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Examining the Connectivity of Antarctic Krill on the West Antarctic Peninsula: Implications for Pygoscelis Penguin Biogeography and Population Dynamics

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Abstract

Antarctic krill (*Euphausia superba*) are considered a keystone species for higher trophic level predators along the West Antarctic Peninsula (WAP) during the austral summer. The connectivity of these populations may play a critical role in predator biogeography, especially for central-place foragers such as the *Pygoscelis* penguins that breed along the WAP during the austral summer. Here, we used a physical ocean model to examine adult krill connectivity in this region using simulated krill with realistic diel vertical migration behaviors across four austral summers. Specifically, we examined krill connectivity around the Adélie gap, a 400 km long region along the WAP with a distinct absence of Adélie penguin colonies, to determine if krill population connectivity around this feature played a role in its persistence. Our results indicate that krill populations north and south of the Adélie gap are nearly isolated from each other and that persistent current features play a role in this inter-region connectivity, or lack thereof. Our results indicate that simulated krill released within the Adélie gap are quickly advected from the region, suggesting that the lack of local krill recruit retention may play a role in the persistence of this biogeographic feature.

1. Introduction

Antarctic krill (*Euphausia superba;* henceforth referred to as krill) populations along the Western Antarctic Peninsula (WAP) are highly dynamic on both spatial and temporal scales[1–6], with cycles of abundance peaking approximately every 4–6-years[7,8]. Recruitment of juvenile krill in the region has been linked to the extent of sea ice in the previous winter[9–12]. Ice dynamics in the spring also play a role in phytoplankton distributions, size, and availability to krill recruits[13,14]. These dynamics on the WAP have been linked to shifts in large scale climate oscillations like the Southern Annual Mode and El Nino Southern Oscillation[6,13,15]. Furthermore, a growing krill fishery has added additional stressors to a delicate system[16,17].

Around the WAP, krill are thought to spawn off the continental shelf where eggs can sink into Circumpolar Deep Water and the heat associated with this water mass can assist in development[18–23]. The resulting larvae migrate upwards and are advected downstream in the Antarctic Circumpolar Current (ACC) and eventually transported onto the continental shelf through trenches to their overwintering grounds under the coastal sea ice[9,12, 24–26]. Both observations and modeling experiments suggest that krill spawning in the Bellingshausen Sea serves as a source of juvenile and adult krill along the central and southern regions of the peninsula, as well as to the South Shetland Islands and islands to the north of the WAP[27–31]. Spawning in the Bellingshausen Sea does not, however, appear to serve as a source of krill to the northern tip of the WAP. Ocean currents around the tip of the WAP may isolate this region from the rest of the Peninsula, which relies instead on krill being fed from the Weddell Sea through the Coastal Current (CC; Fig. 1)[32–34].

During the austral summer, juvenile and non-spawning adult krill are found in coastal waters[30]. While krill distributions along the WAP during this critical season are well studied[2,7,26,30], the connectivity among populations of adult krill during the austral summer is poorly understood. Because krill spawning and resulting recruitment is so spatially heterogeneous[22], connectivity among regions can have an important influence on krill availability for central-place predators such as breeding *Pygoscelis* penguins that feed primarily on krill to help provision their growing chicks. Although all three *Pygoscelis* species breed along the WAP[35–38], there is a notable absence of Adélie penguin colonies along the Peninsula between the west coast of Trinity Peninsula and Anvers Island (orange box in Fig. 1). This region is known as the "Adélie gap" and stretches over 400 km along the coast of the WAP[38,39]. It has been hypothesized that Adélie penguins north and south of the gap rely on different winter habitats in the Weddell and Bellingshausen Seas, respectively[39,40]. However, Adélie penguins are known to range widely in the winter period, so such constraints on winter foraging do not necessarily preclude breeding within the Adélie gap[41]. As such, causal drivers for this biogeographic phenomenon remain poorly understood.

Here we examine how krill populations are connected along the WAP during the austral summer, with a special focus on connectivity across the Adélie gap. Using a physical ocean model, we simulate krill movement through the austral summer across the entire Antarctic Peninsula region from the Marguerite Trough to the Weddell Sea. We hypothesize that krill connectivity in this region of the WAP plays a significant role in *Pygoscelis* penguin population dynamics north and south of the Adélie gap. Adélie penguin populations are growing or stable north of the gap but are performing poorly elsewhere[42,43]. Evidence supporting our hypotheses would suggest that krill population connectivity may help explain this dichotomy and, furthermore, is a factor that may influence the efficacy of regional krill fishing closures.

2. Methods

2.1 Regional Ocean Modeling System

To test how krill populations along the WAP are connected, we used an updated regional WAP implementation of the Regional Ocean Modeling System (ROMS)[44–46]. Simulation parameters are provided in Supplementary Text A. This version of the model has a 1.5 km horizontal resolution and 24 vertical terrain-following layers. Dynamic sea ice and the interactions between floating ice shelves and the underlying waters are included[47,48]. We simulated four austral summers from November to March: 2008–2009, 2009–2010, 2018–2019, and 2019–2020. We refer to each of these summers as a season, using the year in which the summer started to differentiate the simulations. Tidal forcing is from the CATS2008 regional Antarctic tidal model, with nodal corrections applied as necessary[49]. Atmospheric forcing is from the Antarctic mesoscale Prediction System (AMPS)[50]. Spatial resolution of AMPS varied between 15–20 km for the 2008 and 2009 seasons and increased to 8 km for the 2018 and 2019 seasons.

Simulated particles served as a proxy for krill (henceforth referred to as ‘simulated krill’) and were seeded on an approximately 8 km grid throughout the study region (Figure S1). A total of 5,574 simulated krill were released in the study regions (see Section 2.2; Fig. 1) during each release event. A total of 16 release events occurred, starting on 1 November and ending in mid-February of each simulation. Simulated krill were released every 7 days and were tracked for at least 30 days. To mimic the effect of vertical turbulence (which is parameterized in ROMS), simulated krill positions included a vertical random walk[51,52]. Simulated krill were advected at every model time step (50 s) and positions were saved hourly.

To simulate krill behavior, diel vertical migration (DVM) was added to passive particles within ROMS. This behavior was added to ROMS particles previously to simulate both zooplankton[53] and krill[54]. DVM in ROMS was based on local solar angle. When the sun was above the horizon, downward velocities were added to the advective and random vertical velocities in the model if the simulated krill was above a target depth. Inversely, when the sun was below the horizon, an upward velocity was added if the simulated krill was below a target depth (10 m).

Table 1
Previously published krill diel vertical migration (DVM) and *Pygoscelis* penguin foraging depth observations along the West Antarctic Peninsula (WAP) used to inform DVM simulations.

