Variability in transport pathways on and around the South Georgia shelf, Southern Ocean: Implications for recruitment and retention

Emma F. Young,[1] Sally E. Thorpe,[1] Neelofer Banglawala,[1] and Eugene J. Murphy[1]

Received 9 August 2013; revised 19 December 2013; accepted 22 December 2013; published 15 January 2014.

[1] The waters around South Georgia are among the most productive in the Southern Ocean, with zooplankton populations close to the island, in particular Antarctic krill, supporting vast colonies of higher predators. However, our understanding of the processes governing variability in the supply of these food resources is limited by the poor spatial and temporal resolution of available data. Here, we use a numerical modeling approach to examine the underlying physical processes driving the recruitment and retention of zooplankton to the South Georgia shelf. Variability in the magnitude and spatial distribution of recruitment was dominated by the proximity and orientation of the southern Antarctic Circumpolar Current front to the shelf edge. Shelf retention was highest for source sites on the southwest shelf, with the main transport routes off the shelf to the north and northwest. Retention was lowest in the austral summer and winter; in summer increased glacial melt drives stronger off-shelf near-surface currents, while in winter, stronger winds lead to an increase in off-shelf transport. Of particular note was the prediction of a significant increase in retention for particles released throughout the shelf in April and July 2000. This period coincided with the development of pronounced anticlockwise shelf flows, associated with horizontal density gradients due to reduced wind mixing of shelf waters, and differences between shelf and oceanic waters, which significantly reduced off-shelf transport rates. Such findings are crucial for understanding the influence of variability in physical processes on the ecosystem at South Georgia.

Citation: Young, E. F., S. E. Thorpe, N. Banglawala, and E. J. Murphy (2014), Variability in transport pathways on and around the South Georgia shelf, Southern Ocean: Implications for recruitment and retention, *J. Geophys. Res. Oceans*, *119*, 241–252, doi:10.1002/2013JC009348.

1. Introduction

[2] The island of South Georgia is situated in the path of the Antarctic Circumpolar Current (ACC) in the northeast Scotia Sea, Southern Ocean (Figure 1). The waters surrounding South Georgia are among the most productive in the Southern Ocean with increased levels of biomass and production of phytoplankton and zooplankton supporting vast colonies of higher predators that breed on the island, including macaroni and gentoo penguins, and fur seals [e.g., *Atkinson et al*., 2001]. Of particular interest at South Georgia is Antarctic krill (*Euphausia superba*), a species that dominates the pelagic ecosystem and is a key prey item for these local colonies. The krill population around the island is not considered to be self-sustaining, but is instead dependent on the transport of krill into the region in association with the major current flows of the ACC [*Murphy et al*., 2007b]. There is marked interannual variability in the abundance of krill around the island and hence in the availability of krill to the predators, many of which are constrained during their breeding seasons to foraging close to the island to feed their young [*Trathan et al*., 2006]. This generates major fluctuations in the foraging and breeding success of these predators.

[3] Studies into physical drivers of the ecological variability observed at South Georgia have tended to focus on larger-scale environmental fluctuations, such as the El Nino-Southern Oscillation and the Southern Annular Mode, and variability in the regional oceanography [e.g., *Thorpe et al*., 2002; *Meredith et al*., 2003; *Murphy et al*., 2007a]. South Georgia lies between two major fronts of the ACC, the Polar Front to the north and the southern ACC front (SACCF) that approaches South Georgia from the southwest, loops anticyclonically around the island's shelf and then retroflects to the east [*Orsi et al*., 1995; *Thorpe et al*., 2002; *Meredith et al*., 2003]. The SACCF has been shown to be an important transport mechanism for bringing biological material such as Antarctic krill to the South Georgia region from the Antarctic Peninsula [*Hofmann et al*., 1998; *Murphy et al*., 1998, 2004; *Fach et al*., 2006]. However, while the large-scale modeling studies have permitted examination of the main transport pathways and the variability associated with the influx of zooplankton to the

[1]British Antarctic Survey, Natural Environment Research Council, Cambridge, UK.

Corresponding author: E. F. Young, British Antarctic Survey, Natural Environment Research Council, Madingley Road, Cambridge CB3 0ET, UK. (eyoung@bas.ac.uk)

2169-9275/14/10.1002/2013JC009348

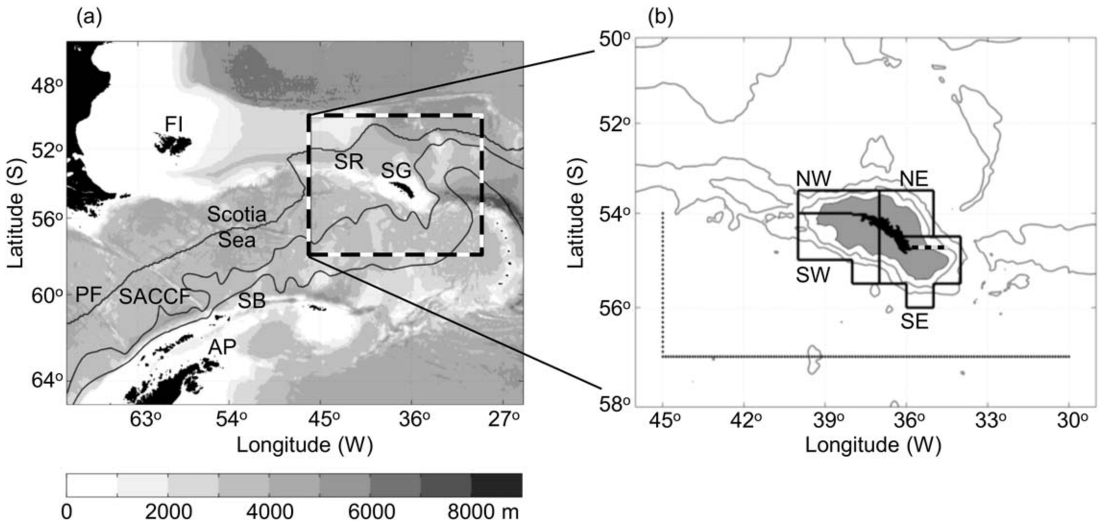

Figure 1. (a) Map showing the location of South Georgia (SG) and Shag Rocks (SR), with the model region indicated with dashed lines. Solid black lines indicate the mean positions of the Polar Front (PF) following *Moore et al*. [1997], the Southern ACC Front (SACCF) and the southern boundary of the ACC (SB), both from *Thorpe* [2001]. AP is Antarctic Peninsula, and FI is Falkland Islands. Bathymetry (shaded at 1000 m intervals) is from *Smith and Sandwell* [1997]. (b) The model region with black lines delineating specific shelf regions used in retention analyses: NW, SW, SE, and NE. Black circles mark the particle release sites used in the off-shelf simulations. The dashed line is the location of the section presented in Figure 4. Gray contours are model bathymetry (contours at 300, 1000, 2500, and 5000 m), and the area shaded gray is the shelf region $\leq$300 m where particles were released in the on-shelf simulations.

region, the resolution of these models has not been sufficient to resolve transfer onto the shelf once in the South Georgia region, and the ensuing retention/exchange of material on the shelf. Further knowledge of these processes, and the drivers of variability in them, is critical for a better understanding of the ecosystem of South Georgia and for management of the area’s fisheries. High-resolution modeling has been shown to be a useful tool for the study of the physical processes influencing the recruitment and retention of krill in the Antarctic Peninsula region [*Pinones et al*., 2013]. This study highlighted the potential importance of interactions between large-scale oceanic flows and the shelf edge for on-shelf transport of krill larvae, in particular through the intrusion of Circumpolar Deep Water, and showed how complex shelf bathymetry could generate regions of retention.

[4] In this study, we use an existing fine resolution model of the South Georgia shelf and the surrounding area [*Young et al*., 2011] that is capable of resolving the finer scale processes that are important in cross-shelf exchange and retention. The high resolution of the hydrodynamic model (approximately 3 km horizontally with 45 terrain-following vertical levels) permits accurate representation of the shelf bathymetry with its deep canyons and the associated vertical motions, simulation of tides and their interaction with the complex bathymetry, and coastal fluxes of freshwater. Detailed flow fields generated by the hydrodynamic model are used with a Lagrangian model to define the characteristics of the transport pathways on and around the South Georgia shelf. This approach allows the identification of the key physical processes impacting the recruitment and retention of planktonic marine biota, including young krill with limited swimming capability. While the model does not include swimming behavior typical of older krill, this study is a key step toward our understanding of the physical processes underpinning the recruitment and retention of krill at South Georgia.

[5] The following section provides details of the hydrodynamic and Lagrangian models used in this study. Section 3 provides a description of the results, including the simulated oceanography and its variability, identification of dominant transport pathways onto the South Georgia shelf, areas of retention on the shelf and key exit routes off the shelf. In section 4, the physical processes driving the simulated variability in recruitment and retention are discussed, and the implications for our understanding of krill populations at South Georgia are considered. Finally, the main results and conclusions are summarized in section 5.

