oceanic transport in the South Orkneys region are also significantly modified by behaviour in the presence of sea ice; upstream sources cover a much wider geographic area, with krill transported from both the northern Weddell Sea and from the Antarctic Peninsula shelf region. Consequently, the flux of krill entering the South Orkneys region is higher than for krill transported in purely oceanic flows. Conversely, when sea ice is present in the South Orkney region, there is a reduction in local recruitment and retention of model krill undergoing sea-ice associated behaviour due to transport away from the region with the dominant northeastward sea-ice movement. However, as sea ice retreats in late spring, transport pathways are dominated by oceanic flows and there is an increase in recruitment and retention. Thus, the timing of the sea-ice cycle is a key driver of variability in the supply and retention of krill at the South Orkney Plateau. Considering the temporal variability in successful transport, recruitment and retention, maximum krill flux is achieved through an interaction between sea-ice cover required for increased regional transport, and timing of sea-ice retreat for successful recruitment and retention. With a 50 d mean transit time for krill with sea-ice associated behaviour, krill passing through the upstream source lines in October combined with sea-ice retreat from the South Orkney Plateau by the end of November, maximises local recruitment and retention. Thus, a combination of krill behaviour in the presence of sea ice and optimal timing of sea-ice retreat generates a peak in krill flux to the South Orkney region in the austral summer. However, whilst the presence of sea ice can generate high levels of krill transport to the region, recruitment and retention show much greater seasonal and interannual variability. Such variability adds uncertainty to estimates of krill influx to the region. In addition, while the ocean-sea ice model used for this study produces a realistic seasonal sea ice cycle, comparisons with observations suggested there is a tendency for sea ice to extend too far north and west in winter, and too far south in summer. Consequently, the predicted transport patterns due to sea ice-associated behaviour may not be a precise representation of the spatial and temporal variability. In particular, the impacts of sea ice-associated behaviour in summer may be greater than predicted, with higher fluxes from upstream sources east of the Antarctic peninsula, but a longer period of reduced local recruitment and retention in early summer. However, the model simulations presented here clearly demonstrate the importance of sea ice-associated behaviour and permit valuable assessments of the potential impacts of such behaviour.

Whilst sea ice-associated behaviour has a strong impact on model krill transport and retention, such behaviour is thought to vary with krill developmental stage, season, geographic location, and sea-ice structure (Brierley and Watkins, 2000; Flores et al., 2012b; Meyer, 2012; Meyer et al., 2017; Quetin and Ross, 1991). In this study we have used one representation of sea-ice associated behaviour, and changes in the assumed behaviour will affect the model results and interpretation. There are few observations of under-ice behaviour, particularly under pack ice due to the inaccessibility of such regions. Observations suggest that larval krill have a strong association with sea ice (Daly, 2004; Meyer et al., 2017) while adult krill are more flexible in their overwintering strategies and may not rely on sea ice to such an extent (Flores et al., 2012a; Kane et al., 2021; Quetin and Ross, 1991; Schmidt and Atkinson, 2016). Thus, the interpretation of the impacts of sea ice-associated behaviour on transport, recruitment and retention in this study are likely of more relevance to larval krill. Adults may experience a mixture of oceanic and sea ice transport, with additional active swimming behaviour, which would lead to a separation in transport pathways, and potentially different source regions, for krill at different developmental stages.

Model krill with sea-ice associated behaviour, particularly relevant to larval krill, can reach the South Orkney region from the majority of points along the upstream source lines, including the northern Antarctic Peninsula, which implies the potential for a wide geographical spread of source areas including from the West Antarctic Peninsula, which has been identified previously as a key spawning site for Antarctic krill from both analyses of a long-term dataset (Perry et al., 2019) and mechanistic life-cycle modelling studies (Green et al., 2021; Hofmann and Hüsrevoğlu, 2003; Thorpe et al., 2019). By contrast, the more limited source regions implied by the simulated oceanic transport pathways suggest that adult krill with a potentially weaker affinity to sea ice may be less likely to reach the South Orkney region from the West Antarctic Peninsula through passive transport; source regions to the south and east in the Weddell Sea are more probable, although active swimming behaviour may act to decouple adult krill movement from oceanic transport to some extent. With the spatial limitations of the oceanographic model used for this study, source regions cannot be identified definitively; exploration of links to upstream sources requires larger-scale modelling, which is the focus of ongoing model investigations, but also more detailed understanding and subsequent representation of age-dependent krill behaviour. Further, in this study we imposed regular particle distributions within release locations. However, interactions between variable flows and heterogeneous krill distributions are likely to be important and should be considered in future studies as appropriate data become available.