Daytime Depths (m)	**Nighttime Depths (m)**	**Location**	**Season**	**Citation**
37–48	NA	Palmer Deep	Summer	Bernard et al 2017[55]
20–200	NA	Palmer Deep	Summer	Nardelli et al 2020[56]
30	NA	Palmer Deep	Summer	Cimino et al 2016[57]
100–140	20–30	South Georgia	Summer	Everson et al 1983[58]
250	Near surface	Marguerite Bay & WAP continental shelf	Fall – Early Winter	Zhou and Dorland 2004[59]
45–100	25–85	Northern WAP/South Shetland Islands	Summer	Godlewska and Klusek 1987[60]
200–400	Upper 200	Wilhelmina Bay	Fall	Espinasse et al 2012[61]
40–80	20–40	Palmer Deep	Summer	Goodrich 2018[62]
50–250	Upper 100	Branford Strait bays	Late spring	Kane et al 2018[63]
10	50	Palmer Deep	Summer	Hudson et al., 2022[53]

Simulated krill migration depths were based on previously published observations of krill DVM along the WAP (Table 1) and *Pygoscelis* penguin foraging depths (Table 2). Based on these observations, simulated krill DVM occurred between a minimum depth of 10 m and a maximum depth that varied between simulations (25, 50, 75, 100, or 150 m). Vertical migration speed was determined using observed krill swimming speeds in body lengths (BL) per second[63]. The mean BL of krill in swarms in the northern WAP and observed in *Pygoscelis* penguin diets near Anvers Island is approximately 43 mm[64,65]. With a mean vertical swimming speed of 0.335 BL s^{-1} in late spring[63], vertical migration speed of simulated krill was set to 0.014 m s^{-1}. Reverse DVM (krill spending time near the surface during the day and migrating down at night) and non-migrating behaviors were not considered here.

Table 2
Previously published *Pygoscelis* penguin foraging depth observations along the West Antarctic Peninsula (WAP) used to inform diel vertical migration (DVM) simulations.

Species	**Forage Depth (m)**	**Location**	**Season**	**Citation**
Adélie	6–82	Palmer Deep	Summer	Pickett et al 2018[66]
Gentoo	6–144	Palmer Deep	Summer	Pickett et al 2018[66]
Chinstrap	25–45	South Orkney & King George Island	Summer	Lishman & Crozall 1983[67]; Kokubun et al 2015[68]

2.2 Regional Connectivity

Connectivity was examined between the following regions: south of Adelaide Island, south of the Adélie gap, the Adélie gap, the northern tip of the WAP, the South Shetland Islands, and Elephant Island (Fig. 1). These regions were based on the location of *Pygoscelis* penguin colonies from the Mapping Application for Penguin Populations and Projected Dynamics (MAPPPD)[69]. Only areas approximately 40 km from these colonies were considered, as this approximates the maximum penguin summer foraging range for most colonies on the peninsula[70]. To estimate penguin populations, population projections for the 2019 season from MAPPPD were used[71]. Two additional regions were considered as potential sources for krill: the north Weddell Sea and the coastal Bellingshausen Sea (Fig. 1). In these potential source regions, all areas where simulated krill were released are considered, regardless of distance to shore. Any simulated krill released in model water points under ice shelves were excluded.

We examined connectivity between the 8 regions using two different metrics: 1) the percentage of simulated krill released in one region that interacted with other regions[72] and 2) the percent of time simulated krill spent in each region. For both metrics, we determined if simulated krill were present in a region using *point.in.polygon* in the R package 'sp'[73]. Metrics were averaged across release events that occurred within the chick-rearing period (December – March). Both metrics were averaged across simulated krill DVM behaviors to account for the variability in observed krill DVM behaviors.

Daily average currents from ROMS and simulated krill paths were examined as possible mechanisms of connectivity. Currents were interpolated to 10, 25, 50, 75, 100, and 150 m to match simulated DVM behaviors and averaged within the chick-rearing period across all seasons at each depth. To visualize simulated krill trajectories throughout the simulations, 20% of released particles with one of five DVM behaviors were randomly selected within each season to account for variability in these behaviors. Tracks were visualized across all seasons. For each persistent current feature, the number of penguin nests for each adjacent colony of the three *Pygoscelis* species were summed to determine the total number of birds impacted by these features. Colonies were considered adjacent to persistent current features if their 40 km foraging range overlapped with the feature.

3. Results

3.1 Regional connectivity

Of the simulated krill released in the Weddell Sea, 40% entered the North WAP region, but they spent little (10%) time there (Fig. 2). Of the simulated krill released in the Weddell Sea, 8 and 7% entered the South Shetland and Elephant Island regions, respectively (Fig. 2a). Twelve percent of the simulated krill released in the Weddell Sea made it to the Adélie gap (Fig. 2). Apart from the North WAP region, simulated krill released in the Weddell Sea rarely spent much time (< 2%) in other regions (Fig. 2b).

The simulated krill released within the Adélie gap and the North WAP spent approximately half (40–54%) of their time within the regions in which they were released (Fig. 2). These simulated krill often entered the South Shetland and Elephant Islands regions, but rarely interacted with other regions apart from the Weddell Sea (Fig. 2). Nearly 40% of simulated krill released in the North WAP entered the Weddell Sea, but they did not spend much of their time there (5%, Fig. 2). Simulated krill released within the South Shetland and Elephant Islands regions spent the largest fractions of their time within their respective regions (18% and 37% respectively; Fig. 2b). These simulated krill rarely (< 5%) entered other regions outside the two island regions (Fig. 2a).

Simulated krill released in the South WAP dispersed more widely than simulated krill released from any other region (Fig. 2). However, simulated krill were relatively self-contained within the South WAP, spending 68% of their time there (Fig. 2b). No more than 16% of simulated krill released in the South WAP moved to any given region to the north while less than 10% moved into more southern regions (Fig. 2a). In addition, simulated krill that moved from the South WAP into other regions spent little time (< 5%) in those other regions (Fig. 2b).

Simulated krill released in the Bellingshausen Sea rarely passed through the other regions and spent little time (< 2%) there when they did (Fig. 2). Only 10% of simulated krill released in this region passed through the South WAP and adjacent Adelaide Island regions (Fig. 2a). Simulated krill originating in the Bellingshausen Sea rarely (< 1%) the Adélie gap, South Shetland Islands and Elephant Island regions (Fig. 2a). Simulated krill originating around Adelaide Island also rarely (< 1%) entered the South Shetland and Elephant Island regions, with most only passing through the South WAP and Bellingshausen Sea regions (Fig. 2a).

Due to the stochastic nature of the ocean dynamics, there were rare exceptions to these overall patterns. Simulated krill released in the Weddell Sea, for example, were advected into the South WAP region in the 2018 and 2019 seasons (Figures S2-3). Simulated krill released in the North WAP made it to the South WAP, albeit rarely in the 2008, 2018, and 2019 seasons (Figures S2-3). The reverse (simulated krill released in the South WAP traveling to the North WAP) was rare but observed in 3 seasons (2008, 2009, and 2019) (Figures S2-3). Simulated krill released around the Islands also only entered the Weddell Sea in the 2008 and 2009 seasons (Figures S2-3). Transport from the Island regions into the South WAP was observed in the 2018 season. In all these exceptions to the overall patterns described above, less than 1% of simulated krill entered these novel regions and these simulated krill spent less than 1% of their time in these regions (Figures S2-3).