2. Numerical Models

2.1. Hydrodynamic Model

[6] Hourly flows from a high-resolution ($\sim$3 km) hydrodynamic model of the South Georgia region [*Young et al*., 2011] were available for the years 1997/1998, 1998/1999, and 2000/2001. These three periods experienced relative extremes in atmospheric forcing over the Southern Ocean, associated with extreme phases of large-scale coupled modes of interannual climate variability [see *Meredith et al*., 2008, for full discussion]. Simulation of these years therefore captures a range of physical variability and allows clear identification of persistent trends. Full details of the development and validation of the hydrodynamic model

may be found in *Young et al*. [2011]; a summary is presented here.

[7] The hydrodynamic model is an application of the Proudman Oceanographic Laboratory Coastal Ocean Modelling System (POLCOMS), a three-dimensional finite difference primitive equation model (described by *Proctor and James* [1996], *Holt and Jame* [2001]), with spherical polar *s*-coordinates [*Song and Haidvogel*, 1994], specifically the terrain-following *s*-coordinate transformation described in *Holt and James* [2001]. The model domain extends from 46°W, 58°S to 29°W, 50°S (Figure 1) and has a grid spacing of 1/20° longitude by 1/40° latitude (~3 km), with 45 layers in the vertical. Lateral open boundary forcing comprised tidal forcing from the Oregon State University global tidal model, TPXO6.2 [*Egbert and Erofeeva*, 2002], and baroclinic forcing derived from 5 day mean fields generated by the Ocean Circulation and Climate Advanced Modelling Project [OCCAM; *Webb et al*., 1998] 1/4° model. Surface fluxes of heat and momentum were calculated from 6 hourly ERA-40 reanalysis data from the European Centre for Medium-Range Weather Forecasts (ECMWF) [*Uppala et al*., 2005], with surface freshwater fluxes calculated by combining daily precipitation rates from ECMWF ERA-40 and the evaporative loss term of the bulk heat flux formulae. Temporal variability in daily freshwater fluxes at the South Georgia coast (predominantly glacial melt) was estimated using a theoretical description of the seasonal melt cycle at South Georgia, based on historical temperature and precipitation data [see *Young et al*., 2011, for full details]. The locations of the dominant freshwater sources were identified using satellite imagery, and the relative magnitude of the sources was determined from the sizes of their catchment areas.

2.2. Lagrangian Model

[8] Hourly flows from the circulation model were used to advect Lagrangian particles representing the planktonic stages of marine biota. The model is based on the particle-tracking scheme described by *Young* [1996], and has been applied previously to studies of fish larvae and zooplankton transport on the South Georgia shelf [*Ward et al*., 2007; *Young et al*., 2012]. In summary, particles were advected at each model time step (5 min) according to the imposed horizontal velocity field using a second-order Runge-Kutta method. Additional horizontal and vertical diffusions were included using a random-walk approach [*Dyke*, 2001], assuming isotropic diffusion, and with horizontal and vertical diffusion coefficients of 10 and 0.0001 $m^2\ s^{-1}$, respectively. These values fall within the range of established values from the published literature and are in accordance with observed values from the Southern Ocean [*Sheen et al*., 2013; *Watson et al*., 2013]. A slip condition was used for particles reaching land, and particles that left the model domain through the open boundary were assumed to have left the region.

[9] Two sets of model experiments were undertaken: (1) simulations with off-shelf release sites were designed to identify key transport routes onto the South Georgia shelf; (2) simulations with on-shelf release sites were used to investigate dominant transport routes off the shelf, and areas of retention on the shelf. Off-shelf release sites were located inside the south and west boundaries of the hydrodynamic model, between latitudes 57°S and 54°S at longitude 45°W, and between longitudes 45°W and 30°W at latitude 57°S (Figure 1). Three particles were released at every 0.1 grid cell (horizontal spacing of ~300 m), one at each of 50, 150, and 250 m depth. For on-shelf simulations, three particles were released at the center of each model grid cell defined as a shelf point (depth <300 m; Figure 1), one at each of 5 m, 25% of the local water depth, and 50% of the local water depth. A total of 12,603 particles were released for each off-shelf simulation and 10,707 particles for each on-shelf simulation. Particles were allowed to move randomly in the vertical, according to the random-walk scheme, between the depths of 2 and 300 m; this range was chosen to encompass the observed vertical distribution of krill swarms in the Scotia Sea [*Tarling et al*., 2009]. Ten time periods were simulated, for durations of 9 months, with start dates of 15 January, 15 April, and 15 July in each of 1997, 1998, and 2000, and an additional run starting on 15 October 1997. The 9 month duration was sufficient time for particles released off-shelf to reach South Georgia, and also for the determination of flushing times for those particles released on-shelf. The choice of time periods, while limited by the availability of the underlying flow fields, permitted analyses of interannual and seasonal variability.

[10] A variety of model analyses were performed to identify persistent features and levels of variability in predicted particle transport, recruitment and retention. Dominant transport pathways for particles released both on- and off-shelf were determined by calculating the number of particles that passed through each model grid cell ("unique occupancy"). Off-shelf simulations were analyzed for key aspects of recruitment, specifically the proportion of particles successfully recruiting to the shelf (defined as depth <300 m), the geographical origin of these particles, and the location at which they entered the shelf. On-shelf simulations were used to investigate patterns in retention and loss, specifically flushing (e-folding) time, the locations at which particles exited the shelf, and their depth on exit. The mean length of time particles occupied each model grid cell ("mean occupancy") was calculated to illustrate regions of retention on the shelf. Interannual variability in the observed patterns was assessed by comparing model results from particle releases in April and July in the 3 study years. Seasonal variability was investigated by comparing model results for releases at 3 monthly intervals between July 1997 and April 1998.

3. Results

3.1. Hydrodynamic Simulations

[11] Comparisons with observational data have shown the model to reproduce key features of the oceanography around South Georgia [*Young et al*., 2011]. Variability in the large-scale oceanography is predicted by the model, in particular the high degree of temporal and spatial variability in the position of the SACCF [*Meredith et al*., 2003]. A strong and persistent full-depth northward flow between the South Georgia and Shag Rocks shelves is also predicted, in agreement with observed drifter tracks [*Young et al*., 2012]. The seasonal cycle in stratification is reproduced, with horizontal density gradients driving a temporally variable shelf

break front, in agreement with observations [*Meredith et al*., 2005]. The accuracy of model predictions is limited by uncertainties in the open boundary forcing, and lack of interannual variability in freshwater fluxes [*Young et al*., 2011]. However, these comparisons demonstrate the ability of the numerical model to reproduce key observed features of the oceanography around South Georgia.

[12] The SACCF is predicted to approach the South Georgia shelf from the southwest, looping anticyclonically around the shelf before continuing to the northeast. However, the orientation of the front with respect to the southern shelf edge, and the location where the strongest flows impact the shelf edge, are variable. Considering the 3 monthly mean flows for April to June (Figure 2), the SACCF in 1998 had a more east/west orientation, only weakly impacting the southern shelf. By contrast, in 1997 and 2000 the SACCF had a strong northward component as it impacted the southwest shelf, before turning toward the southeast. On the northern side of the SACCF, flows turn northward along the western shelf edge, with the strength of these flows dependent on the position and orientation of the SACCF as it approaches the shelf. With a more east/west SACCF orientation in 1998, these flows were weaker.

[13] An underlying feature of the South Georgia on-shelf flows is a tendency for anticlockwise flows around the island from the south and southeast shelf, continuing on the northern shelf before exiting the shelf to the north and northwest (Figure 3). Flows from the southwest shelf tend to be northward, either joining the aforementioned off-shelf flows or turning eastward along the southern shelf. To the west of South Georgia, flows tend to be weaker and more variable. However, overlying these broad patterns, there is significant seasonal and interannual variability in the flows. During the austral summer and autumn, when there are increased freshwater inputs from glacial melt, strong vertical salinity gradients and enhanced near-surface off-shelf flows are predicted on the northern shelf. A strengthening of flows around the southeast tip of the island is also predicted, due to glacial freshwater inputs to the southern shelf and the subsequent generation of horizontal density gradients (Figure 4). The location of the strongest off-shelf flows varies both seasonally and interannually, with a suggestion of off-shelf flows further west in the austral autumn (Figure 3), and generally further east in April and July 1998 relative to the same months in 1997 and 2000. Of particular note is the prediction of an anticlockwise shelf current circumnavigating the island in the austral winter 2000, which is likely to aid retention during this period.