4.2. Impacts of environmental change

Studies of long-term trends in climate indices such as the Southern Annular Mode (SAM) and El Niño Southern Oscillation (ENSO), and environmental variables including water temperature and sea ice, suggest that they will negatively impact krill populations (Atkinson et al., 2022; Flores et al., 2012a; Loeb and Santora, 2015; Murphy et al., 2007a; Murphy et al., 2007b; Saba et al., 2014). However, the underlying mechanisms driving such influences are complex and there remain significant knowledge gaps (Meyer et al., 2020). Model simulations presented here suggest that oceanic transport of krill to the South Orkney region from upstream sources is impacted by the strength and direction of regional winds, with an increase in predicted transport during periods of stronger westerly and northerly winds. Such wind anomalies are associated with the positive phase of SAM (Meredith et al., 2008). Positive SAM is characterised by a poleward displacement of the mid-latitude westerly wind jet, and manifests as an increase in cyclonic wind stress in the Weddell Sea region, and an acceleration of the Weddell Gyre (Jullion et al., 2010; Simpkins et al., 2012). Previous modelling studies have suggested that krill transport from the northwest Weddell Sea to the South Georgia region is increased under positive SAM conditions, with decreased transport to the Bellingshausen Sea (Renner et al., 2012). Experiments with simulated surface drifters suggested that such changes in transport were related to an acceleration of the Weddell Gyre and consequent strengthening of the Antarctic Slope Current (Youngs et al., 2015). The results of our study suggest that krill transport to the South Orkney region may be similarly increased under wind conditions typical of a positive SAM phase. We hypothesise that associated winds enhance the eastward component of near-surface currents in the northwest Weddell Sea, while acceleration of the Weddell Gyre strengthens flows associated with the Weddell Front. Together, these drive an increase in the transport of particles to the South Orkney region from the northwest Weddell Sea. By contrast, simulations also suggest that stronger westerly and northerly winds are associated with a decrease in local recruitment and retention. Thus, for winds characteristic of positive SAM conditions, the transport and availability of krill at the South Orkney Islands is likely to be a balance between the contradictory influences of increased regional transport and decreased local recruitment and retention. However, this inference assumes passive oceanic transport of krill and neglects the strong affinity of krill with sea ice, most notably during the larval phase.

Positive SAM is further associated with a decreased sea-ice concentration in the northwest Weddell Sea between December and May, and a reduced northward sea-ice extent from June to November (Simpkins et al., 2012). Such trends arise from the increased advection of warm air from the north and southward ice drift, with enhanced air-sea heat fluxes during colder seasons increasing sea surface temperatures and impacting sea ice formation. Analyses of seasonal trends in SAM (1957–2018) showed statistically significant increases in summer and autumn (Fogt and Marshall, 2020). However, whilst significant negative correlations between observed (1979–2004) September sea-ice extent in the Weddell sector and SAM have been found (Lefebvre and Goosse, 2008), recent studies suggest a seasonally varying relationship (Kumar et al., 2021) and additional drivers of sea-ice variability including ENSO and ocean-ice interactions are likely important (Murphy et al., 2014; Simpkins et al., 2012). Analyses of sea-ice extent from 1979 to 2004 showed a change to the timing of the seasonal sea-ice cycle in the northwest Weddell Sea, with an earlier retreat in spring, a later advance in autumn, and a shorter sea-ice season (Stammerjohn et al., 2008). In this study we have demonstrated how the timing and distribution of sea ice, combined with sea-ice associated behaviour, may have a strong impact on krill flux to the South Orkney region from the northwest Weddell Sea and Antarctic Peninsula, and on local recruitment and retention. Specifically, transport of krill from upstream sources is significantly increased if sea ice-associated behaviour is included and sea ice is present in the northwest Weddell Sea. Conversely, the presence of sea ice in the South Orkneys region reduces the local recruitment and retention of sea ice-associated krill. Thus, the earlier sea-ice retreat associated with positive SAM conditions may reduce transport of sea-ice associated krill from upstream sources in spring but increase local recruitment and retention at the South Orkney Plateau.

Analysis of model projections from the most recent phase of the Coupled Model Intercomparison project (CMIP6) found that for socio-economic pathways with middle to high greenhouse gas emissions, SAM will continue increasing, most strongly in autumn (Deng et al., 2022). This suggests there could be ongoing strengthening of westerly and northerly winds during the 21st century and further reductions in sea-ice extent and the length of the sea-ice season. Indeed, the multi-model mean projection is for sea-ice area loss in all forcing scenarios, for both summer and winter, by the end of the 21st century (Holmes et al., 2022). Under a strong forcing scenario, models project a near-total loss of sea ice in summer and a loss of 40% of sea-ice area on average in winter, by the end of the 21st century. A southward displacement of the marginal ice zone would impact the geographical extent of sea-ice influence on transport pathways for sea ice-associated krill. Lower sea-ice concentrations or a shorter period of sea-ice cover in the northwest Weddell Sea and Antarctic Peninsula could decrease the flux of krill to the South Orkney region. Conversely, delayed sea-ice advance in the Weddell Sea may promote recruitment and retention of krill on and around the South Orkney Plateau later into autumn. However, such effects would be modified by the contradictory impact of winds associated with positive SAM and assume a strong affinity to sea ice, which is typically associated more with larval and juvenile krill.