3.2 Features driving connectivity

We identified 6 oceanic pathways in the model that promote or inhibit connectivity between regions of the WAP: the North WAP Loop Current (NWLC), Antarctic Circumpolar Current (ACC), Low Island Loop Current (LILC), Bransfield Current System (BCS), Bismarck and Gerlache Straits (BGS), and Cross Shelf Currents (CSC). Spaghetti plots (Fig. 3), animations (Supplemental Movies 1–8), and across season average currents (Figs. 4, S4-5) illustrated consistent features in the coastal ocean that drive patterns of connectivity among the regions examined here. These features are highlighted in Fig. 5.

North WAP Loop Current (NWLC)

The NWLC consisted of the CC moving out of the Weddell and around the tip of the Peninsula on the north and east (Figs. 4a, 5; Movies S1, 4). A southward current between the D’Urville and Joinville Islands and the tip of the peninsula completed the loop to the east of James Ross Island (Fig. 4, Movies S1, 4). This feature moved at ~ 20 cm s^{-1} (Figs. 4, S4-5). The NWLC helped retain simulated krill within the North WAP and Weddell Sea regions (Fig. 3a, d; Movies S1, 4).

Antarctic Circumpolar Current (ACC)

Some simulated krill from the regions south of the Adélie gap (Bellingshausen Sea, Adelaide Island, and South WAP) were advected along the continental shelf via the ACC (Fig. 3f-h, Movie S5-6, 8). This feature facilitated the transport of simulated krill from these southmost regions to the South Shetland and Elephant Island regions (Fig. 3f-h, Movie S5-8) and moved rapidly (> 20 cm s^{-1}) along the continental shelf break (Fig. 4b). It also transported some simulated krill along the north shore of the South Shetland Islands from the LILC (see below; Fig. 3d-f, h).

Bransfield Current System (BCS)

The BCS consisted of 1) a northeasterly current along the south coast of the South Shetland Islands toward Elephant Island; 2) a southward current from Elephant Island towards the tip of the peninsula; 3) the CC moving out of the Weddell and to the southeast along the peninsula; and 4) a northward current between Tower and Astrolabe Islands (Figs. 4a, 5). These currents moved rapidly (~ 20 cm s^{-1}) and were relatively consistent (Figs. 4a, S4). The BCS facilitated most of the transport from the South Shetland Islands to Elephant Island and helped retain simulated krill around the Adélie gap (Fig. 3b-c, e; Movie S3-5).

Bismarck & Gerlache Straits (BGS)

The BGS between Anvers Island and the Antarctic Continent served as the primary feature connecting the South WAP and Adélie gap regions (Figs. 3f, 5). Water moved rapidly through this tight channel (~ 20 cm s^{-1}; Fig. 4b; Movie S6).

Cross Shelf Currents (CSC)

The CSC consisted of persistent currents moving from the continental shelf inshore (Figs. 3f, h; 4b; 5). These shoreward currents had relatively consistent speeds (~ 10 cm s^{-1}) across the depths considered (Figs. 4b, 5). Unlike other features described here, the CSC refers to a set of three similar current systems along the continental shelf of the WAP. These currents facilitated the transport of simulated krill from the Bellingshausen Sea and Adelaide Island regions into the South WAP region, and likely helped retain simulated krill within the South WAP (Fig. 3f-h, Movies S6-8).

3.3 Penguins impacted by persistent features

To determine the impacts each of these features has on local *Pygoscelis* penguin populations, we calculated the total number of penguins adjacent to them from MAPPPD predictions (Table 3; Fig. 5). The ACC supported nearly 250,000 chinstraps across 73 colonies along the north shore of the South Shetland and Elephant Islands (Table 3). The CSC and BGS supported approximately 15,000 gentoo penguins combined across many small colonies (Table 3). While the CSC supported many small Adélie colonies, no Adélie colonies were present in the BGS (Table 3). Of the regions considered, BCS supported the largest number of chinstrap and gentoo penguins on the WAP (Table 3). North of the Adélie gap, the NWLC supported nearly a million Adélie penguins, the largest number of penguins across all features and species (Table 3). The LILC supported nearly 300,000 penguins with most of them being chinstraps (Table 3). The BGS supported the second largest number of gentoo penguins (Table 3). The total number of penguins supported by each feature increased moving south to north (Table 3).

Table 3
Number of nests (and number of colonies) adjacent to persistent current features on the West Antarctic Peninsula (WAP). Data are from Mapping Application for Penguin Populations and Projected Dynamics (MAPPPD) predictions.

Penguin species	**Current Feature**					
	Cross Shelf Currents (CSC)	***Bismarck & Gerlache Straits (BGS)***	***Low Island Loop Current (LILC)***	***Bransfield Current System (BCS)***	***Antarctic Circumpolar Current (ACC)***	***North WAP Loop Current (NWLC)***
Adélie	12,987 (35)	0 (0)	0 (0)	7,521 (8)	0 (0)	970,536 (24)
Chinstrap	3,727 (16)	11,208 (35)	273,214 (58)	421,762 (72)	248,777 (73)	20,568 (5)
Gentoo	22,344 (21)	33,198 (24)	20,286 (8)	43,477 (13)	3,347 (2)	10,810 (15)
Total	39,058 (72)	44,406 (59)	293,500 (66)	472,760 (93)	252,124 (75)	1,001,914 (44)

4. Discussion

Pygoscelis penguins primarily consume krill during the austral summer[66,74,75]. Krill distributions along the WAP are spatially and temporally heterogeneous[1–6, 26] and, therefore, could play a role in penguin biogeography around the Adélie gap. This area is a 400 km long region along the coast of the WAP where no Adélie penguin colonies are present, despite foraging and migration behaviors that do not inhabit these penguins from inhabiting the region[40,41]. Here, we used an ocean circulation model to determine how simulated krill are connected across coastal regions along the WAP. We specifically focused on how krill populations are connected north and south of the Adélie gap to determine if connectivity, or lack thereof, plays a role in penguin population dynamics in the region.

Simulated krill generally moved from south to north along the WAP. Simulated krill populations originating from points south of the Adélie gap generally remained within the region with a small fraction advected north to the South Shetland Islands via the ACC. For simulated krill originating just south of the Adélie gap in the South WAP, the BGS and LILC also moved simulated krill north to the South Shetland Islands. North of the gap, simulated krill were advected from the Weddell Sea to the Adélie gap via the CC. From here, simulated krill were advected north to the South Shetland Islands via the LILC. Occasionally, simulated krill returned to the Adélie gap via the BCS.

Here, we found that simulated krill south and north of the Adélie gap are, for the most part, isolated from each other. Connectivity between these regions is limited by a northward current around Low Island within the Adélie gap. This current, like many along the WAP, appears to be bathymetrically driven, following the contours of Boyd Strait between Low Island and the South Shetland Islands (Fig. 1)[32]. This current likely acts as a boundary between the Bransfield Strait and the rest of the peninsula, which have very different water column structures and water mass properties[76].