3.2. Recruitment

[14] The transport pathways of particles released at off-shelf release sites were analyzed to identify patterns in recruitment to the South Georgia shelf. Unique occupancy plots (Figure 5), which reveal dominant particle transport pathways, show some clear general trends, in particular a dominant north-eastward transport from the release sites in the southwest toward the South Georgia shelf. Once they reach the shelf, the majority of particles travel to the east along the southern edge of the South Georgia shelf, and continue around the shelf edge to the north of South Georgia, with some particles recruiting to the shelf, and a minority traveling to the west and north along the western South

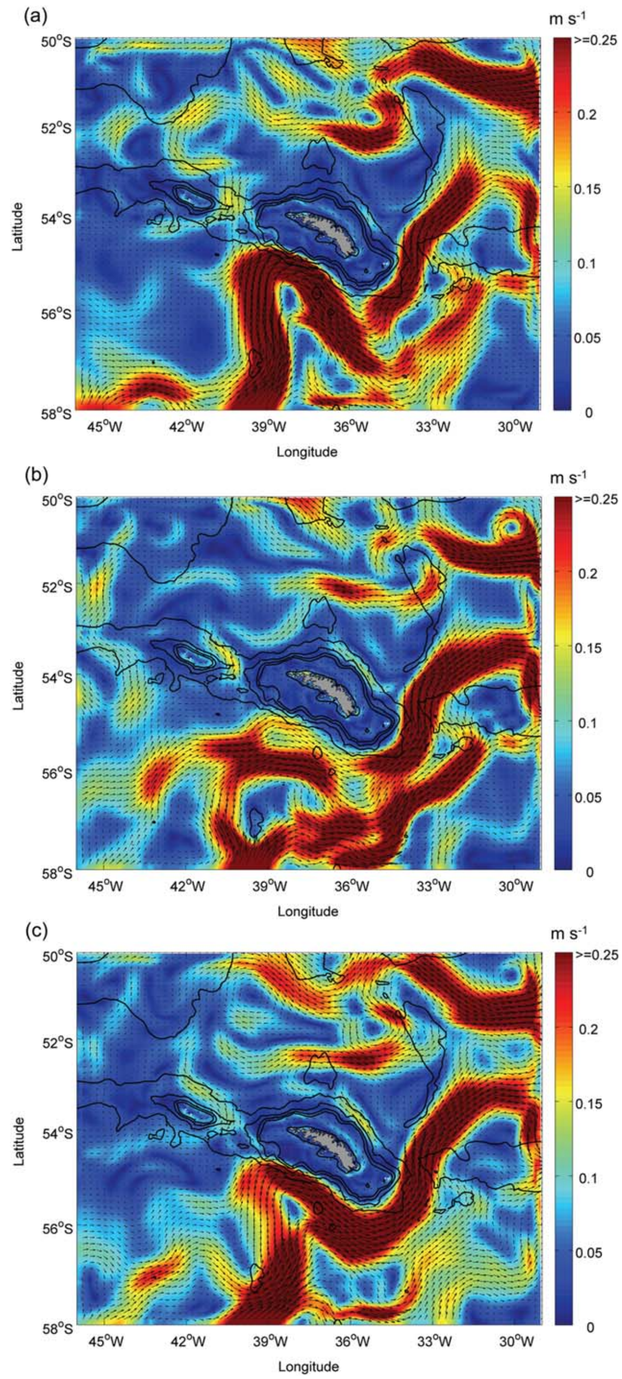

Figure 2. Predicted 3 monthly mean near-surface flows for 15 April to 15 July (a) 1997, (b) 1998, and (c) 2000. Every fifth flow vector is shown, and the color bar indicates mean speed (m s^{-1}). Solid black lines are model bathymetry contours at 100, 300, 500, 1000, 2500, and 5000 m.

Georgia shelf edge. However, overlying this general picture are high levels of seasonal and interannual variability. For example, a large number of particles pass through the southern and eastern shelf following their release in April 1997 (Figure 5a), whilst the unique occupancy plot for particles released in April 1998 (Figure 5b) shows very little recruitment to the shelf. Particle trajectories for this period (not shown) reveal a tendency for a more southerly

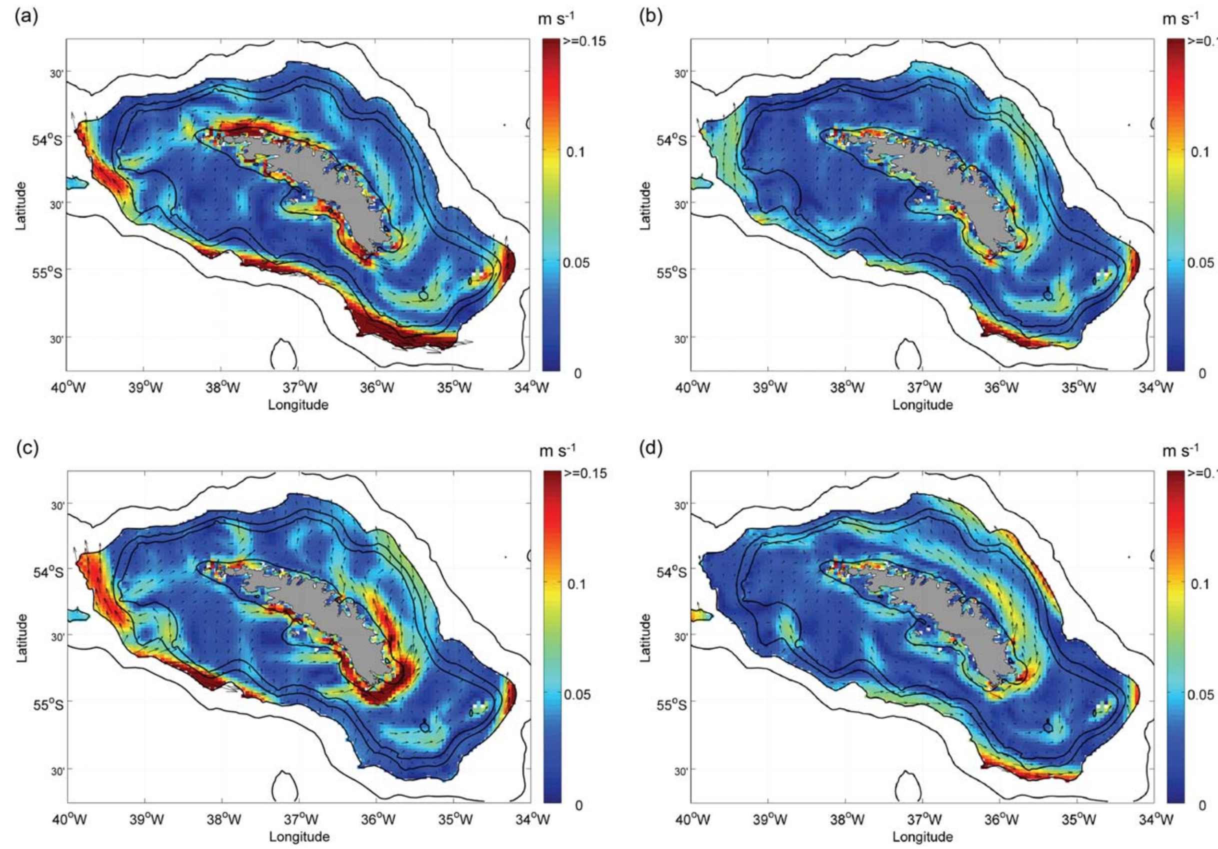

Figure 3. Predicted monthly mean near-surface flows for (a) 15 July to 15 August 1997, (b) 15 October to 15 November 1997, (c) 15 January to 15 February 1998, and (d) 15 April to 15 May 1998. Every third flow vector is shown, and the color bar indicates mean speed (m s^{-1}). Solid black lines are model bathymetry contours at 100, 300, 500, 1000, 2500, and 5000 m. Off-shelf regions deeper than 1000 m are masked.

transport pathway, further from the shelf edge, and without the strong northward component seen at other times.

[15] Particles successfully recruiting to the South Georgia shelf tend to originate from release sites to the southwest. However, within this general pattern, there is considerable interannual and seasonal variability in the distribution of these particles, and in the proportion of particles released off-shelf that successfully recruit. Comparing the distribution of particle origins for April 1997, 1998, and 2000 (Figure 5), the highest concentration is along the southern boundary in 1997 but has a more "L-shaped" distribution in both 1998 and 2000 with more particles originating from the southern half of the western boundary. The level of seasonal variability in particle origins is similar to that seen in the interannual comparison; while there is again a tendency for an "L-shaped" distribution pattern, there is variability in the distribution of the highest concentration of particles. Highest concentrations are along the southern boundary for July 1997, along the western boundary for October 1997/January 1998, and in the southwest corner for April 1998.

[16] The levels of seasonal and interannual variability in the proportion of particles successfully recruiting to the South Georgia shelf are very similar, with ranges of 1.9–7.6%, 1.7–9.2%, and 1.9–9.2% for the April, July, and seasonal (July 1997 to April 1998) comparisons, respectively (Table 1). Highest recruitment was predicted for particle releases in April and July 1997, with least for April and July 1998.

[17] Particles tend to recruit to the South Georgia shelf in higher numbers on the southern side, with highest numbers of particles frequently predicted in the vicinities of (38.5°W, 54.7°S) and (34.5°W, 55°S) (Figure 6). However, the distribution of entry points also shows seasonal and interannual variability. For example, superimposed on these general trends, there is a region of increased entries in the middle of the southern shelf in January 1998 (Figure 6c), and fewer entries to the south-western shelf in April 1998 (Figure 6d). In addition, although the majority of particles tend to enter the shelf on the southern side, on occasion a significant number of particles are predicted to enter the shelf on the northern side (e.g., July 1997; Figure 6a).