The impacts of environmental variability on transport pathways highlighted by this study contribute to a growing understanding of the environmental drivers of krill population variability and response to climate change. Observational and modelling studies have highlighted the importance of the seasonal extent of sea ice for successful larval recruitment, with enhanced survival in years with extensive sea-ice cover, especially in late autumn and early winter (Atkinson et al., 2004; Meyer et al., 2020; Thorpe et al., 2019). Recent studies have suggested that krill have a nuanced response to changing sea-ice dynamics, responding to changes in sea ice quality, such as ice thickness and ridging rate, but within the underlying constraints of sea-ice extent and timing (Melbourne-Thomas et al., 2016; Veytia et al., 2021). Declining sea ice may impact krill recruitment through multiple and possibly cumulative effects, including its role as a transport platform, a shelter for predator avoidance, and a feeding ground. A southward contraction of the winter sea-ice zone would reduce ice algal productivity and the extent of ice edge blooms in spring due to lower light availability at higher latitudes, thus impacting the availability of food and subsequent krill growth and survival (Flores et al., 2012a). A latitudinal shift in the sea-ice edge would also affect the distribution of krill as they leave the marginal ice zone when sea ice retreats in spring. This would influence subsequent oceanic transport paths and destinations, with implications for the supply of krill to downstream populations (Mori et al., 2019). In addition to a decline in sea ice, climate change is projected to increase ocean temperatures and storminess, the latter related to more positive SAM. Together, these could lead to changes in primary productivity and the distribution of successful spawning habitat, with the potential for a mismatch between krill biological timings and food availability (Piñones and Fedorov, 2016; Veytia et al., 2020).

To date, studies have examined the roles of subsets of environmental or behavioural drivers to project the response of krill populations to a changing climate. This study has demonstrated how changes to winds and sea ice associated with a more positive SAM could have a contradictory impact on krill transport pathways in the South Orkneys region, with further complexity introduced by differing krill behaviours in the presence of sea ice. More realistic projections of the response of krill populations to future climate change requires development of a krill life cycle model within a Lagrangian framework to better represent the temporally- and spatially-varying response of different life stages to a changing environment.

4.3. Implications for management

Penguins breeding at the South Orkney Islands have been observed to forage both on the plateau and at the shelf break (Lowther et al., 2020; Lynnes et al., 2002; Warwick-Evans et al., 2018). The foraging distribution of chinstrap penguins depends on the breeding phase, with a more constrained foraging area during the brood and creche phases, and also on the location of the colonies (Warwick-Evans et al., 2018). Chinstrap colonies along the southern coasts tend to have foraging distributions on the plateau and the western shelf edge, whilst those to the north and northwest tend to forage along the shelf edge to the north and northwest. Thus, the potential overlap with the krill fishery, which is concentrated along the shelf edge to the northwest of the islands (Santa Cruz et al., 2022), will vary with both the colony location and the breeding phase.

Predators foraging to the northwest likely have the greatest overlap with fishing activity. For example, the distribution of highest density chinstrap foraging lies along the shelf edge to the northwest of the South Orkney Islands, coinciding with the region of most intense fishing activity (Warwick-Evans et al., 2018). Simulated flow fields show strong currents along the shelf edge and a coincident concentration of transport pathways, which together suggest there may be a rapid flux of krill around the edge of the plateau towards the northwest. Replenishment rates may therefore be high along the shelf edge, which may explain in part the observed tendency of chinstraps to travel towards the shelf edge to forage (Warwick-Evans et al., 2018). The modelling suggests that the retroflection in transport pathways to the south of Pirie Bank could also contribute to high krill availability to the northwest of the South Orkneys. Observations have described a hotspot for foraging and fishing associated with canyons on the northwest South Orkney Plateau (Krafft et al., 2015). Although this lies within a broad region of high predicted krill flux, the mechanisms underpinning the hotspot are unclear. The canyons are small bathymetric features that are not well resolved by the regional model presented here; further studies with a nested very high-resolution model are required to clarify the underlying physical processes.