Rare exceptions to these patterns were observed across all four seasons simulated. These outlying events generally occurred in either the 2008–2009 seasons or 2018–2019 seasons. The coupling of these patterns in adjacent seasons suggests that changes in forcing dynamics may play a role. Possible forcing changes include wind, stratification, or eddying dynamics. Changes in the spatial resolution of atmospheric forcing may have also played a role. Further work is necessary to examine how changes in these forcing mechanisms may affect future connectivity north and south of the Adélie gap.

Despite these outlying events, overall patterns of connectivity between the regions studied here are remarkably consistent, with low variability, across four different austral summers. The current features highlighted here are persistent mechanisms for this connectivity and most are associated with bathymetric features. The CSC, for example, are driven by troughs and canyons crossing the continental shelf and the BCS follows bathymetric contours in the region. Persistent features were not found in areas on the continental shelf without strong bathymetry changes, illustrating the importance of bathymetry, and the resulting bathymetric steering of ocean currents in this region[77–79].

A majority of the persistent current features described here that drive krill connectivity along the WAP, including the ACC[32,80], CSC[77–79], BGS[32,81], BCS[33,34, 81–83], and LILC[80–82], have been observed along the WAP. Both the LILC and BCS have their components described in detail but are not often considered closed loop systems as we have described them here (Fig. 5). Entrainment of simulated krill by both these features is present, albeit not persistently in our observations. Therefore, more observations of these systems are necessary to determine if these features persist as closed loop systems or are simply connecting different current systems.

While the northward component of the NWLC associated with the CC has been observed previously (Fig. 1)[34,80,84], observations suggest that flow between the D’Urville and Joinville Islands and the tip of the WAP is northward, rather than southward as model simulations suggest[83,84]. Animations of daily simulated krill locations illustrate that occasional northward transport of simulated krill is possible through this region despite mean southward flows (Fig. 4a, Movies S1, 4). Local water mass properties suggest that northward currents through this region is unlikely[85]. Therefore, additional observations are necessary to determine if the southward component of the NWLC is present and persistent feature during the austral summer.

The addition of DVM to simulated krill, in addition to the persistence of current features across seasons, also likely helped drive the persistence of krill transport mechanisms. Ocean currents are highly variable in the surface due to the influences of wind on the surface mixed layer while the influence of wind is less prevalent in deeper waters which results in more consistent currents (see Movie S9-10 for examples within the Adélie gap). The addition of DVM to our simulated krill likely helped keep krill in these persistent current features and helped them avoid the variability associated with near-surface flows. The persistence of currents at depth may explain why simulated krill were well entrained within the BCS and LILC along the outside of the bathymetric features associated with each current system. This may be why these current features appeared as the closed loop systems observed and interactions with the mesoscale eddies associated with features like the BCS[32,34] were not as common.

It is critical to note that in modeling krill behavior, we made three assumptions that may impact our results. The first and foremost is that krill are only actively swimming in the vertical and are passive drifters in the horizontal. Krill form massive swarms and have been observed swimming in the horizontal on small scales[63,65]. However, the directionality of this horizontal movement is unknown on the same horizontal scales of the model (1.5 km). While random walks have net zero displacement in the horizontal, previous krill movement modeling studies using monthly 1 km climatologies of surface currents have illustrated that random walks can impact krill distributions[86]. Furthermore, individual based, small scale krill models have shown that horizontal movement can help krill move towards food (phytoplankton) and avoid predation[86–88]. Therefore, future work should construct and incorporate a realistic krill horizontal movement model into simulations and determine its impact on krill transport and connectivity.

The second assumption made in this analysis is that krill regularly perform DVM to the depths simulated (25, 50, 75, 100, and 150 m). DVM is highly variable in krill throughout the WAP (Table 1). While we averaged krill accumulation metrics over our DVM behaviors to account for a portion of this variability, we did not simulate deeper DVM which has been shown to increase transport and/or retention by deep current features[53] to make sure that simulated krill were available to penguins within their vertical foraging ranges (Table 2). In addition, the krill have been shown to reduce or completely stop DVM over the austral summer in response to changing photoperiod[89,90]. We also did not consider simulated krill without DVM behaviors, or reverse DVM. Reverse DVM, where simulated krill spend days in the surface feeding and migration downwards at night[89], may reduce the impact during the summer of the persistent current features identified as influencing population connectivity, since near-surface currents are heavily influenced by winds.

Our third assumption was that krill are homogeneously distributed throughout the WAP. As discussed previously, krill have high spatial and temporal variability along the WAP[2–6, 26,30]. Therefore, it is important to interpret these results, not as absolute connectivity, but potential connectivity between the regions studied here. Future simulations should consider krill distribution and catch data from sources such as KRILLBASE to determine how the heterogenous distribution of krill along the WAP impacts these results. Areas previously defined as regions of high recruitment along the WAP[29] should also be considered. We hypothesize that the relative importance of the current features defined here will be directly correlated to krill spawning success in both the Weddell and Bellingshausen Seas.

One further limitation of our analysis is the modeling of the coastal buoyancy forces in ROMS. This iteration of the WAP circulation model is known to underestimate water column stratification, resulting in ocean currents with greater barotropic (depth-driven) and smaller baroclinic (density-driven) components than *in situ* observations suggest[44,76]. This impacts the modeled CC around the tip of the WAP and along the coast, which is driven primarily by buoyancy due to coastal ice melt and coastal precipitation[91]. Improved modeling of the CC, especially down the coast of the WAP, may increase connectivity between regions north and south of the Adélie gap[91].

Our results illustrate that adult krill populations in the Bellingshausen and Weddell Seas are only weakly connected to the rest of the Antarctic Peninsula waters. Penguin populations north of the Adélie gap have been doing well in recent years[42,43]. The NWLC supports a number of Adélie penguins an order of magnitude greater than anywhere else in our study region (Table 3)[43]. Colony sizes along the peninsula decrease as they become farther away from the Weddell Sea and the persistent features (NWLC and BCS) that transport krill out of this region. Therefore, the Weddell Sea may provide ample resources for the penguin colonies north of the gap via the NWLC, providing a compelling explanation for the aggregation of many large Adélie penguin colonies in this region.

Penguin populations south of the Adélie gap, however, do not receive krill from the Weddell, instead receiving krill from the Bellingshausen Sea and points south on the peninsula. Previous modeling studies show that the Bellingshausen Sea serves as a source of larval and juvenile krill[27]. *Pygoscelis* penguin colonies, including the new gentoo colonies that have formed in this region in the 21st century[36], are generally smaller south of the Adélie gap than those to the north.