3.3. Retention

[18] The transport pathways of particles released at on-shelf release sites were analyzed to identify the key features of transport and retention on the South Georgia shelf. Unique occupancy plots show that more particles pass across the northern shelf than the southern (Figure 7). Particle density plots at 1, 3, and 6 months after release show that this is due to a general trend for transport from the southern to the northern shelf. Preferred off-shelf transport

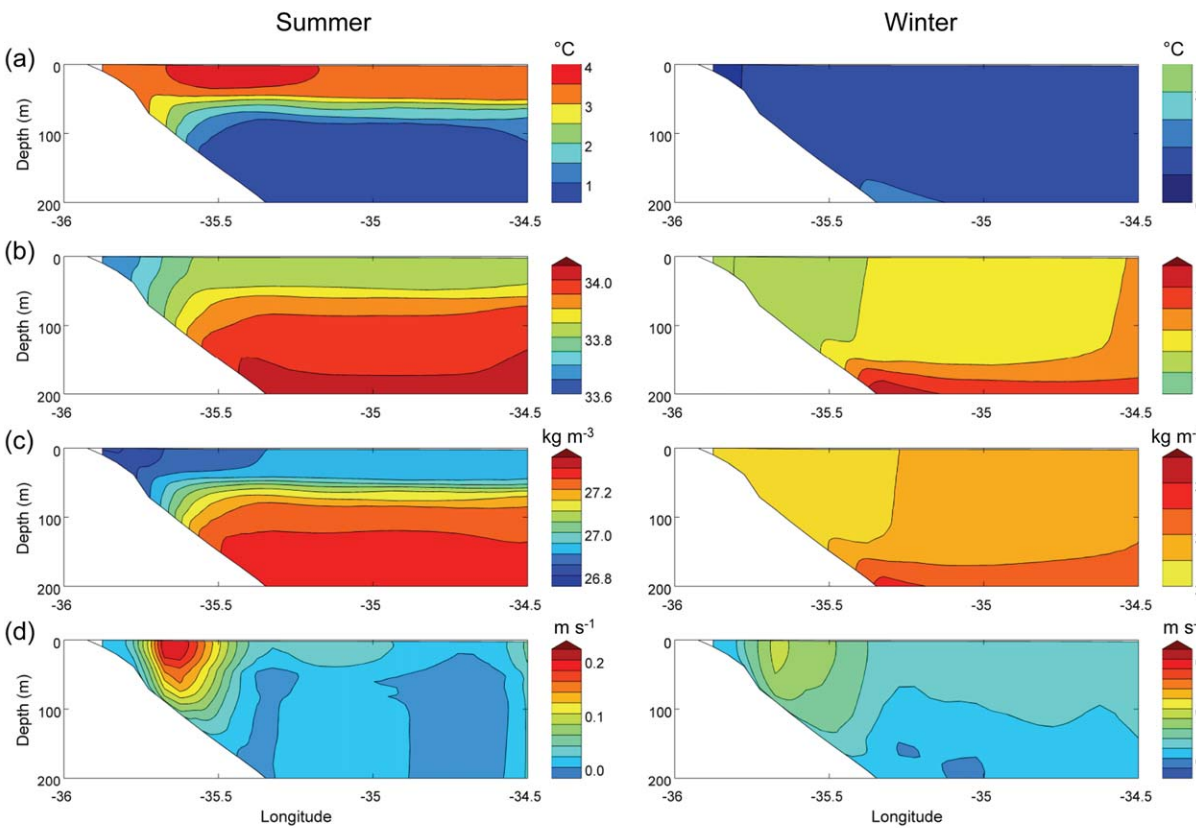

Figure 4. Vertical sections of monthly mean (a) potential temperature, (b) salinity, (c) potential density anomaly, and (d) northward current speed, for a section east of South Georgia (Figure 1). The left plot corresponds to the period 15 January 1997 to 15 February 1997 (summer), and the right plot corresponds to the period 15 July 1997 to 15 August 1997 (winter).

pathways are to the north and northwest, with consistently higher numbers of particles exiting the South Georgia shelf from the northern shelf. However, overlying these general trends are significant levels of seasonal and interannual variability. An interannual comparison of the unique occupancy plots for particle releases in April and July shows higher occupancy on the southern shelf in 2000 relative to 1997 and 1998 (Figure 7). Seasonal variability in transport on the shelf can be inferred from the distribution of retained particles 6 months after release, with highest densities in the northwest for the July 1997 and October 1997 runs, in the northeast for the April 1998 run, and in the southwest for the January 1998 run. Particle density plots at 3 monthly intervals from the start of the April simulations reveal variability in the location of the dominant off-shelf transport route. While most particles exit from the middle of the north shelf in 1997, the main off-shelf transport route moves from northwest to north during the course of the 2000 simulation, and is further east in 1998. Particle depth on exit is consistently shallower on the northern shelf. This is due to particles originating from the southern shelf having passed over relatively shallow bathymetry. This forces them to a shallower trajectory, which tends to persist and influences the mean exit depths from the northern shelf.

[19] Shelf flushing times over the period of the model simulations show considerable seasonal and interannual variability, with a distinctive "zigzag" pattern (Figure 8). Seasonally, the shortest flushing times are predicted for the July and January runs, with the slowest flushing (longest retention) predicted for the October and April runs. Comparing the results for the April and July simulations, flushing times are similar in 1997 and 1998, but considerably longer in 2000.

[20] Considering the geographical variability in retention, in all the simulations, the average length of time a particle spent in each grid cell ("mean occupancy") is higher on the southern shelf, and in particular in the southwest, with particles predicted to transit the northern shelf more rapidly (Figure 9). The near-coast region, most notably near the north coast of South Georgia, also has higher mean occupancy times, and there is a small region of consistently higher mean occupancy toward the southeast corner of the shelf. The regions of lowest mean occupancy are consistently around the northwest and southeast tips of the island. Some variability is predicted within these general trends. Mean occupancy times in the southwest region are slightly higher in 2000 than in the comparable 1997 and 1998 simulations. There are also temporal differences in the predicted mean occupancy along the southern shelf edge, as illustrated by the slower transit times in the southeast in the January 1998 simulation (Figure 9). Although tides on the South Georgia shelf are weak and thus do not significantly impact larval transport and retention, previous work [*Young et al.*, 2011] identified potential areas of increased retention

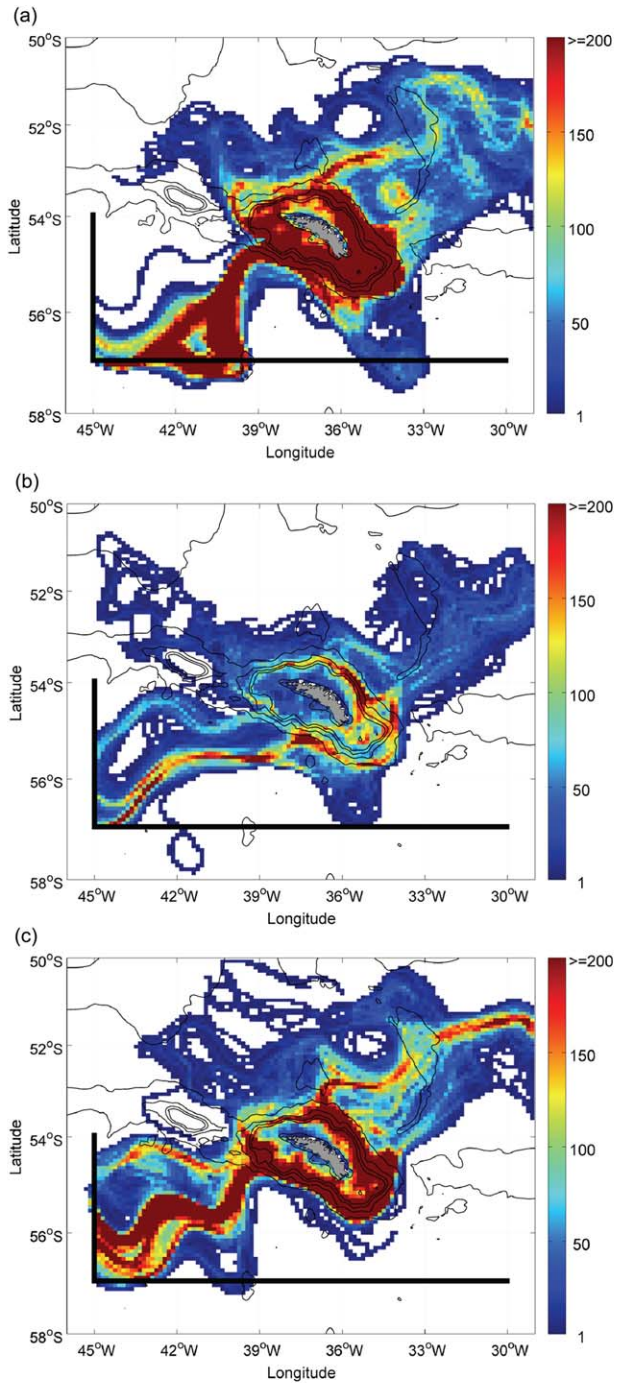

Figure 5. Unique occupancy of particles released at off-shelf sites on 15 April in (a) 1997, (b) 1998, and (c) 2000. Here, the unique occupancy calculation considers only those particles that reach the South Georgia shelf, and particle numbers are integrated onto a coarse-scale grid of one-third the resolution of the underlying hydrodynamic grid. The location of release sites is indicated by the black lines.

along the shelf edge associated with diurnal tides. However, no evidence for these features could be identified in the present study.