Although high predicted krill transport and replenishment rates in the northwest region could mitigate potential impacts of krill fishing on foraging success, the supply of krill is ultimately dependent on the strength of upstream sources. As discussed in Section 4.1, the location of upstream sources depends on the behavioural response of krill to the presence of sea ice, which is not well known and is likely dependent on the stage of development (Meyer et al., 2017). Estimates of the strength of potential sources can be derived from climatological compilations (KRILLBASE; Atkinson et al., 2017), large-scale synoptic surveys (Krafft et al., 2021), and local-scale monitoring programs (Krafft et al., 2018). However, whilst climatologies and synoptic surveys have broader spatial coverage than local-scale monitoring programs, there are still areas with limited observations, including the Weddell Sea (Atkinson et al., 2009), which introduces uncertainties in biomass estimates in potentially important source regions. Further, climatological data do not capture interannual variability in krill density, which can vary by an order of magnitude between consecutive years (Siegel, 2005). Influx is also dependent on the survival of krill during the austral winter when food resources are more limited. Larval krill have low lipid reserves and are vulnerable to extended periods of starvation (Hagen et al., 2001). In this modelling study, we have demonstrated that both environmental variability and krill behaviour can influence the transport of krill to the South Orkney region; however, simulation of variability in the magnitude of krill flux is currently limited by the uncertainties surrounding age-dependent krill behaviours and the size of source populations. Further development of biophysical models to provide information of more direct relevance to krill fishery management requires a better understanding and integration of key age-dependent krill behaviours and representation of the full krill life cycle, underpinned by observations and monitoring.

5. Conclusions

Management of the Antarctic krill fishery requires an understanding of variability in the distribution and supply of krill whilst also considering the spatially- and temporally-varying foraging demands of higher predators. In this study, we have highlighted the roles of environmental variability and behaviour in krill transport, recruitment, and retention in the South Orkney region.

The strength and direction of winds affect the transport, recruitment and retention of krill, and subsequent availability of krill for land-based predators and the local krill fishery. Weaker westerly and stronger southerly winds increase retention of krill on the plateau. However, increased recruitment to the South Orkneys region is associated with stronger westerly and northerly wind components, which drive changes to near-surface flows that reduce the transport of particles across the South Scotia Ridge via the Antarctic Slope Current. These environmental drivers influence the supply of krill on seasonal and interannual timescales, and respond to large-scale climate indices such as the SAM. The seasonal sea-ice cycle also responds to climate variability, with reduced sea-ice extent and earlier fast-ice breakout associated with a positive SAM (Murphy et al., 2014; Simpkins et al., 2012). Here, our model experiments have demonstrated that variability in sea-ice extent coupled with sea-ice associated behaviour impacts krill transport patterns, and subsequent recruitment and retention. When sea ice is present, local retention is reduced but transport and recruitment from upstream sources is increased, with optimum recruitment achieved for krill in the northwest Weddell Sea when sea ice retreats from the South Orkney Plateau by the end of November. Thus, the regional-scale flux of krill and local recruitment and retention have complex and often opposing responses to winds and sea ice, and the effect of large-scale climate patterns, such as the SAM, on these key environmental variables may also have contradictory influences on krill transport patterns. A better understanding of the role of a changing climate on the krill population at the South Orkney Islands requires multi-decadal model simulations such that the relative influences of seasonal, interannual and longer-term changes can be determined.

The effect of sea ice is strongly dependent on krill behaviour, which is in part dependent on age and stage of development (Meyer, 2012). Predicted oceanic transport pathways suggest that adult krill with a potentially weaker affinity to sea ice may be less likely to reach the South Orkneys region from the Antarctic Peninsula, although active swimming behaviour may act to decouple adult krill movement from oceanic transport. In this study, interpretation of the impacts of sea ice has assumed a set of behaviours that are not yet well-understood, and the simplified representation is likely to be over-estimating the impacts. A better understanding of the role of krill behaviour in modifying transport patterns requires more field studies of age- and environment-specific krill behaviour to refine the model representation of such behaviours. Further, the magnitude of the krill flux to the South Orkneys region is also dependent on the strength of upstream sources. Consideration of upstream sources requires large-scale models and representation of the full krill life cycle, underpinned by greater understanding of the drivers of krill recruitment. Model development guided by targeted observations will allow more focussed modelling studies and further improve our understanding of the roles of behaviour and environmental processes on krill population dynamics, the potential impact of future climate change, and contribute to more informed management of the Antarctic krill fishery.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

This research was supported by a grant from the Antarctic Wildlife Research Fund and British Antarctic Survey National Capability funding to the Ecosystems and Polar Oceans science programmes. AHHR's contribution was supported by The Research Council of Norway through the SWARM project (grant no. 26716). Modelling studies were performed on the British Antarctic Survey high performance computing facility. We thank J. Midoli Goto for contributing additional model runs. The UK Foreign, Commonwealth and Development Office funded the South Orkneys regional model development, which used the ARCHER UK (www.archer.ac.uk) National Supercomputing Service. We thank J. M. van Wessem for providing RACMO output, and the National Oceanography Centre, Southampton for access to global NEMO model output. We thank two anonymous reviewers, whose comments helped us improve the original manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jmarsys.2023.103920.

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