Penguins on both sides of the Adélie gap are adjacent to persistent current features that could potentially bring krill within their foraging ranges. Therefore, we hypothesize that the volume of resources available within each of these current features is likely highly heterogeneous and may be differentially impacted by changes to the environment observed over the last several decades. The Weddell Sea may serve as a krill sanctuary due to the extent and persistence of sea ice in the region, whereas sea ice – a critical overwintering habitat for krill[9–12] – is declining in the Bellingshausen[42,92,93]. Significantly higher resource availability north of the Adélie gap from the Weddell Sea may be the cause of the significantly larger colonies there. Changing krill stocks and distributions as a result of climate change[1,2,94], albeit debated[95,96], have been linked to penguin population declines[16,97], changes in diet compositions in gentoos[98], and reproductive success of other krill predators such as the Antarctic fur seal (*Arctocephalus gazella*)[99] throughout the WAP, suggesting that krill availability may be declining to predators. However, recent modeling work and observations suggest that prey resources are not currently limiting for penguins south of the Adélie gap[66,100]. Therefore, more studies are needed to determine if resource availability north and south of the Adélie gap is truly different and driving penguin population trends in these regions.

The larger penguin colonies north of the Adélie gap could persist due to transport of other prey species. Antarctic silverfish (*Pleuragramma antarcticum*) are considered another important prey species to *Pygoscelis* penguins[101–104]. All life stages of the silverfish are strongly dependent on sea-ice extent[105].

Therefore, the Weddell Sea may also serve as an important refuge for silverfish, in addition to overwintering krill. Previous modeling studies have illustrated that larval silverfish can be transported from the Weddell Sea to the North WAP and Adélie gap, likely through the NWLC and BE described here[106]. In addition, the LILC may continue to act as a barrier to transport south of the Adélie gap[106]. Increased availability of silverfish via the persistent current features described here, therefore, may be an additional driver of penguin population dynamics north of the Adélie gap. Silverfish are noticeably absent from penguin diets south of the WAP. However, the presence of smaller persistent current features may retain enough krill near penguin colonies to allow them to persist[54,101,107].

While our results illustrate that krill populations are not connected north and south of the Adélie gap and provide a plausible hypothesis for distinct penguin population dynamics on either side of this feature, they do not immediately discern why this biogeographic feature is present. Previous analysis of the US Antarctic Marine Living Resources long term monitoring program suggests that the Bransfield Strait between the South Shetland Islands and the coast of the WAP is a hotspot for krill recruitment[29]. This suggests that prey resources should be plentiful enough to facilitate successful penguin foraging and colony establishment in the Adélie gap. Our results indicate that simulated krill released within the Adélie gap spent, on average, less than half of their time (40%) in the gap. If this region is a krill recruitment hotspot, recruits are presumably spawned in the Weddell Sea and subsequently transported into the Adélie gap region through the CC. Our results suggest that these krill recruits may be quickly advected out of the Adélie gap and into the South Shetland Islands and Elephant Island regions via the BCS. In addition, simulated krill released in other regions did not spend much time (< 17%) in the Adélie gap, if they entered this region at all. Therefore, we hypothesize that rapid currents in this region impede local recruit retention. Future work should test these hypotheses to determine if resource limitation via a lack of recruit retention is driving the *Pygoscelis* penguin population dynamics observed in the Adélie gap.

Not only do these results provide a testable hypothesis on driving mechanisms behind the Adélie gap but also are valuable for understanding the implications of krill fishery closures in different regions along the WAP. Our results suggest that closures north and south of the Adélie gap may only impact local krill stocks and have little influence elsewhere, with the exception of the South Shetland Islands. Therefore, proposed closures should take the connectivity of populations in account in order to have the desired effects on krill stocks.

Declarations

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Data Availability Statement

Bounding boxes for the regions used in this study, indexes used to subset simulated krill released within each region, and the code used to conduct connectivity calculations are available on GitHub (https://github.com/klgallagher/connectivity). Simulated krill trajectories (https://www.usap-dc.org/view/dataset/601655) and current velocity and direction data (https://www.usap-dc.org/view/dataset/601656) are archived at the United States Antarctic Program Data Center.

Author Contributions Statement

K.L.G. and H.J.L. conceived the presented idea. M.S.D. provided the version of ROMS used. K.L.G. ran model simulations and performed the analysis. All authors contributed to writing the manuscript.

Additional Information

Competing Interests Statement: The authors declare no competing interests.