[21] To further examine geographical variability in retention, the South Georgia shelf was divided into the four regions detailed in Figure 1. Local retention was assessed by calculating the loss of particles from a particular region, released within that region, but not necessarily lost from the wider shelf area ("quadrant flushing time"). The contribution of each region to overall shelf retention was evaluated by calculating the loss of particles from the shelf following release within a particular region ("quadrant-shelf flushing time"). The use of e-folding time to calculate flushing times means that the results are independent of the areal coverage of each quadrant, and of the number of particles released therein, and are thus comparable between quadrants. The ranking of regions by quadrant flushing time is consistent for the January, April, and October simulations, with longest flushing times for the southwest region, coincident with the higher mean occupancy times for this region, followed by the northwest and southeast regions, and with most rapid flushing of the northeast region. However, the order of quadrant flushing times for the July runs does not follow this pattern, and is inconsistent between the 3 years. Considering the ranking of regions by quadrant-shelf flushing times, the southwest region again tends to have the longest flushing time, with the exception of the January 1997 and July 2000 simulations (Figure 8). However, the ranking of the other regions is variable. The shortest quadrant-shelf flushing times are generally predicted for either the northwest or northeast region, but the southeast region is most rapidly flushed in the April 2000 simulation.

[22] By considering the destination of particles released from specific regions at 3 and 6 months after release, further aspects of the variability in on-shelf transport can be inferred. Comparing the simulations for April 1997, 1998, and 2000, the predictions for 1997 and 1998 are broadly similar. However, in 2000 a greater proportion of particles released in the northwest reach the southwest and southeast regions after 3 and 6 months, and more particles released in the northeast reach the same regions after 6 months. Similar differences are seen in a comparison of the July simulations, with a higher proportion of particles released in the northwest and northeast regions reaching the southwest after 3 and 6 months in 2000. Additionally, transport from the northeast to the northwest region after 1 and 3 months is higher in this year, and a greater proportion of particles released in the southwest are transported to the southeast region, with fewer entering the northwest region.

Table 1. The Percentage of Particles Released Off-Shelf That Successfully Reach the South Georgia Shelf During a 9 Month Simulation

Particle Release Date	Successful Recruitment (%)
15 Jan. 1997	5.4
15 Apr. 1997	7.6
15 Jul. 1997	9.2
15 Oct. 1997	3.4
15 Jan. 1998	4.5
15 Apr. 1998	1.9
15 Jul. 1998	1.7
15 Jan. 2000	2.6
15 Apr. 2000	6.1
15 Jul. 2000	4.2

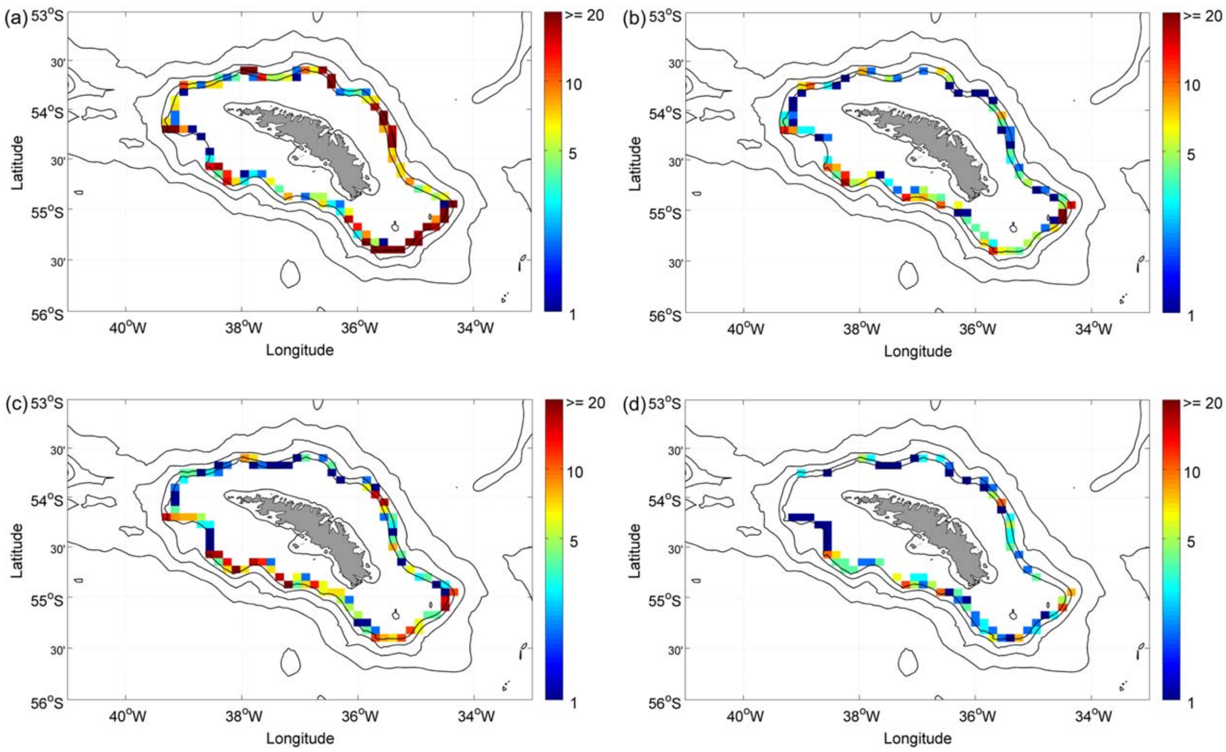

Figure 6. Distribution of shelf entry points for particles released at off-shelf sites, expressed as number of particles per coarse grid cell (one-third the resolution of the underlying hydrodynamic model). Simulation start dates are (a) 15 July 1997, (b) 15 October 1997, (c) 15 January 1998, and (d) 15 April 1998.

4. Discussion

4.1. Recruitment

[23] Large-scale transport and recruitment patterns around South Georgia are dominated by the path of the ACC, and in particular the position of the SACCF. The mean path of the SACCF is north-eastward across the Scotia Sea, looping anticyclonically around the South Georgia shelf before retroflecting to the east. This is reflected in the tendency for particles recruiting to the shelf to originate along the southwest boundaries, and in the dominant anticyclonic pathway illustrated in the unique occupancy plots (Figure 5). On reaching the shelf from the southwest, the change of direction of the SACCF from a north-eastward to an eastward flow generates an on-shelf near-surface flow and a persistent area of increased particle entries. At the eastern extremity of the shelf, the SACCF often clips the shelf edge, generating a second region of enhanced entry to the shelf. Although theoretically the predominantly westerly winds in the region could enhance recruitment to the southern shelf through generation of a northward Ekman transport, the strength and complexity of the large-scale geostrophic flows are far more significant.

[24] However, mesoscale variability in the proximity and orientation of the SACCF to the South Georgia shelf drives high levels of seasonal and interannual variability in patterns of recruitment. During periods when the SACCF has a strong northward component as it approaches the southwest shelf (e.g., 15 April to 15 July 1997; Figure 2a), the resultant enhanced on-shelf flows lead to increased recruitment to the southern shelf, and particle origins are concentrated along the southern boundary (Figure 5a). By contrast, when the SACCF is located further to the south and has a more eastward orientation (e.g., 15 April to 15 July 1998; Figure 2b), recruitment to the shelf is reduced, with more particles originating from the western boundary. The latter SACCF configuration also changes the distribution of peak particle entries; the flows impact the southern shelf most strongly further to the east, reducing the influx to the south-western shelf (e.g., April 1998; Figure 6d). On occasion, flows on the northern side of the SACCF are predicted to continue further around the South Georgia shelf edge to the northwest before retroflecting to the east. When this occurs, a significant number of particles are predicted to enter the shelf on the northern side (e.g., July 1997; Figure 6a).

4.2. Retention

[25] Retention on the South Georgia shelf shows a high degree of seasonal variability. Retention is lower during the austral summer and winter, with consistently shorter shelf flushing times predicted for particle releases in January and July (Figure 8). During the summer, coastal freshwater inputs (glacial melt) peak, with a corresponding increase in near-surface, off-shelf flows from the northern shelf, and more rapid anticlockwise currents around the southeast tip of the island due to the development of strong horizontal density gradients (Figure 4). During the austral winter, stronger winds generate an increase in current speeds, most notably around the tips of the island (Figure 3), which increases flushing rates. Thus, during the austral

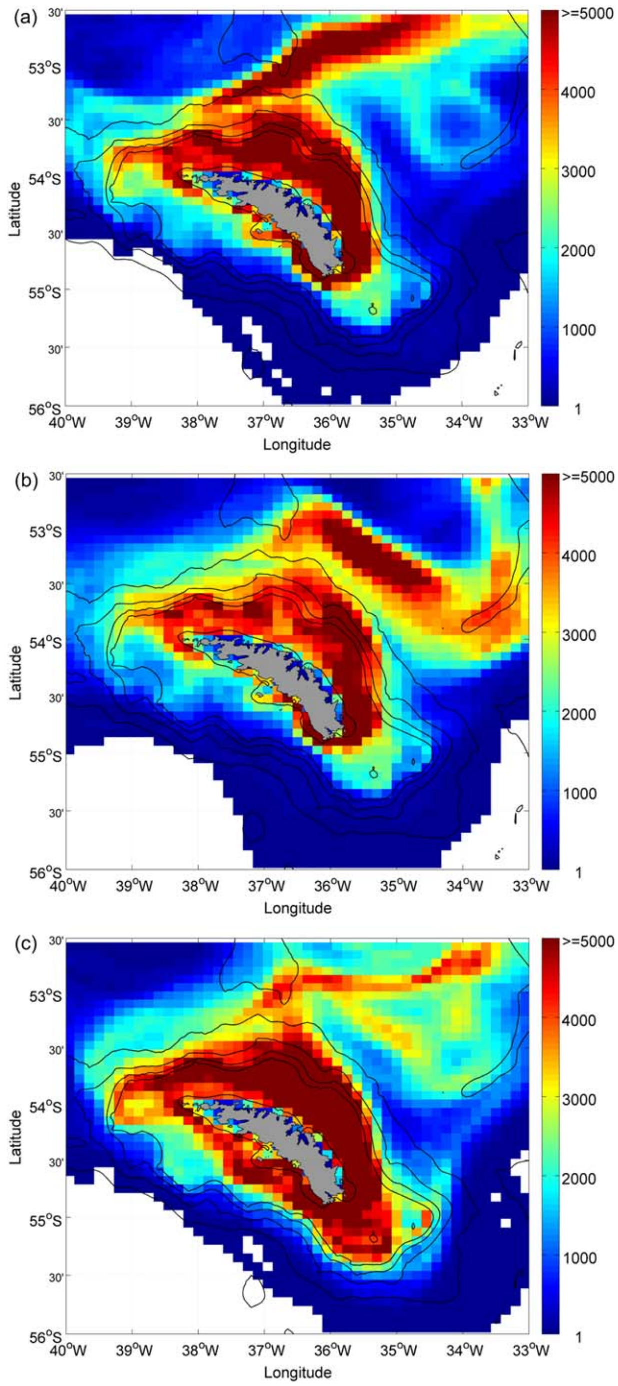

Figure 7. Unique occupancy of particles released on the South Georgia shelf on 15 July in (a) 1997, (b) 1998, and (c) 2000. Here, particle numbers are integrated onto a coarse-scale grid of one-third the resolution of the underlying hydrodynamic grid.

summer and winter more rapid flushing of both the southern and northern regions of the shelf occurs.

[26] Considering the effect of winds in more detail, monthly and 3 monthly mean wind speeds for South Georgia for the periods following each particle release were extracted from the ECMWF ERA-40 reanalysis (which was used to force the hydrodynamic model) and compared with the predicted shelf and quadrant flushing times. Significant negative correlations were found for the 3 monthly mean wind speed and flushing times for the shelf ($r^2 = 0.43$, $p = 0.040$), southeast quadrant ($r^2 = 0.60$, $p = 0.008$), and northeast quadrant ($r^2 = 0.41$, $p = 0.047$). For the monthly mean wind speed, a significant negative correlation was found for the northwest quadrant ($r^2 = 0.51$, $p = 0.021$). Thus, increased wind speed during the period following particle release is associated with more rapid flushing of the shelf, with the northwest region, which tends to have a shorter flushing time (Figure 8), responding to winds over a shorter time period than the other quadrants. No significant correlations between wind speed and retention in the southwest quadrant were found. However, retention in this region was significantly positively correlated with the 3 monthly mean wind direction ($r^2 = 0.49$, $p = 0.025$); mean winds with a more southerly component are associated with slower flushing of this quadrant.

[27] Flushing rates on the South Georgia shelf show considerable variability between regions. The northwest and northeast quadrants tend to have the shortest flushing times (Figure 8). The dominant off-shelf transport routes are from the northern shelf, thus particles released in these quadrants have the shortest distance to the main exit routes, and are retained for a shorter time period. The longest flushing times are predicted for the southwest quadrant. Particles released here travel either to the north before exiting the shelf, or to the east, traveling along the southern shelf before turning northward and exiting the shelf. The latter particles have a considerably longer transit route before exiting the shelf than those released in other quadrants, and thus are retained for longer. Mean occupancy is also longer in the southwest quadrant (Figure 9), indicative of generally weaker flows, with consequently longer flushing times.

[28] Overlaying the patterns described above, there is distinct interannual variability in retention. Of particular note is the considerably higher retention for April and July

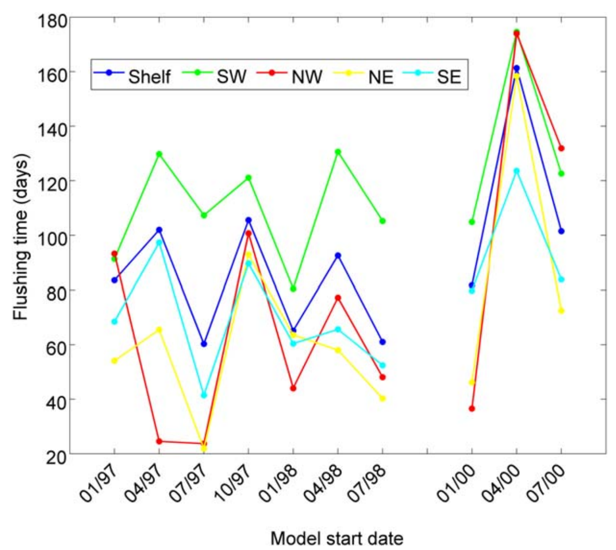

Figure 8. Predicted flushing (e-folding) time for model simulations with particles either released throughout the shelf (defined as depth ≤300 m) or within one of four shelf regions (SW, NW, NE, SE; Figure 1).

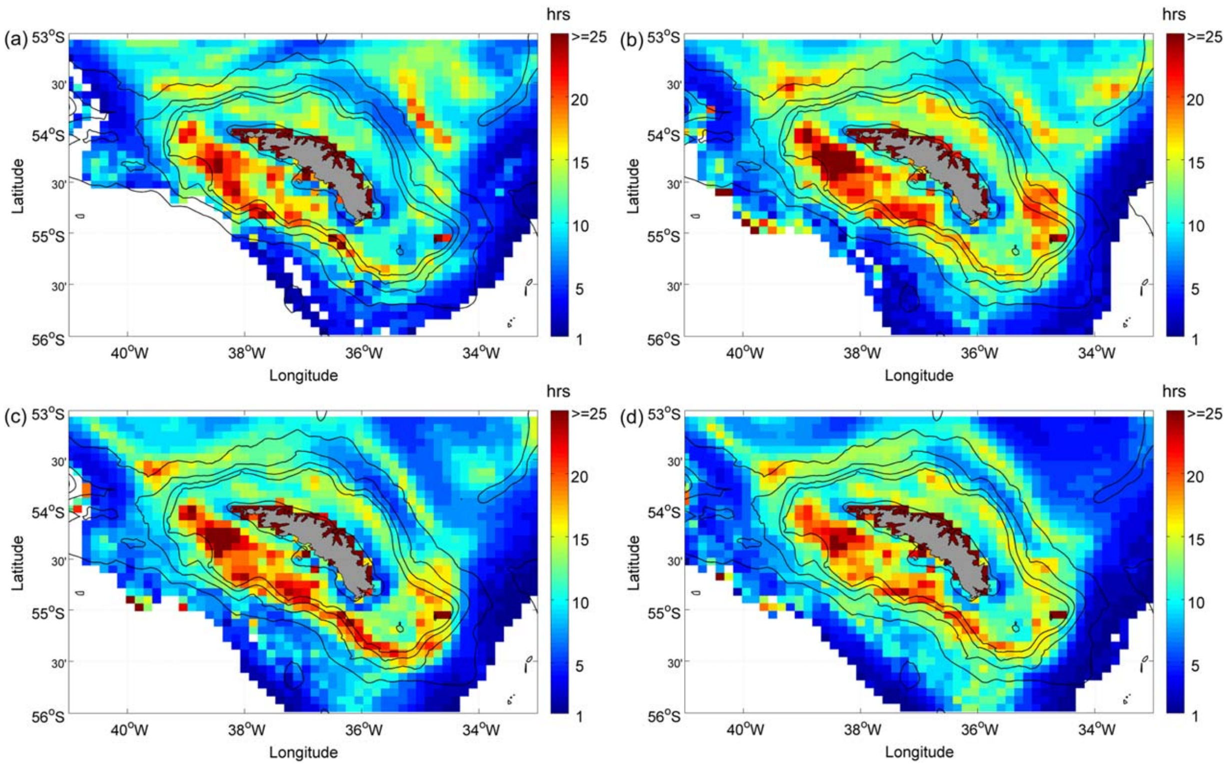

Figure 9. Mean occupancy (hours) of particles released on the South Georgia shelf on (a) 15 July 1997, (b) 15 October 1997, (c) 15 January 1998, and (d) 15 April 1998. Here, mean particle occupancy is averaged onto a coarse-scale grid of one-third the resolution of the underlying hydrodynamic model.

2000 compared with the equivalent particle releases in 1997 and 1998 (Figure 8). During the austral autumn and winter in 2000, an anticlockwise circulation was predicted on the South Georgia shelf, circumnavigating the island, which reduced the off-shelf transport of particles. This flow was driven by horizontal density gradients from two origins. First, weaker winds during the austral autumn and winter in 2000 relative to 1997 and 1998 caused reduced mixing, resulting in the persistence of residual density gradients due to coastal freshwater inputs. Second, during the latter part of this period, density gradients between shelf and oceanic waters, with fresher water on the shelf, were predicted. Variability in the latter horizontal density gradients and associated flows have been observed previously [*Meredith et al*., 2005], and this study clearly demonstrates the importance of this circulation feature for retention of planktonic organisms on the shelf.