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Figures

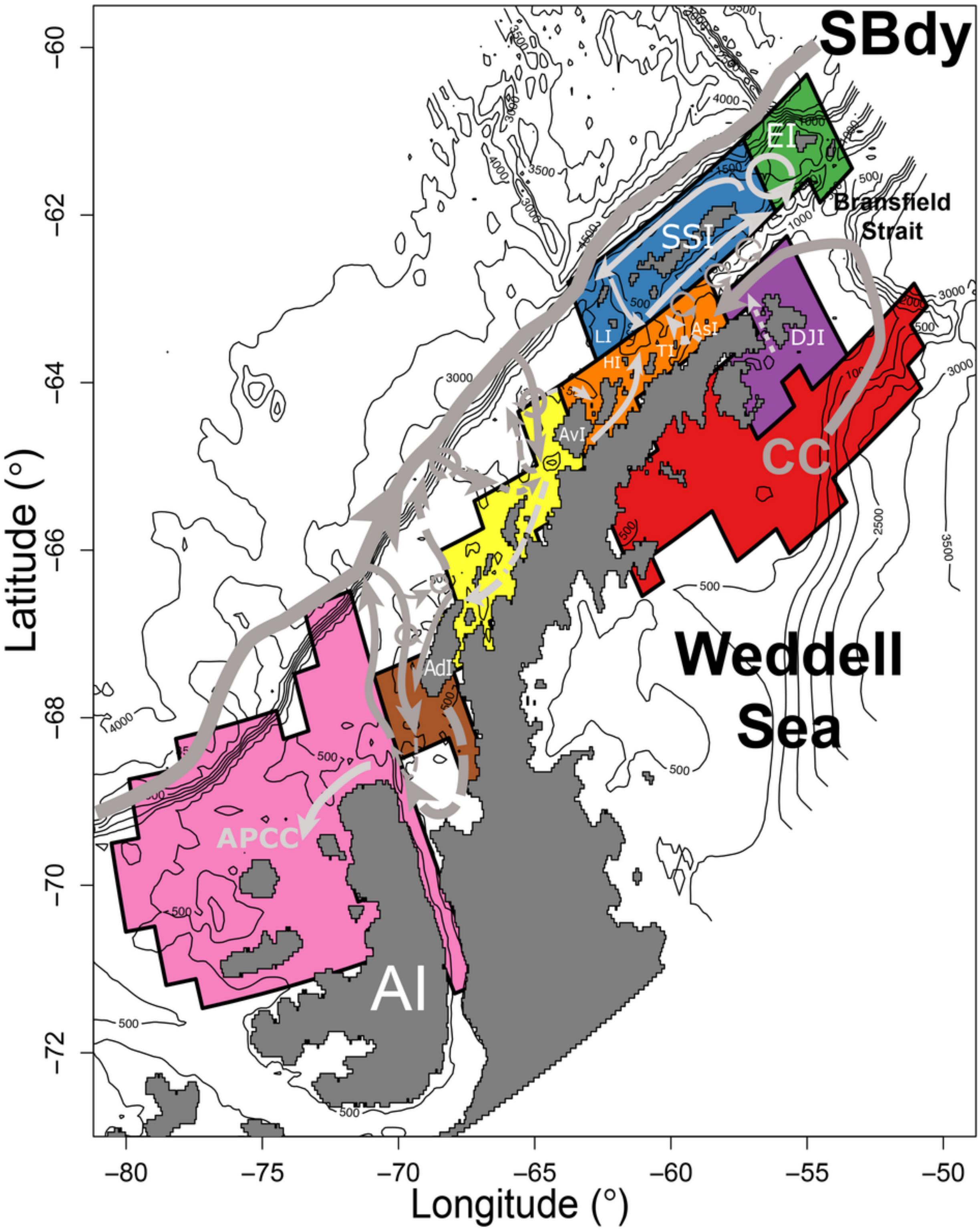
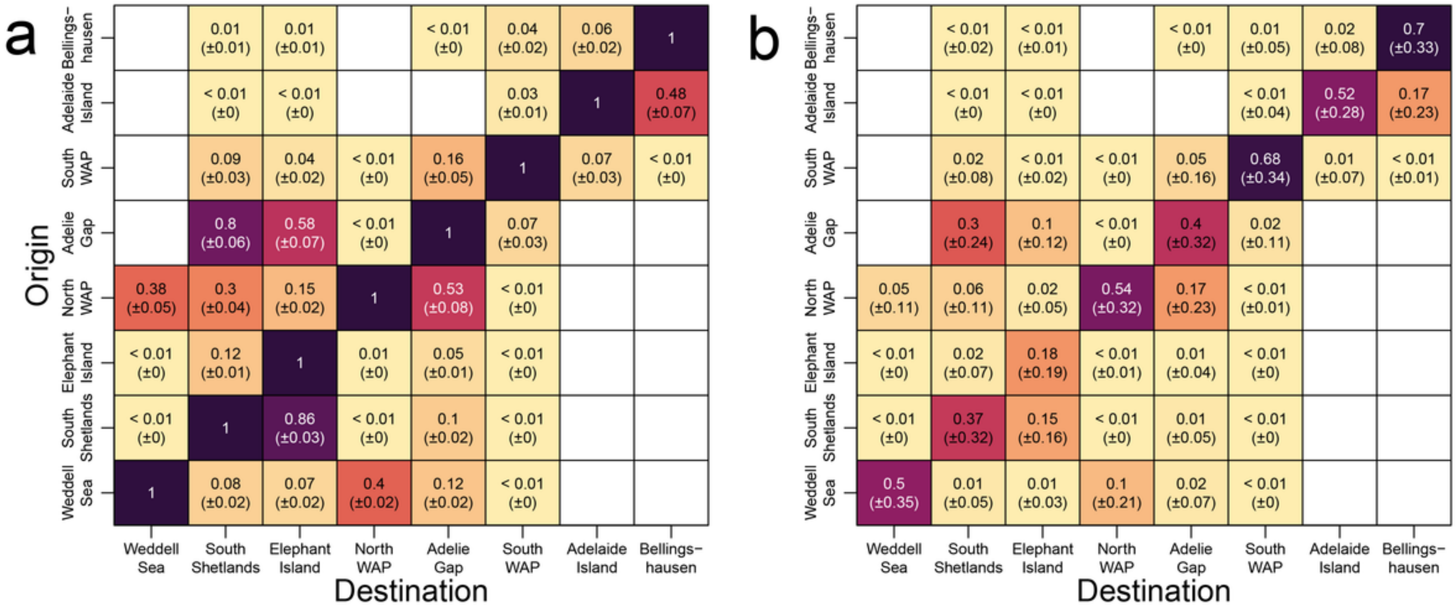


Figure 1

Map of the Antarctic Peninsula, including land masks and bathymetry from the Regional Ocean Modeling System (ROMS). Boxes illustrate the 8 regions used to estimate connectivity: Bellingshausen Sea (pink), Adelaide Island (brown), South Western Antarctic Peninsula (WAP; yellow), Adélie gap (orange), North WAP (purple), South Shetland Islands (blue), Elephant Island (green), and Weddell Sea (red). Grey arrows illustrate an overview of the WAP circulation from Moffat & Meredith (2018)[32]. Abbreviations indicate relevant current systems and islands: SBdy, Southern ACC Boundary; APCC, Antarctic Peninsula Coastal Current; CC, Antarctic Coastal Current; EI, Elephant Island; SSI, South Shetland Islands; DJI, D'Urville and Joinville Islands; AsI, Astrolabe Island; TI, Tower Island; HI, Hoseason Island; LI, Low Island; AvI, Anvers Island; AdI, Adelaide Island; AI, Alexander Island.



a

Origin \ Destination	Weddell Sea	South Shetlands	Elephant Island	North WAP	Adelie Gap	South WAP	Adelaide Island	Bellings–hausen
Bellings–hausen		0.01 (±0.01)	0.01 (±0.01)		< 0.01 (±0)	0.04 (±0.02)	0.06 (±0.02)	1
Adelaide Island		< 0.01 (±0)	< 0.01 (±0)			0.03 (±0.01)	1	0.48 (±0.07)
South WAP		0.09 (±0.03)	0.04 (±0.02)	< 0.01 (±0)	0.16 (±0.05)	1	0.07 (±0.03)	< 0.01 (±0)
Adelie Gap		0.8 (±0.06)	0.58 (±0.07)	< 0.01 (±0)	1	0.07 (±0.03)		
North WAP	0.38 (±0.05)	0.3 (±0.04)	0.15 (±0.02)	1	0.53 (±0.08)	< 0.01 (±0)		
Elephant Island	< 0.01 (±0)	0.12 (±0.01)	1	0.01 (±0)	0.05 (±0.01)	< 0.01 (±0)		
South Shetlands	< 0.01 (±0)	1	0.86 (±0.03)	< 0.01 (±0)	0.1 (±0.02)	< 0.01 (±0)		
Weddell Sea	1	0.08 (±0.02)	0.07 (±0.02)	0.4 (±0.02)	0.12 (±0.02)	< 0.01 (±0)		

b

Origin \ Destination	Weddell Sea	South Shetlands	Elephant Island	North WAP	Adelie Gap	South WAP	Adelaide Island	Bellings–hausen
Bellings–hausen		< 0.01 (±0.02)	< 0.01 (±0.01)		< 0.01 (±0)	0.01 (±0.05)	0.02 (±0.08)	0.7 (±0.33)
Adelaide Island		< 0.01 (±0)	< 0.01 (±0)			< 0.01 (±0.04)	0.52 (±0.28)	0.17 (±0.23)
South WAP		0.02 (±0.08)	< 0.01 (±0.02)	< 0.01 (±0)	0.05 (±0.16)	0.68 (±0.34)	0.01 (±0.07)	< 0.01 (±0.01)
Adelie Gap		0.3 (±0.24)	0.1 (±0.12)	< 0.01 (±0)	0.4 (±0.32)	0.02 (±0.11)		
North WAP	0.05 (±0.11)	0.06 (±0.11)	0.02 (±0.05)	0.54 (±0.32)	0.17 (±0.23)	< 0.01 (±0.01)		
Elephant Island	< 0.01 (±0)	0.02 (±0.07)	0.18 (±0.19)	< 0.01 (±0.01)	0.01 (±0.04)	< 0.01 (±0)		
South Shetlands	< 0.01 (±0)	0.37 (±0.32)	0.15 (±0.16)	< 0.01 (±0)	0.01 (±0.05)	< 0.01 (±0)		
Weddell Sea	0.5 (±0.35)	0.01 (±0.05)	0.01 (±0.03)	0.1 (±0.21)	0.02 (±0.07)	< 0.01 (±0)		

Figure 2

Heat maps of the mean (± 1 standard deviation) proportion of simulated krill that interacted with a region (a) and the mean (± 1 standard deviation) proportion of time spent in each region (b). Rows indicate region of origin and columns indicate destination regions. Blank squares indicate no connection between regions.