4.3. Implications for Recruitment and Retention of Antarctic Krill

[29] Variability in the krill population at South Georgia has been linked to fluctuations in the influx of krill to the region, and to changes in the source populations upstream of the island [*Hofmann and Murphy*, 2004; *Thorpe et al*., 2004; *Fach et al*., 2006; *Murphy et al*., 2007b; *Thorpe et al*., 2007]. The current view is that during cold periods more krill enter the area around South Georgia, becoming entrained in the region as part of the local population, and that growth conditions are enhanced [*Atkinson et al*., 2006]. Larval krill overwinter in sea ice covered regions around the Antarctic Peninsula and the northern Weddell/southern Scotia Sea [*Daly*, 1990]. During the spring, when the sea ice retreats, the general oceanic advection disperses krill in the upper ocean across the Scotia Sea. These krill are more likely to arrive in the vicinity of South Georgia when conditions are generally cooler and the edge of the sea ice occurs further north during late winter and early spring [*Thorpe et al*., 2007]. The combined effect of these processes generates marked fluctuations in the abundance of krill at South Georgia [*Murphy et al*., 2007b]. Current understanding is that this variability is driven by years of successful recruitment separated by periods of low recruitment, which can result in years of extremely low krill abundance [*Murphy et al*., 2007b; *Thorpe et al*., 2007; *Reid et al*., 2010].

[30] The model simulations described in this paper demonstrate that, in addition to these larger-scale influences, local physical processes can impact the krill population at South Georgia. Simulations of particles released to the southwest of South Georgia have illustrated how the proximity and orientation of the SACCF to the southern South Georgia shelf influences the recruitment of marine biota to the South Georgia system, with stronger recruitment at times. Although these particles lack aspects of behavior typically seen in older krill, simulated recruitment is relevant to young krill with reduced swimming capability. The model prediction of high levels of recruitment to the South Georgia shelf in winter and spring 1997 is in agreement with data from predator diet samples (Table 1; particles released off-shelf took, on average, approximately 4 months to reach the shelf). The length-frequency distribution of krill in the diet of macaroni penguins (*Eudyptes*

chrysolophus) in summer 1997/1998 had a bimodal distribution with peaks at krill lengths of 16 and 42 mm (C. M. Waluda, BAS, unpublished data, 2013). The presence of the smaller size class suggests that there was an influx of young krill to South Georgia prior to this season. Poor recruitment to the shelf region was predicted for particle releases in autumn and winter 1998 (Table 1), with reduced winter retention of material that successfully reached the shelf (Figure 8). Together this would imply the successful importation of relatively few young krill to the South Georgia shelf system prior to the 1998/1999 predator breeding season. Diet samples from macaroni penguins for the 1998/1999 summer season show a single peak in the length-frequency distribution at a relatively large size (58 mm; C. M. Waluda, BAS, unpublished data, 2013). This suggests that there was no significant recruitment of young krill to the South Georgia population prior to this period, which is consistent with the model predictions from this study.

[31] The slowest shelf flushing rates predicted by the model were of the order 5.5 months. By comparison, the size of krill found in predator diet data suggests that krill can be retained for much longer than this at South Georgia [order of a few years, *Reid et al*., 2010]. However, this study did not consider the effect of zooplankton (krill) behavior on retention. Retention rates predicted by this study are therefore more appropriate for young krill with reduced swimming capability, or other weakly motile zooplankton. Older krill are capable of maintaining horizontal swimming speeds of at least 0.2 m s^{-1} [*Kils*, 1981], which would allow them to modify their transport. *Cresswell et al*. [2007] used numerical modeling to demonstrate how krill could modify their position on the South Georgia shelf by varying their swimming speed and turning rate in response to environmental cues. Krill also perform vertical migration, and are known to feed near the sea bed [*Schmidt et al*., 2011]. A modeling study of larval fish transport and retention at South Georgia [*Young et al*., 2012] found that diel vertical migration increased retention rates, and it is likely that this behavior would also increase the retention of krill. Due to vertical current shear, krill feeding near the sea bed would be exposed to weaker currents, which again is likely to increase retention. Thus, there are several behavioral mechanisms that could allow older krill to modify their transport on the South Georgia shelf; these will be investigated as part of ongoing research into krill populations at South Georgia.

5. Summary and Conclusions

[32] Previous modeling studies have demonstrated how large-scale physical processes, such as sea ice extent and climate variability, may influence the marine ecosystem at South Georgia by, for example, affecting the local krill population. However, such studies were unable to resolve local recruitment and retention processes. In this study, high-resolution numerical models were used to identify the key physical processes driving transport, recruitment, and retention to the South Georgia shelf.

[33] Recruitment variability was dominated by the proximity and orientation of the SACCF to the South Georgia shelf. During periods when the front had a more east-west orientation and was positioned further south, recruitment to the shelf was significantly reduced. Previous modeling studies have highlighted the role of the SACCF in transporting krill from the Antarctic Peninsula to the South Georgia region and this study further emphasizes the importance of the SACCF in the recruitment of krill to the South Georgia population. The maintenance of the local krill population will be affected by variability in shelf retention. Flushing rates for the shelf are highly variable, both spatially and temporally. The southwest region generally has the slowest flushing rate, with most rapid flushing of the northern shelf, coincident with the dominant transport routes off the shelf. Retention is reduced in the Austral summer and winter, due to freshwater inputs and increased wind speeds, respectively. However, horizontal density gradients, both on the shelf and between shelf and oceanic waters, can generate flows that increase the retention of particles. Flushing rates for the period following recruitment to the shelf will modify the size of the imported population, such that strong recruitment may not necessarily lead to high numbers of imported krill if subsequent retention is very poor.

[34] Although this regional modeling study did not take account of upstream variability in krill populations, or biological processes such as the behavior, growth and mortality of krill, simulated recruitment success for young krill prior to the 1997/1998 and 1998/1999 breeding seasons is broadly in agreement with predator diet data. This result is promising and suggests that it would be valuable to simulate recruitment for a longer time period to examine the ability of the model to reproduce the observed variability in krill recruitment, and to identify the underlying physical influences. Further development of the models to take account of upstream processes and key aspects of krill biology, including behavior, could also be considered to enhance model predictions. In addition, the present model configuration uses large-scale atmospheric forcing from reanalysis, which does not adequately resolve fine-scale processes, in particular the effect of island blocking. This may generate features such as wind jets around the island tips, and a region of decreased wind speeds in the island wake [e.g., *Chelton et al*., 2004], and may thus impact retention on the shelf. Development of a high-resolution atmospheric model to adequately account for such features would be advantageous for future studies of the region. This study has identified key physical processes influencing recruitment and retention of zooplankton to the South Georgia shelf, which is a fundamental step toward understanding the role of variability in physical processes on ecosystem dynamics at South Georgia.

[35] **Acknowledgments.** We thank M. P. Meredith (BAS) for his advice on interpretation of the output of the hydrodynamic model, and C. M. Waluda (BAS) for analysis and discussion of macaroni penguin diet data. We thank the three anonymous reviewers whose constructive comments helped improve the original manuscript. This work was carried out as part of the Ecosystems Programme at the British Antarctic Survey, Natural Environment Research Council.

References

Atkinson, A., M. J. Whitehouse, J. Priddle, G. C. Cripps, P. Ward, and M. A. Brandon (2001), South Georgia, Antarctica: A productive, cold water, pelagic ecosystem, *Mar. Ecol. Prog. Ser.*, *216*, 279–308.

Atkinson, A., R. S. Shreeve, A. G. Hirst, P. Rothery, G. A. Tarling, D. W. Pond, R. E. Korb, E. J. Murphy, and J. L. Watkins (2006), Natural growth rates in Antarctic krill (*Euphausia superba*). II: Predictive models based on food, temperature, body length, sex, and maturity stage, *Limnol. Oceanogr.*, *51*(2), 973–987.

Chelton, D. B., M. G. Schlax, M. H. Freilich, and R. F. Milliff (2004), Satellite measurements reveal persistent small-scale features in ocean winds, *Science*, *303*(5660), 978–983, doi:10.1126/science.1091901.

Cresswell, K. A., G. A. Tarling, and M. T. Burrows (2007), Behaviour affects local-scale distributions of Antarctic krill around South Georgia, *Mar. Ecol. Prog. Ser.*, *343*, 193–206, doi:10.3354/Meps06908.

Daly, K. L. (1990), Overwintering development, growth, and feeding of larval *Euphausia superba* in the Antarctic marginal ice-zone, *Limnol. Oceanogr.*, *35*(7), 1564–1576.

Dyke, P. (2001), *Coastal and Shelf Sea Modelling*, 257 pp., Kluwer Acad., Boston, Mass.

Egbert, G. D., and S. Y. Erofeeva (2002), Efficient inverse Modeling of barotropic ocean tides, *J. Atmos. Oceanic Technol.*, *19*(2), 183–204.

Fach, B. A., E. E. Hofmann, and E. J. Murphy (2006), Transport of Antarctic krill (*Euphausia superba*) across the Scotia Sea. Part II: Krill growth and survival, *Deep Sea Res., Part I*, *53*(6), 1011–1043, doi:10.1016/j.dsr.2006.03.007.

Hofmann, E. E., and E. J. Murphy (2004), Advection, krill, and Antarctic marine ecosystems, *Antarct. Sci*, *16*(4), 487–499, doi:10.1017/S0954102004002275.

Hofmann, E. E., J. M. Klinck, R. A. Locarnini, B. Fach, and E. Murphy (1998), Krill transport in the Scotia Sea and environs, *Antarct. Sci.*, *10*(4), 406–415.

Holt, J. T., and I. D. James (2001), An *s* coordinate density evolving model of the northwest European continental shelf. 1: Model description and density structure, *J. Phys. Oceanogr.*, *106*(C7), 14,015–14,034.

Kils, U. (1981), Swimming behavior, swimming performance and energy balance of Antarctic krill *Euphausia superba*, *Biomass Sci. Ser.*, *3*, 1–122.

Meredith, M. P., J. L. Watkins, E. J. Murphy, P. Ward, D. G. Bone, S. E. Thorpe, S. A. Grant, and R. S. Ladkin (2003), Southern ACC front to the northeast of South Georgia: Pathways, characteristics, and fluxes, *J. Geophys. Res.*, *108*(C5), 3162, doi:10.1029/2001jc001227.

Meredith, M. P., M. A. Brandon, E. J. Murphy, P. N. Trathan, S. E. Thorpe, D. G. Bone, P. P. Chernyshkov, and V. A. Sushin (2005), Variability in hydrographic conditions to the east and northwest of South Georgia, 1996–2001, *J. Mar. Syst.*, *53*(1–4), 143–167, doi:10.1016/j.jmarsys.2004.05.005.

Meredith, M. P., E. J. Murphy, E. J. Hawker, J. C. King, and M. I. Wallace (2008), On the interannual variability of ocean temperatures around South Georgia, Southern Ocean: Forcing by El Nino/Southern Oscillation and the Southern Annular Mode, *Deep Sea Res., Part II*, *55*(18–19), 2007–2022, doi:10.1016/j.dsr2.2008.05.020.

Moore, J. K., M. R. Abbott, and J. G. Richman (1997), Variability in the location of the Antarctic Polar Front (90 degrees-20 degrees W) from satellite sea surface temperature data, *J. Geophys. Res.*, *102*(C13), 27,825–27,833.

Murphy, E. J., J. L. Watkins, K. Reid, P. N. Trathan, I. Everson, J. P. Croxall, J. Priddle, M. A. Brandon, A. S. Brierley, and E. Hofmann (1998), Interannual variability of the South Georgia marine ecosystem: Biological and physical sources of variation in the abundance of krill, *Fish. Oceanogr.*, *7*(3–4), 381–390.

Murphy, E. J., J. L. Watkins, M. P. Meredith, P. Ward, P. N. Trathan, and S. E. Thorpe (2004), Southern Antarctic Circumpolar Current Front to the northeast of South Georgia: Horizontal advection of krill and its role in the ecosystem, *J. Geophys. Res.*, *109*(C1), C01029, doi:10.1029/2002jc001522.

Murphy, E. J., P. N. Trathan, J. L. Watkins, K. Reid, M. P. Meredith, J. Forcada, S. E. Thorpe, N. M. Johnston, and P. Rothery (2007a), Climatically driven fluctuations in Southern Ocean ecosystems, *Proc. R. Soc. B*, *274*(1629), 3057–3067, doi:10.1098/rspb.2007.1180.

Murphy, E. J., et al. (2007b), Spatial and temporal operation of the Scotia Sea ecosystem: A review of large-scale links in a krill centred food web, *Philos. Trans. R. Soc. B*, *362*(1477), 113–148, doi:10.1098/rstb.2006.1957.

Orsi, A. H., T. Whitworth, and W. D. Nowlin (1995), On the meridional extent and fronts of the Antarctic Circumpolar Current, *Deep Sea Res., Part I*, *42*(5), 641–673.

Pinones, A., E. E. Hofmann, K. L. Daly, M. S. Dinniman, and J. M. Klinck (2013), Modeling the remote and local connectivity of Antarctic krill populations along the western Antarctic Peninsula, *Mar. Ecol. Prog. Ser.*, *481*, 69–92, doi:10.3354/Meps10256.

Proctor, R., and I. D. James (1996), A fine-resolution 3D model of the southern North Sea, *J. Mar. Syst.*, *8*, 285–295.

Reid, K., J. L. Watkins, E. J. Murphy, P. N. Trathan, S. Fielding, and P. Enderlein (2010), Krill population dynamics at South Georgia: Implications for ecosystem-based fisheries management, *Mar. Ecol. Prog. Ser.*, *399*, 243–252, doi:10.3354/Meps08356.

Schmidt, K., et al. (2011), Seabed foraging by Antarctic krill: Implications for stock assessment, bentho-pelagic coupling, and the vertical transfer of iron, *Limnol. Oceanogr.*, *56*(4), 1411–1428, doi:10.4319/lo.2011.56.4.1411.

Sheen, K. L., et al. (2013), Rates and mechanisms of turbulent dissipation and mixing in the Southern Ocean: Results from the Diapycnal and Isopycnal Mixing Experiment in the Southern Ocean (DIMES), *J. Geophys. Res.*, *118*, 2774–2794, doi:10.1002/jgrc.20217.

Smith, W. H. F., and D. T. Sandwell (1997), Global sea floor topography from satellite altimetry and ship depth soundings, *Science*, *277*(5334), 1956–1962.

Song, Y. H., and D. Haidvogel (1994), A semiimplicit ocean circulation model using a generalized topography-following coordinate system, *J. Comput. Phys.*, *115*(1), 228–244.

Tarling, G. A., T. Klevjer, S. Fielding, J. Watkins, A. Atkinson, E. Murphy, R. Korb, M. Whitehouse, and R. Leaper (2009), Variability and predictability of Antarctic krill swarm structure, *Deep Sea Res., Part I*, *56*(11), 1994–2012, doi:10.1016/j.dsr.2009.07.004.

Thorpe, S. E. (2001), Variability of the southern Antarctic Circumpolar Current in the Scotia Sea and its implications for transport to South Georgia, Ph.D. thesis, 212 pp., Univ. of East Anglia, Norwich.

Thorpe, S. E., K. J. Heywood, M. A. Brandon, and D. P. Stevens (2002), Variability of the southern Antarctic Circumpolar Current front north of South Georgia, *J. Mar. Syst.*, *37*(1–3), 87–105, doi:10.1016/S0924–7963(02)00197-5.

Thorpe, S. E., K. J. Heywood, D. P. Stevens, and M. A. Brandon (2004), Tracking passive drifters in a high resolution ocean model: implications for interannual variability of larval krill transport to South Georgia, *Deep Sea Res., Part I*, *51*(7), 909–920, doi:10.1016/j.dsr.2004.02.008.

Thorpe, S. E., E. J. Murphy, and J. L. Watkins (2007), Circumpolar connections between Antarctic krill (*Euphausia superba* Dana) populations: Investigating the roles of ocean and sea ice transport, *Deep Sea Res., Part I*, *54*(5), 792–810, doi:10.1016/j.dsr.2007.01.008.

Trathan, P. N., E. J. Murphy, J. Forcada, J. P. Croxall, K. Reid, and S. E. Thorpe (2006), Physical forcing in the southwest Atlantic: Ecosystem control, *Conserv. Biol. Ser.* (12), 28–45, doi:10.1017/Cbo9780511541964.004.

Uppala, S. M., et al. (2005), The ERA-40 re-analysis, *Q. J. R. Meteorol. Soc.*, *131*(612), 2961–3012, doi:10.1256/Qj.04.176.

Ward, P., M. Whitehouse, R. Shreeve, S. Thorpe, A. Atkinson, R. Korb, D. Pond, and E. Young (2007), Plankton community structure south and west of South Georgia (Southern Ocean): Links with production and physical forcing, *Deep Sea Res., Part I*, *54*(11), 1871–1889, doi:10.1016/j.dsr.2007.08.008.

Watson, A. J., J. R. Ledwell, M. J. Messias, B. A. King, N. Mackay, M. P. Meredith, B. Mills, and A. C. N. Garabato (2013), Rapid cross-density ocean mixing at mid-depths in the Drake Passage measured by tracer release, *Nature*, *501*(7467), 408–411, doi:10.1038/Nature12432.

Webb, D. J., B. A. de Cuevas, and A. C. Coward (1998), The first main run of the OCCAM global ocean model, *Tech. Rep.*, 44 pp., Southampton Oceanogr. Centre, UK.

Young, E. F. (1996), Environmental influences on bivalve recruitment in The Wash, Ph.D. thesis, 279 pp., Univ. of East Anglia, Norwich.

Young, E. F., M. P. Meredith, E. J. Murphy, and G. R. Carvalho (2011), High-resolution modelling of the shelf and open ocean adjacent to South Georgia, Southern Ocean, *Deep Sea Res., Part II*, *58*(13–16), 1540–1552, doi:10.1016/j.dsr2.2009.11.003.

Young, E. F., J. Rock, M. P. Meredith, M. Belchier, E. J. Murphy, and G. R. Carvalho (2012), Physical and behavioural influences on larval fish retention: Contrasting patterns in two Antarctic fishes, *Mar. Ecol. Prog. Ser.*, *465*, 201–215, doi:10.3354/Meps09908.