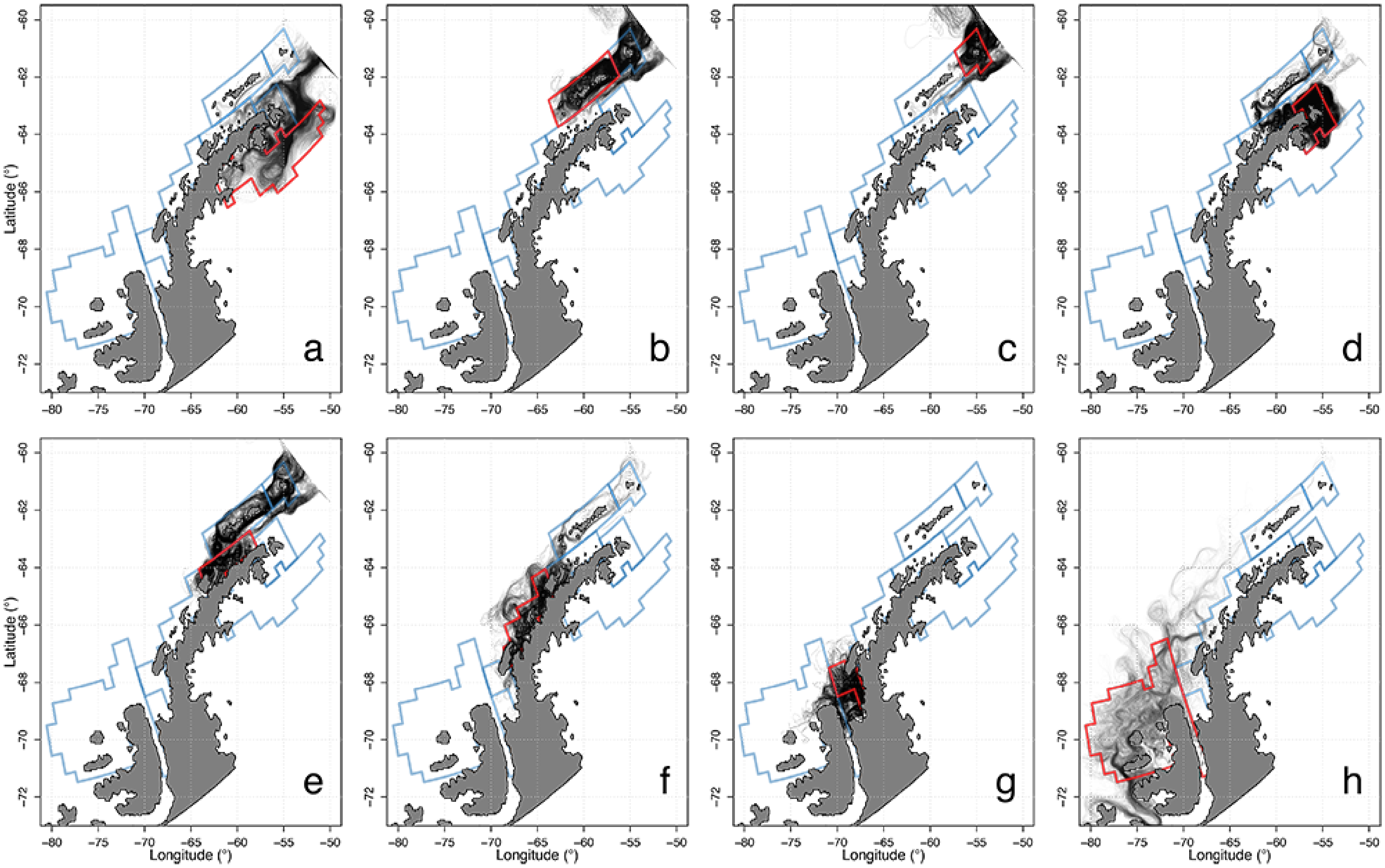


Figure 3

Spaghetti plots illustrating major connectivity pathways between the eight study regions: Weddell Sea (a), South Shetland Islands (b), Elephant Island (c), North WAP (d), Adélie gap (e), South WAP (f), Adelaide Island (g), Bellingshausen Sea (h). Regions outlined in red illustrate the region of origin.

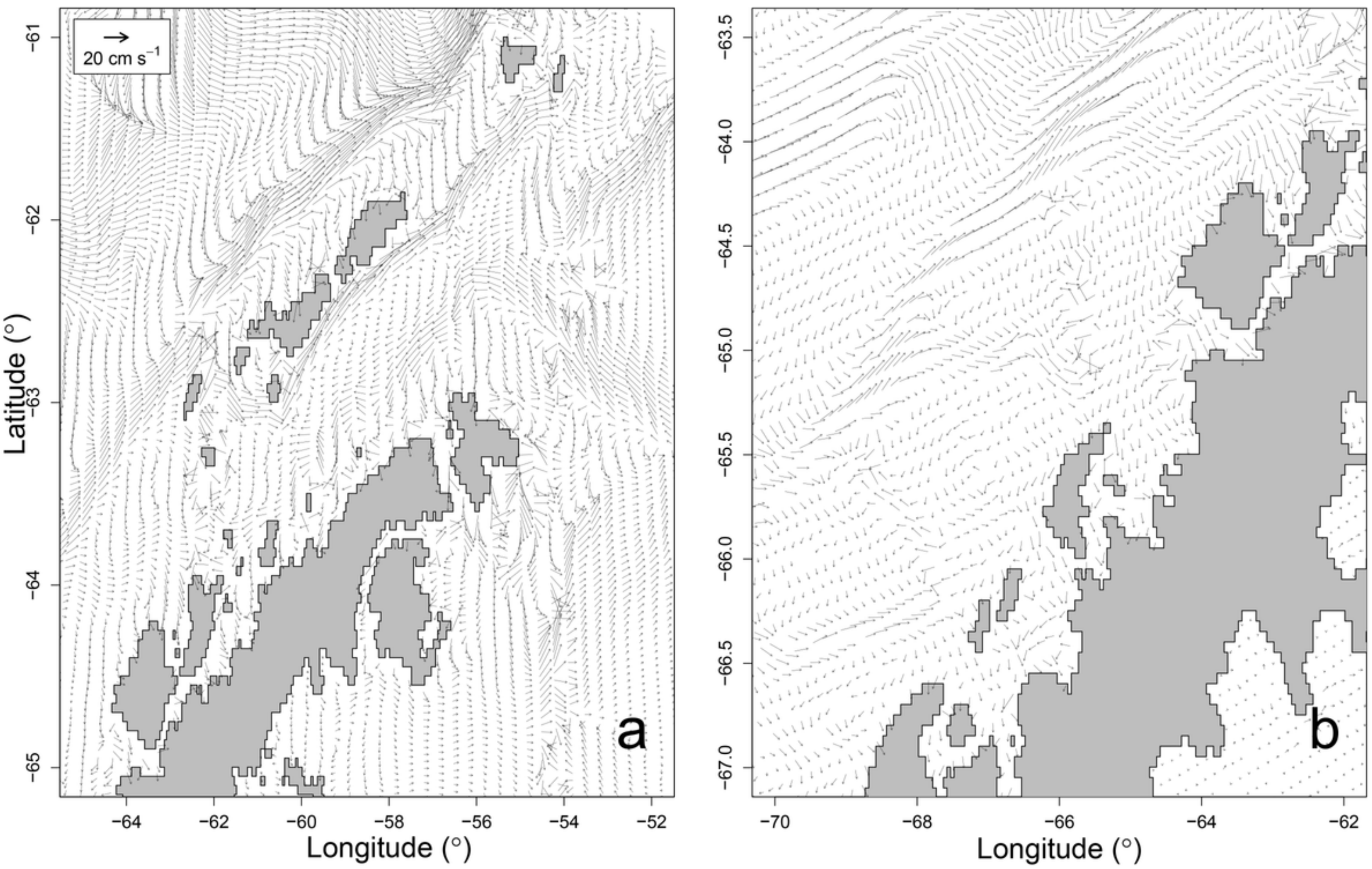


Figure 4

Mean current velocities and directions in the (a) northern and (b) southern areas of the study region illustrating persistent current features. Every 30th vector (representing ~20 km horizontal resolution) is plotted in panel a and every 25th vector (representing ~ 17 km resolution) is plotted in panel b. Current velocities and directions were averaged across the 4 simulated seasons during the chick-rearing period (December – March) and over the top 150 m of the water column.

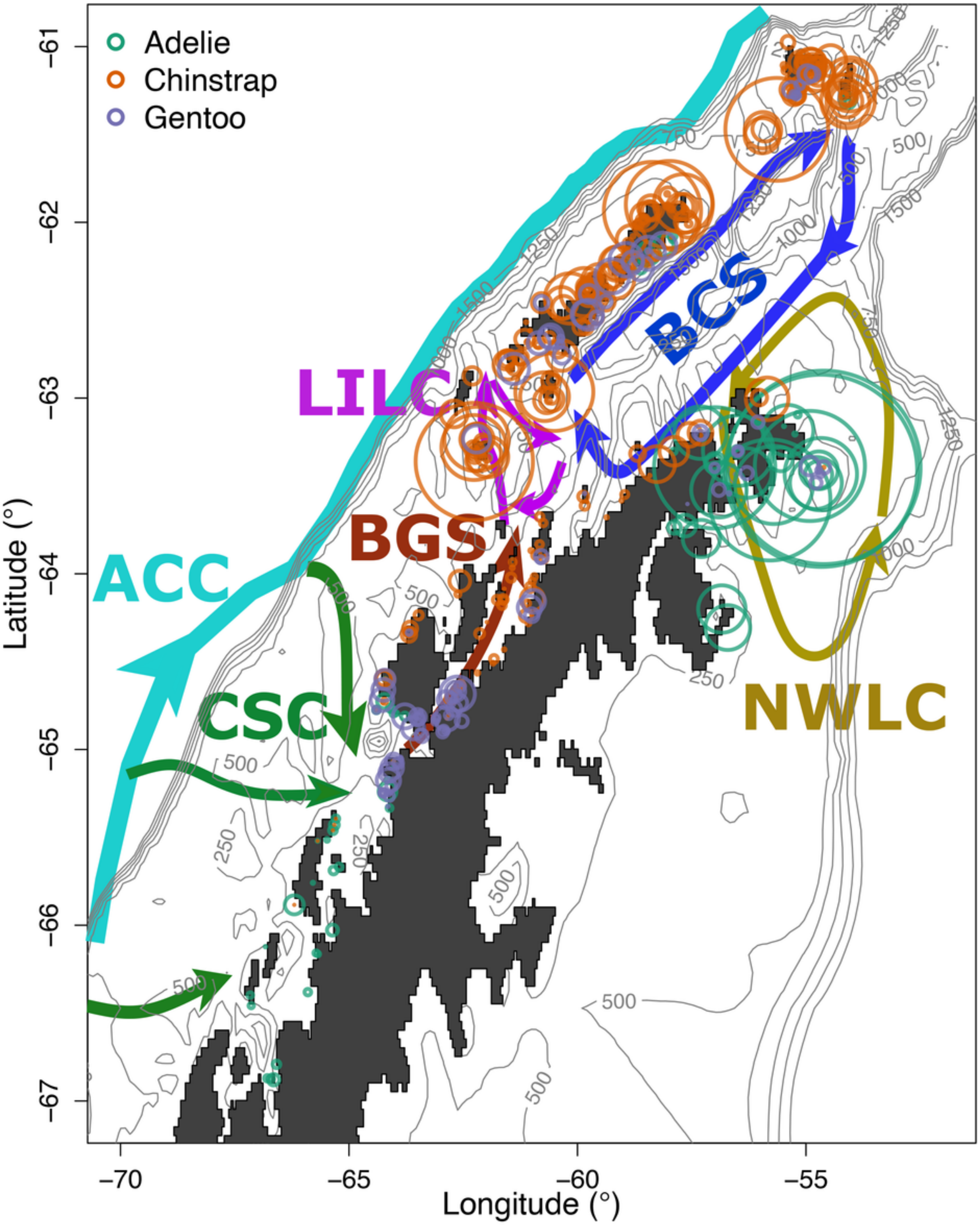


Figure 5

Persistent current features along the West Antarctic Peninsula. Circles illustrate the relative size of Adélie (green), chinstrap (orange), and gentoo (purple) penguin colonies based on population estimates from the Mapping Application for Penguin Populations and Projected Dynamics (MAPPPD). Currents are from Moffat and Meredith (2018)[32] when applicable. ACC, Antarctic Circumpolar Current; CSC, Cross Shelf

Currents; BS, Bismarck Strait; LILC, Low Island Loop Current; BE, Bransfield Eddy; NWLC, North West Antarctic Peninsula Loop Current

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

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- movieS9.gif
- movieS10.gif
- SupplementConnectivityGallagheretal.docx